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# Decades of warming alters maturation and reproductive investment in fish

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## Abstract

How does warming affect maturation and reproductive investment in ectotherms? Younger age and smaller size at maturation, as well as altered reproduction processes, have been found in a few species subjected to elevated temperatures. These observations, however, come from studies that do not distinguish effects of warming on maturation from those on growth, are also restricted to single generation responses to warming, or have additional stressors besides warming in the study system. Here, we study warming effects on maturation and reproductive investment in wild, unexploited fish populations using a whole-ecosystem heating experiment. The experiment is conducted on Eurasian perch (*Perca fluviatilis*) in a heated and control area (with >5°C temperature difference) in the Baltic Sea. We compare female perch size at maturation using estimated probabilistic maturation reaction norms (PMRNs) and the gonado-somatic index over 17 years of heating, spanning approximately five to eight perch generations. Using the PMRN approach, we show that warming has substantial effects on maturation size independent of warming-induced changes in body growth. We found that young fish mature at a smaller size and invest more in developing their gonads in the heated population than in the unheated population. Our findings suggest that warming effects on reproductive investment may initially compensate for the cost of warming-induced decrease in maturation size caused by the trade-off between early maturation and size-dependent fecundity. After multiple additional generations of warming, maturation and reproduction traits in perch differed from those in the first generations following the onset of warming, which suggests that warming-induced evolution may have occurred. Our study is particularly relevant in the context of climate change because of the unusually large temperature difference between the areas and the fact that the heating occurred on an ecosystem level. We call for experimental studies resolving mechanisms of trait responses to warming across generations, complemented with genomic analyses, to aid understanding of organisms' long-term responses to climate change.

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**KEYWORDS**
climate change, evolution, gonado-somatic index, life history traits, *Perca fluviatilis*, probabilistic maturation reaction norm, reproduction, size at maturation, temperature, trade-offs, whole-system experiment

## INTRODUCTION

Temperature has a pervasive influence on ectotherms, whose body temperature depends on their ambient thermal environment. Temperature directly influences physiological traits such as metabolic rate, growth rate, development rate, and hormone regulation, and key processes such as survival (reviewed in Angilletta, 2004; Huss et al., 2019). Still, temperature effects on key life history traits such as age- and size at maturation and energy allocation to reproductive versus somatic growth are not well understood (Audzijonyte et al., 2016). Age- and size at maturation are to a large extent determined by juvenile growth rate and in turn, affect adult growth rate, lifetime reproductive success, and mortality (Berrigan & Charnov, 1994; Stearns, 1992). As resources are limited, the allocation of energy to reproduction upon maturation will lead to slower somatic growth, especially in organisms with indeterminate growth, such as fish. Hence, fish adult size is largely dependent on size at maturation. Larger size at maturation in fish is often linked to higher fecundity, higher offspring fitness, and lower mortality due to lower predation risk following the larger body size. However, a larger (adult) body size also costs fish more energy and resources to maintain (Roff, 1992). The opposite holds for smaller size at maturation, which is associated with smaller adult body size and lower fecundity (Roff, 1992), but also lower maintenance costs. Moreover, the differences in maintenance costs between large- and small-sized fish increase if the temperature is high (Lindmark, Ohlberger, et al., 2022). Early maturation, commonly concurring with smaller maturation size, can increase the number of reproduction events in a lifetime for multiple spawning fish. Smaller maturation size is thus the result of optimizing fitness by balancing fecundity and predation risk against maintenance cost and potentially, reproductive lifespan. Reproductive investment, that is, energy allocated to reproduction such as developing gonads, is another trait that directly affects fish reproduction and recruitment success (Rosecchi et al., 2001). Such investment is traded off against somatic growth, survival, and future spawning success (Kozlowski, 1996; Stearns, 1992). Because the processes underlying these trade-offs depend on temperature, warming could induce changes in these key life history traits. Due to global warming's potentially profound impacts on populations and food webs (Audzijonyte et al., 2013), it is especially important to understand how warming affects fish maturation and reproductive traits, including both immediate and long-term responses.

Maturation describes the process of an organism reaching maturity, whereas maturity is the life stage an organism enters thereafter. Fish often need to exceed a size threshold to mature (Hutchings, 2002; Figure 1a,d). Warming could therefore cause fish to mature earlier (at a younger age) if growth rates increase with temperature (Angilletta, 2004; Berrigan & Charnov, 1994; Sandström et al., 1995; Figure 1d). If the size threshold for maturation also depends on age, changes in growth would alter both age- and size at maturation (Figure 1e,f). Growth rate related changes in age- and size at maturation induced by warming have been supported by theoretical models (Zuo et al., 2012) and observed in controlled experiments (Jonsson et al., 2013). In the wild, warming has been associated with both decreased age- and smaller size at maturity in fish (Ottersen et al., 2006; Shapiro Goldberg et al., 2019). The opposite, increased water temperature leading to later fish maturation, has however also been observed (Otero et al., 2012), including larger size at maturation after multiple generations of experimental warming (Loisel et al., 2019). Changes in maturation traits can thus occur as a direct consequence of warming effects on growth.

Evidence shows, however, that temperature can affect fish maturation independently from its influence on juvenile body growth (Dhillon & Fox, 2004; Kuparinen et al., 2011). By quantifying the probability of an individual to mature using probabilistic maturation reaction norms (PMRNs; Dieckmann & Heino, 2007), such direct impacts of warming on maturation can be disentangled from changes related to juvenile growth rates or mortality. Direct effects of warming on maturation can arise through responses in physiological processes, shifting the PMRNs without altering body growth (Figure 1a–c). Such responses are likely associated with higher temperature, which modifies fish endocrine profiles and affects gonad development (Kraak & Pankhurst, 1997) and increased development rates (Wootton et al., 2021). If temperature increases further, however, the reverse response—larger size and older age at maturation—can be observed (Dhillon & Fox, 2004), likely because temperatures exceed species' maximum tolerance. Warming can thus affect maturation size and age via physiological changes

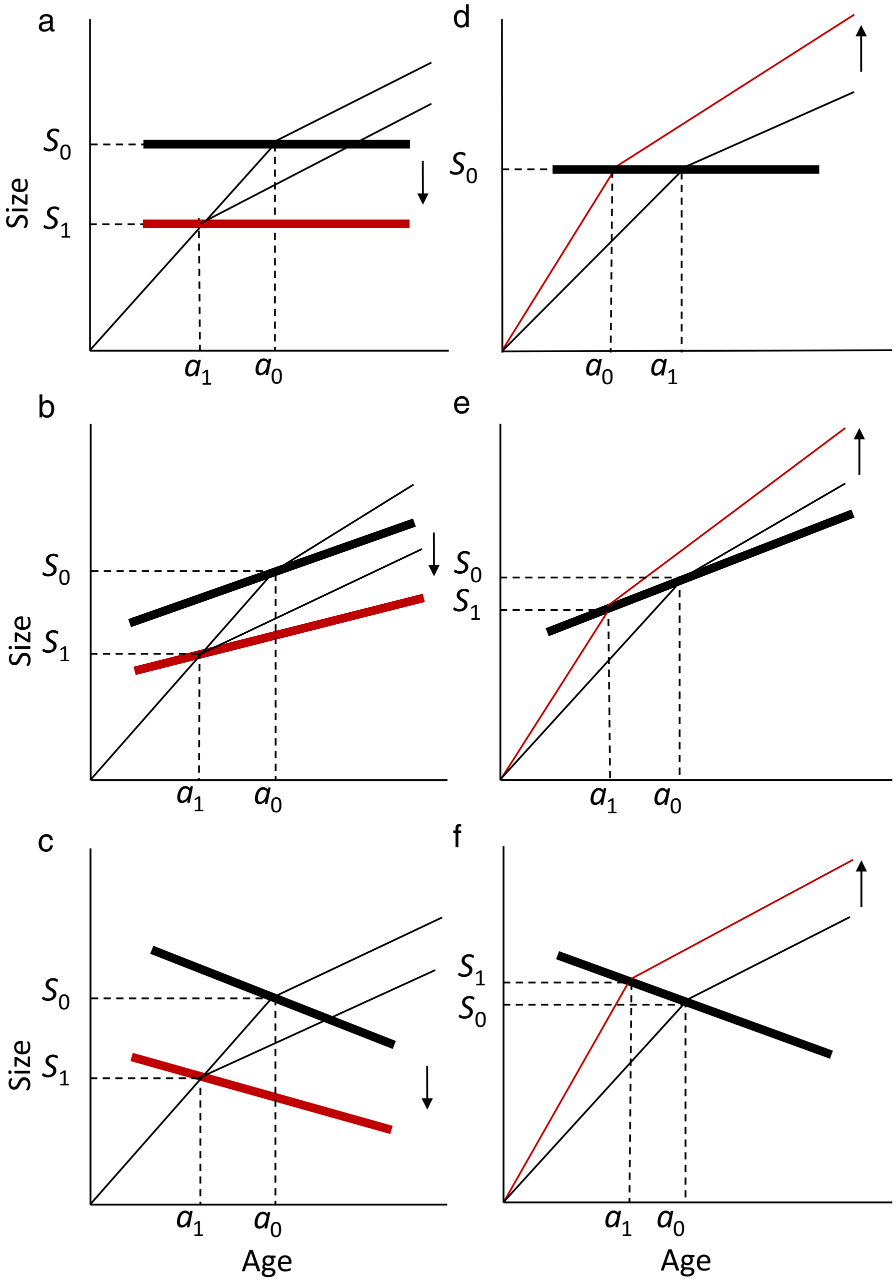

**FIGURE 1** Probabilistic maturation reaction norms (PMRNs; thick lines) reflect direct changes in maturation schedules of individuals in relation to their age and size, independent of changes in juvenile growth (thin lines) rates or mortality. Changes (from black to red lines; follow the directions of the arrows) in both PMRNs (thick lines in subplots a, b, and c) and growth rates (thin lines in d, e, and f) can alter age and/or size at maturation (from $a_0$ to $a_1$ and/or $s_0$ to $s_1$), whereas changes in growth rate will not affect the PMRNs (d, e, and f).

in growth or maturation reaction norm, or both (Figure 1).

Can warming also induce evolutionary changes in phenotypic maturation traits in addition to them changing plastically? Size- and age at maturation have genetic components in fish (Hutchings, 2002). As warming can induce strong phenotypic responses in fish age- and size at maturation (Dhillon & Fox, 2004; Kuparinen et al., 2011; Loisel et al., 2019), it is likely a strong selection pressure and thus a potential evolutionary driver (Crozier & Hutchings, 2014). Most experiments studying warming effects on fish maturation, however, focus on single generation responses. To our knowledge, no study has analyzed the effect of warming lasting multiple generations on maturation traits, independent of effects via growth, in wild fish populations.

In this study, we analyze how warming affects fish maturation and reproductive investment in Eurasian perch (*Perca fluviatilis*) over 17 years (approximately five to eight generations) in an unexploited wild population that has been consistently subjected to elevated water temperatures. Perch sampled from an artificially heated, enclosed coastal area were compared with those from an adjacent control area with natural water temperatures. We examined whether and to what extent multigenerational warming has (1) caused fish to mature at a smaller size or younger age, independent of growth effects (by using PMRNs); (2) altered reproductive investment as indicated by the mass of their gonads relative to their body weight; and (3) if the effect of warming on these traits has changed over time.

# MATERIALS AND METHODS

## Study area and species

We studied effects of warming on fish maturation and reproduction using a whole-ecosystem experimental setup with a chronically and artificially heated enclosed coastal area and its adjacent unheated control area in the Baltic Sea (Appendix S1: Figure S1). The enclosure was constructed in 1977 with the intention to study the future effect of heated water discharge from a nuclear power plant on fish and other organisms in comparison with an unheated area used as control (Thoresson, 1992). Since 1980, the enclosure has been receiving cooling water discharge (flow rate of 80–100 $m^3/s$), making its water temperature 5–10°C higher than in the adjacent control area (Appendix S1: Figure S1). A grating at the outlet of the heated area prevented the exchange of fish bigger than 10 cm between the areas (Adill et al., 2013). Its removal in 2004 increased the probability of larger organisms dispersing between the areas, although the strong current likely prevents the immigration of small or poorly swimming organisms into the heated area. Any kind of exploitation, except for test fishing (see below), has been forbidden in both areas since 1977. The most abundant fish species in both areas is Eurasian perch (Adill et al., 2013). Female perch can become mature from two to five years of age (Heibo & Magnhagen, 2005; Sandström et al., 1995). The onset of spawning in perch depends on temperature and in our study area usually takes place in March to early June (Lukšienė et al., 2000), following gonad development from late autumn to spring (Scharnweber & Gårdmark, 2020). There are considerable regional genetic differences between Baltic Sea perch populations, which can be related to perch being a stationary species with natal homing behavior, variation in temperature, and other environmental variables (Olsson et al., 2011). Perch populations in the heated and control areas show both phenotypic and genetic differentiation. In the heated area, perch have larger size with age, higher growth rates when small (Huss et al., 2019), higher mortality (Lindmark, Karlsson, et al., 2022; Lindmark, Ohlberger, et al., 2022), and more advanced gonad development at a given time of year (Lukšienė et al., 2000). Within the first five years of heating, the youngest age and smallest size at maturity (which is different from *maturation*) have declined for perch in the heated area in comparison with perch in the unheated area (Sandström et al., 1995). Following the separation from the original population, the perch population in the enclosed area has shifted the allelic composition of MHC class II genes related to selection imposed by parasites (Björklund et al., 2015) and has higher expression levels of mitochondrial genes than perch in the surrounding area (Pichaud et al., 2020). Perch in the heated area has thus diverged phenotypically, and possibly also genetically, from perch in the adjacent unheated control area.

## Data

Test fishing with a consistent type of multi-mesh gillnets has been conducted regularly to monitor life history traits of perch in the unheated area since 1970 and in the heated area since 1977 (i.e., after its construction). Test fishing is carried out in parallel in both areas at the same depth range and similar distances to shore (Thoresson, 1992). The secchi depth, often used as a eutrophication indicator, is at similar levels in both areas (Sandström & Karås, 2002 and more details in Appendix S1: Comparison of the areas: similarities). Thus, not only are the two areas adjacent to each other and share the same air temperature, but they are generally also subjected to similar levels and trends in key Baltic Sea environmental drivers (HELCOM, 2009, 2013).

To compare short- and long-term heating effects within this time series, we chose to focus on female perch of age two to five born during the two time periods 1980–1984 and 1991–1996 to estimate their maturation schedule and reproductive investment. We chose these periods to be as distant in time as possible while still being before the grating removal in 2004, so that perch in the two areas were still physically separated. The periods and age range of the perch chosen jointly guaranteed that all perch were caught no later than 2003, such that the exchange and gene flow between the heated and unheated areas perch was minimal. This resulted in that the two periods are 7 years apart, equivalent to a separation by about two to three generations of perch (based on perch age at *maturity* in this area, Sandström et al., 1995, because there is no information on age at *maturation*), allowing us to study warming-induced changes in maturation and reproductive investment occurring between multiple generations. We group perch born in different years into two periods to enable large enough sample sizes as well as the presence of both immature and mature perch at each age in each area during each period, which is required for robust calculations of PMRNs (see *Probabilistic maturation reaction norms*, below). In the first period, 1980–1984, in the heated area, perch were either the first generation to be exposed to heating or offspring of those who had been exposed to heating for about one or two generations. In the later period, 1991–1996, they were all offspring of perch that had been exposed to heating since 1980, that is, for 11–17 years, which is equivalent to about five to eight generations. In total, 3060 perch were sampled, and there were more than 400 individuals sampled per heated or unheated area and per first or second period (Appendix S1: Table S1). We focus on females because only their sample size enabled analyses of heating effects over multiple generations, whereas there are none or too few ages of immature males from the period during which they were sampled (Appendix S1: Table S1). As perch displays sexual size dimorphism (Heibo & Magnhagen, 2005), our sex-specific analyses also ensure that any changes in maturation and reproduction are not confounded by shifts in sex ratio in the population or samples.

Measurements of sampled females were carried out identically in both areas, including body size at capture (in millimeters), age (discrete year), and back-calculated size at each age (in millimeters) from measurements of growth ring distances on the operculum bone, gonad weight (to the nearest 0.01 g), maturation status (mature/immature) from gonad examination, and total body weight (in grams) (see Appendix S1 for detailed descriptions of calculations and examinations).

Reproductive investment is commonly indicated by gonad mass relative to total body weight, the so-called gonado-somatic index (GSI = gonadal weight/total body weight × 100%; Rizzo & Bazzoli, 2020). Female perch GSI from the selected cohorts ranged from 0% to 30.6% (Appendix S1: Figure S2). To capture potential changes in gonad investment among spawning individuals, we filtered out perch sampled well outside the spawning season because their gonads would likely be nondeveloping or spent. We therefore chose sampling weeks 10–30 to capture the peak of gonad development (Appendix S1: Figure S2). To separate prespawning gonads from undeveloped ones, we examined GSI distribution during these weeks. It is bimodal (see Appendix S1: Figure S3) with the two clusters separated at $\text{GSI} \approx 10\%$. We therefore assigned perch with $\text{GSI} > 10\%$ as mature with prespawning or spawning stage gonads for the analyses.

## Maturity ogives

Maturity ogive ($o(a, s)$), the proportion of mature individuals in a population in each age group ($a$) and size class ($s$), is commonly estimated in fish stocks to provide information about reproduction and fecundity per age group. Because of the binary nature of maturation status (being immature or mature), maturity ogive is often modeled as a probability using the logistic regression as a function of age, or size, or both. Once the relationship between maturity ogive, age, and size is estimated in a population, the probability of an individual of any age and size in the population *being* mature can be predicted (Heino et al., 2002). As we need to estimate the PMRNs (see the below section) of individual perch from the two areas and two periods, maturity ogive of an individual at age $a$ (which is the age at capture) and age $a-1$ are needed (Heino et al., 2002). To best describe maturity ogive as a function of age and/or size for each area and period separately, we employed model selection using the logistic regression model (Equation 1) and data on maturation status (0 or 1), age ($a$), and size ($s$) at capture of perch sampled from each area and period,

$$\text{logit}[o(a,s)] \sim \alpha_0 + \alpha_1 a + \alpha_2 s + \alpha_3 a \times s, \tag{1}$$

where $\alpha_1$, $\alpha_2$, and $\alpha_3$ are estimated parameters. We selected the best model for each dataset from models including all combinations of age, size, and their interaction as the one with the lowest Akaike information criterion (AIC; Burnham & Anderson, 2002; Appendix S1: Table S2). To allow for comparisons between areas and periods, we used $o \sim \alpha_0 + \alpha_1 a + \alpha_2 s + \alpha_3 a \times s$ as the best model throughout to predict maturity ogives for the PMRN calculations in the next step (Appendix S1: Figure S4). Model assumptions were checked using diagnostic plots (Appendix S1: Figures S6 and S7). We estimated Nagelkerke's $R^2$ for each model (Appendix S1: Table S2) as a measure of the variation explained (Nagelkerke, 1991).

## Probabilistic maturation reaction norms

Data on perch body size and maturity status at capture give no direct information on the maturation schedule of an individual, that is, the exact age and size when fish have or will become mature. It is important to appreciate the distinction between age- and size at *maturation* and age- and size at *maturity*. The latter can be the age and size of any already mature individual, information that can be easily obtained at capture. We, however, lack data on the former because gonad examination at capture can only provide information on whether a perch has become mature or not but reveals no information about whether a mature fish became mature last year or many years ago. However, estimating PMRNs—the probability of an individual maturing at a given age as a function of size—enables us to investigate individual maturation schedules, for example, size at maturation per age, and by comparing the heated and unheated population, how warming has affected them independently from changes in maturity resulting from changes in growth or mortality. We derived PMRNs for each individual using its size at capture, age, and growth (back-calculated size at age) and the maturity ogive model (Equation 1) to predict its corresponding maturity status. We then calculated the probabilities of an individual becoming mature $m(a, s)$ at a given age $a$ and size $s$ using

$$m(a,s) = \frac{o(a,\, s) - o(a-1,\, s-\Delta s(a))}{1 - o(a-1,\, s-\Delta s(a))}, \tag{2}$$

where $o(a, s)$ and $o(a-1, s-\Delta s(a))$ are the maturity ogives of fish at a given age and size in the year of capture and the previous year, respectively, and $\Delta s(a)$ is the individual growth increment in between (Barot et al., 2004). We focus on two- to five-year-old females, as perch are commonly found to be mature at these ages, and this age range meets the data requirements for the Barot et al. (2004) approach best. Most importantly, this approach requires the presence of both immature and mature individuals at each age, and at each age, there should be at least 100 individuals altogether. Instead of fitting von Bertalanffy's growth curves to calculate an average size-at-age of the population, we used individual growth data, that is, back-calculated individual size-at-age $a$ and $a-1$ derived from their size at capture and operculum structure (for details see Appendix S1). Using these individual growth trajectories rather than a population mean size at age, we calculate each individual's probability of maturing, $m(a, s)$, rather than a population mean $m(a, s)$ per age, which is a population mean PMRN. This reveals variation in PMRNs among individuals between areas and periods, thereby providing more information on changes in maturation schedules than the commonly available population mean in studies of PMRNs (e.g., Vainikka et al., 2009). Therefore, we are able to study how warming may affect not only mean but also within-population variation in perch maturation.

## Statistical modeling of PMRNs and GSI

To investigate if warming and duration of warming affect probability of maturing (and hence size at maturation), we modeled $m(a,s)$ as a function of area (heated or unheated), time period (early, 1980–1984, 5-year warming or late, 1991–1996, after multigeneration warming), age (2–5), and size using binomial generalized linear models (GLMs). Model assumptions were checked, and validation was performed using diagnostic plotting (Appendix S1: Figure S8). Pairwise differences in maturation probabilities between the heated and unheated areas and time periods were assessed using nonparametric Mann–Whitney *U* test. The early period would mainly represent plastic effects of warming as most perch were the first or second generation to experience warming. In the late period, most perch were about the fifth or sixth generation that had been subjected to warming, which would therefore reflect long-term and potentially evolutionary warming effects.

We fitted GSI as a function of area, time period, age (3–5), size, and all combinations of the interactions of the four terms using GLMs. Due to scarcer sampling of gonad weights than gonad status, less GSI data was available for two-year-old perch (Appendix S1: Table S3). We assumed a Gaussian-distributed residual pattern for the models as the data captured the gradual gonadal development from autumn to spring. Student *t*-tests were used to assess differences in GSI between the areas or periods. Model validation was checked by inspecting diagnostic plots (Appendix S1: Figure S9).

For both $m(a,s)$ and GSI, we ran null and full models, respectively, as a function of only age, size, and age × size and as a function of age, size, area, period, and all their possible interactions. We selected the models manually through a stepwise process, working backward from the full model (Appendix S1). We consider the best model to be the one with the lowest AIC, and all models with $\Delta\text{AIC} < 2$ to that model to be indistinguishable. To illustrate consequences of maturation probabilities for maturation size, we derived the predicted perch body size with 50% probability of maturing (Lp50) for each age, using the best model. All data processing and statistical analyses were conducted in R, version 4.0.2 (R Core Team, 2014). Data visualization and processing were done using packages within the tidyverse collection (Wickham et al., 2019). Derivation of Lp50 from the best PMRN model was done using package "rje" (Evans & Drton, 2022).

Whether area or period is included in the best model for either maturation probabilities or reproductive investment indicates whether warming or its duration plays a role for fish maturation and reproduction.

# RESULTS

## Maturation

Area (heated vs. unheated) was retained in the best PMRN model (Table 1, Appendix S1: Table S4; as well as in all models with $\Delta$AIC $< 2$, Appendix S1: Table S8), implying that temperature has affected the maturation probability of female perch (Figure 2). The heating effect on maturation has also changed over about five generations, as the duration of heating (period) was included in the best model (Table 1). Both area and period were included in the best model as well as 2-, 3-, and 4-way interactions with age and size. Importantly, this suggests that heating effects varied over ontogeny and across generations.

Both the probability of becoming mature (Figure 2) and the predicted maturation size (Lp50; Figure 3), differ between the heated and unheated areas. Within the first five years of warming, fish of a given body size have a higher probability of maturing at early ages (Figure 2a,b; Mann–Whitney $U$ test, $p < 0.05$, $\eta^2_{\text{age2}} = 0.30$, $\eta^2_{\text{age3}} = 0.08$) and thus mature at a smaller size at age two and three in comparison with fish in the control area (Figure 3a). Over age, the difference in $m(a, s)$ between perch in the areas decreases, such that predicted Lp50 at age four and five in the two areas are more similar (overlapping CI in Figure 3a; see Appendix S1: Table S5 for significance level and effect size).

Compared with the Lp50 of perch born during the first five years of warming, perch Lp50 is even smaller after multigenerational heating at age two to four (Appendix S1: Figure S10; $p < 0.05$, $\eta^2$ is 0.30, 0.39, and 0.04 for respective ages). Two-year-old perch in the heated area showed an even greater probability of maturation ($p < 0.05$, $\eta^2 = 0.73$; Figure 2e), and thus a smaller maturation size (Figure 3b), than same-aged contemporaries in the unheated area. In contrast, for three-year-old perch the maturation size was similar in both areas (overlapping CI at age three; Figure 3b). Interestingly, four- and five-year-old perch in the heated area had lower probability of maturing ($p < 0.05$, $\eta^2$ is 0.70 and 0.64 for age four and five; Figure 2g,h) and larger maturation size (Figure 3b) than those in the unheated area. Moreover, after the multigenerational heating, the variation in probability of maturing for three- to five-year-old perch is substantially greater than for perch in both the unheated area and those that have only experienced the initial five-year heating (Appendix S1: Figure S11). Notably, maturation size changed between the two periods in the unheated area as well. That is, in the late period, perch matured at smaller size at all ages compared with the early period (Figure 3).

## Reproductive investment

Area was retained in the best GSI model (Table 2, Appendix S1: Table S6, as well as in all models with $\Delta$AIC $< 2$ to the best model, Appendix S1: Table S9), implying that temperature is important to explain female perch reproductive investment. Different levels of interaction between area, period, age, and size were also included in the best model (Table 2). Perch in the heated area invested relatively more in reproduction at age four after five years of heating than perch in the control area ($p < 0.05$, Cohen's $d > 1$; Figure 4a). GSI of five-year-old individuals, however, overlapped substantially between the

**TABLE 1** Model selection results for probability maturation reaction norms of two- to five-year-old female perch across both areas (heated vs. unheated) and periods (early 1980–1984 and late 1991–1996).

| Model | Formula | df | AIC | Residual deviance[a] |
|---|---|---|---|---|
| Null | $m \sim$ age + size + age:size | 2951 | 3301 | 619 |
| Full | $m \sim$ age + size + age:size + area + age:area + size:area + age:size:area + period + area:period + age:period + size:period + age:size:period + age:area:period + size:area:period + age:size:period:area | 2939 | 2152 | 150 |
| Best | $m \sim$ age + size + age:size + area + age:size:area + period + area:period + age:period + age:size:period + age:area:period + size:area:period + age:size:period:area | 2942 | 2143 | 153 |

*Note*: Null model (without effects of area or period), full model (effects of age, size, area, and period and all their interactions), and the best model based on the lowest AIC are displayed (for models with AIC within 2 units of the best model's; Appendix S1).

Abbreviation: AIC, Akaike information criterion.

[a] The null deviance of the model that includes only the intercept is 863.

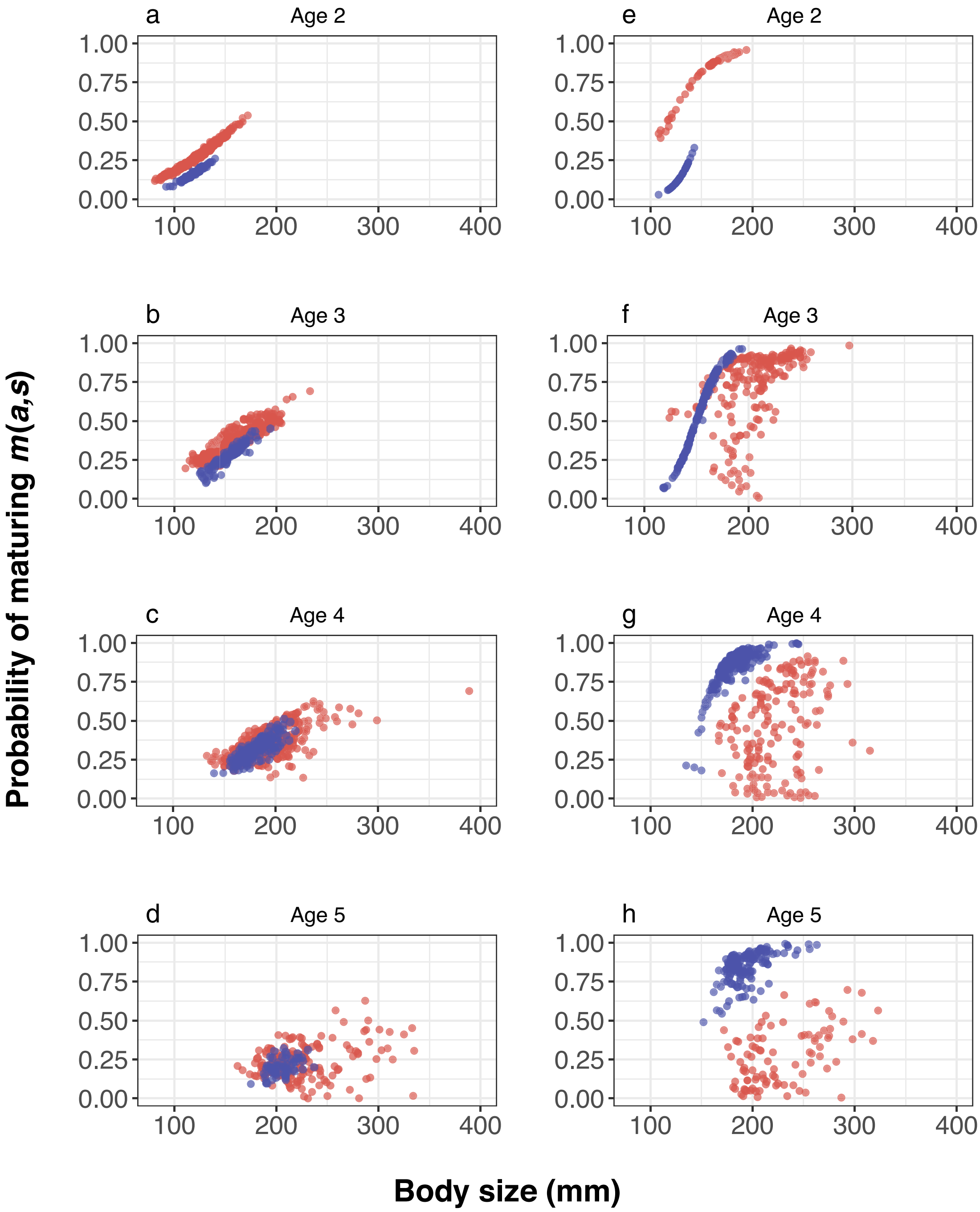

**FIGURE 2** Probabilities of maturing ($m(a,s)$) of female perch from the heated coastal area (red) and the adjacent unheated area (blue) for two-year-old (subplots a and e), three-year-old (b and f), four-year-old (c and g) and five-year-old (d and h) individuals. Maturation probabilities differ between perch from the early period (a–d) following the onset of heating (cohorts 1980–1984) and the late period (e–h), after about five to eight generations of heating (cohorts 1991–1996).

areas ($p = 0.57$; Figure 4b). The effect of warming on GSI changed over time (Appendix S1: Table S7). After multigenerational heating, GSI was similar in the two areas for both four- and five-year-olds ($p > 0.5$; Figure 4c,d). In the heated area, four-year-old perch had smaller GSI after the long-term warming than after only five years of warming ($p < 0.01$, Cohen's $d = 0.86$; see Appendix S1: Figure S12).

## DISCUSSION

We found that warming has a direct impact on both fish maturation and reproductive investment in the wild, beyond shifts caused by temperature-induced changes in growth. Fish in the heated area generally had a higher probability of maturing, hence a smaller size at

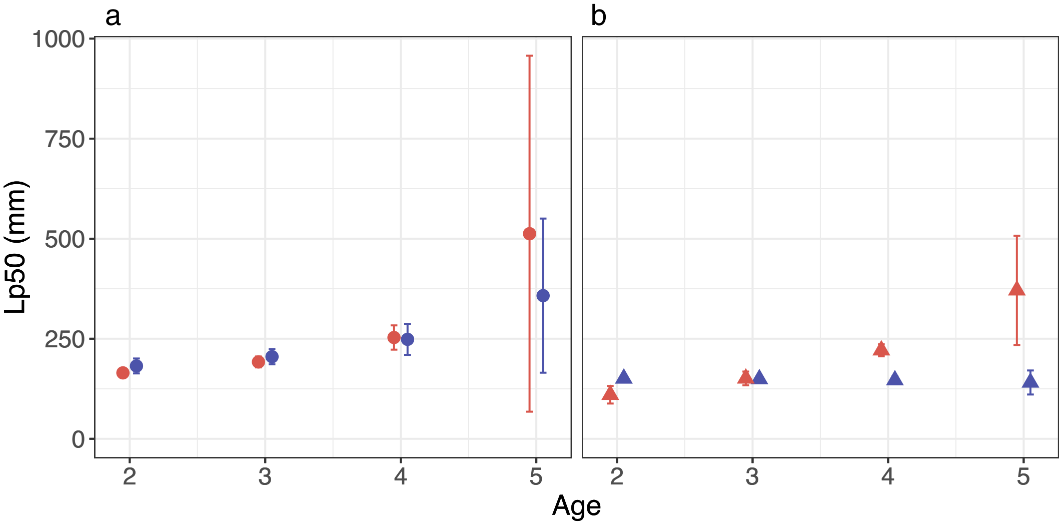

**FIGURE 3** Body size (mm) of female perch with 50% probability of maturing (Lp50), for two- to five-year-olds in the heated (red) and unheated area (blue), for the early period (subplot a, cohorts 1980–1984; circles) and the late period (b, cohorts 1991–1996; triangles). The 95% confidence interval of Lp50 for each age, area, and period combinations are illustrated as bars.

**TABLE 2** Model selection results for selection of variables explaining the building up of gonads of three- to five-year-old female perch, across both areas (heated vs. unheated) and time periods (early 1980–1984 and late 1991–1996).

| Model | Formula | df | AIC | Residual deviance[a] |
|---|---|---|---|---|
| Null | GSI ~ age + size + age × size | 446 | 2383 | 5134 |
| Full | GSI ~ area × age × size × period | 434 | 2362 | 4652 |
| Best | GSI ~ age + size + area + period + age:size + age:area + age:period + size:period + age:size:area + age:size:period + age:area:period + size:area:period | 437 | 2358 | 4672 |

*Note*: The null, full, and best models are displayed here (models with AIC within 2 units of the best model can be found in Appendix S1).
Abbreviation: AIC, Akaike information criterion.
[a]Null deviance for the model including only intercept is 5183.

maturation, and initially also invested more in reproduction than fish in the unheated population. The temperature effect on maturation size and reproductive investment varied over fish ontogeny, as shown by different responses in these life history traits to warming in fish of different ages. By tracking trait changes in perch across generations under constant heating, we also found that the effect of warming on both traits varied over time, and had a different relationship with age (ontogeny) after multiple generations of heating. This suggests that warming-induced evolution may have occurred, but evidence on underlying adaptive genetic changes is needed.

Within the initial five years of heating, young female perch in the heated area were more likely to mature at a smaller size and have larger relative gonad size than those in the unheated population. Warming-induced decrease in size at maturation, beyond any effect of growth, has been found in several fish species under laboratory conditions when studied within a single generation (Dhillon & Fox, 2004; Kuparinen et al., 2011). Uniquely to our study, we also found this in a wild fish population exhibiting multigenerational heating at an ecosystem scale. Warming may directly alter maturation-regulating hormones and development rates at different life stages (Miranda et al., 2013; Wootton et al., 2021), resulting in advanced maturation. Higher food availability, therefore improved body condition, is also associated with higher size-specific maturation probabilities, independent of growth (Uusi-Heikkilä et al., 2011). In our system, perch food abundance in the heated area may have increased initially due to warming (Sandström, 1991; whereafter we lack prey data), although this may not always be the case in other heated systems. Thus, the higher probability of maturation and smaller maturation size could result from both a direct effect of higher temperatures on fish physiology and an indirect effect via improved food conditions. Given more food in the heated area, perch might also be better able to afford diverting of

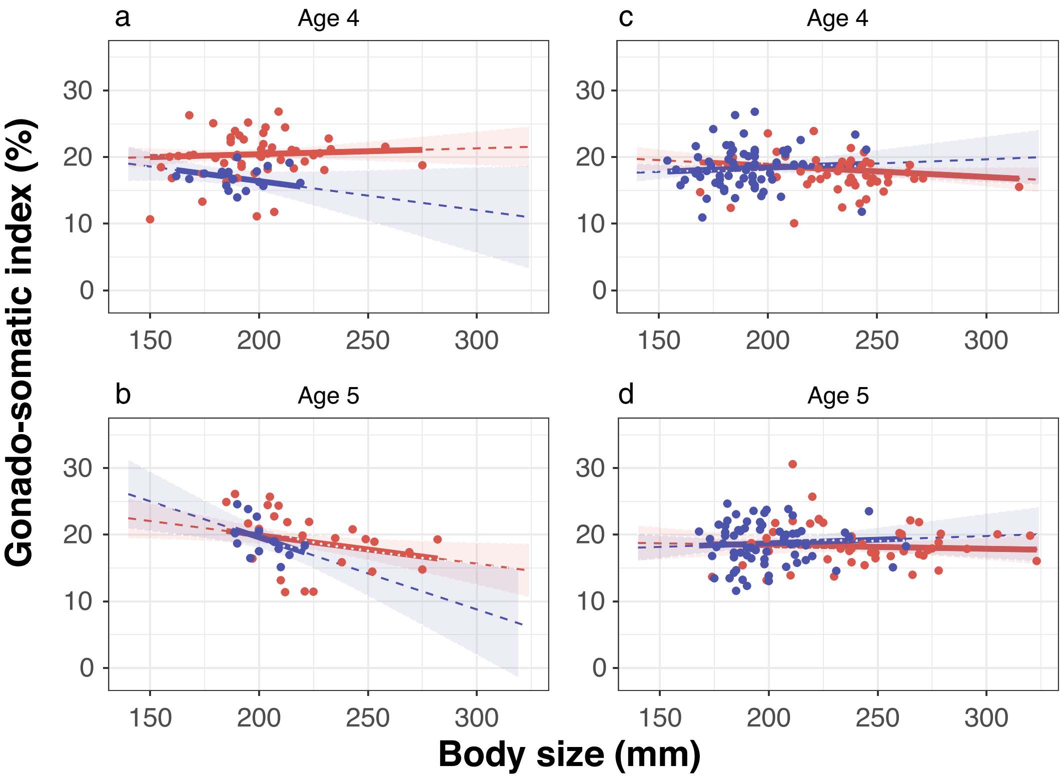

**FIGURE 4** Gonado-somatic index (GSI) predicted for female perch from the heated area (red; solid part of the lines corresponds to the size range of the empirical dataset) and from the unheated area (blue) for age four (a and c) and five (b and d), respectively, for the early period: cohorts 1980–1984 (a and b) and the late period: cohorts 1991–1996 (c and d). The 95% confidence intervals are added for the whole length range as shading. Observed GSI of perch are shown as red (heated area) and blue (unheated area) points.

energy to reproductive investment (McBride et al., 2015) at a smaller size, explaining the increased GSI (Wootton et al., 2022). Previous studies found a negative relationship between increased temperature and absolute gonad size in ectotherms (Donelson et al., 2010), but temperature effects on relative gonad mass (as in our study) are rarely looked at. Larger relative gonad size can be beneficial in warmer environments if the increase in gonad size corresponds to increased egg size, which can result in higher offspring survival in warmer waters (Jonsson & Jonsson, 2019). Another explanation is that investing more energy into reproduction at a young age might compensate for lowered fecundity due to the smaller body size that results from the warming-induced decrease in size at maturation and thus smaller adult size (Roff, 1992). This largely corresponds with our findings in the first five years of warming. Although for the youngest ages displaying the greatest reduction in maturation size, our sample size for gonad weights was too small to allow comparisons between areas. Our whole-ecosystem warming experiment reveals that warming for up to two generations can decrease maturation size. To our knowledge, few studies have addressed long-term warming impacts on both maturation schedules and reproductive investments (but see Wootton et al., 2022 for a laboratory experiment on this). Our joint analyses of these suggest that reproductive investment of fish in the wild may respond to warming in relation to concurrent changes in size at maturation.

In the heated area, after long-term (from 1980 to 1991–1996) warming, corresponding to at least three additional generations of perch exposed to warming following the first five years of warming, maturation size of perch of all ages decreased compared with perch born during the initial years of warming (from 1980 to 1984). This is the first time that warming has been associated with changes in fish maturation over generations in the wild, independent of growth effects induced by warming. Shifts in the PMRNs, following multigenerational warming, could result from a heritable genetic component associated with selection favoring a decrease in maturation size, as inferred in PMRN studies on other selection pressures (reviewed in Dieckmann & Heino, 2007; Gobin et al., 2021). From a life history perspective, smaller maturation size can be beneficial under warming, as it results in a smaller adult size when energy is diverted to reproductive development than somatic growth (Roff, 1992). The benefits can be lower maintenance costs (Forster et al., 2012), especially in warming waters where the metabolic rate of ectotherms inevitably increases. A younger age at maturation can enable more reproductive events, which can increase reproductive success in unpredictable environments (i.e., bet hedging; Slatkin, 1974). Furthermore, if lifespan decreases due to a warming-induced increase in mortality (Pershing et al., 2015), it may be beneficial to mature and spawn as early as possible. The increased mortality in our heated area (Lindmark, Karlsson, et al., 2022; Lindmark, Ohlberger, et al., 2022; Sandström et al., 1995) may thus partly explain the smaller perch maturation size therein. We cannot, however, rule out maternal effects (e.g., silver spoon effect; reviewed in Jonsson & Jonsson, 2014). Genome-wide screens of footprints of selection of perch from the two areas sampled would be one potential step to distinguish if warming has exerted selection on genetic components.

In contrast to most PMRN studies, we derived maturation probabilities for individual fish using back-calculated individual size at age trajectories instead of predicted mean sizes at age based on a growth model fitted at the population level. This enabled us to reveal that warming has affected variation in maturation within the heated population. After multigenerational heating, variation in maturation probability increased for three- to five-year-old perch. This would be expected if fish have adapted to long-term warming using alternative evolutionarily stable strategies (some maturing at smaller size with higher fecundity, others maturing at larger size but with a smaller reproductive investment). This supports findings from a laboratory experiment showing that fish had larger size at maturation and higher fecundity after six generations of warming than fish that experienced warming for a single generation (Loisel et al., 2019). Alternatively, the variation in maturation can stem from the fact that water temperature in the heated area exceeded perch optimal temperatures (especially for large-sized individuals; see fig. S1 in Huss et al., 2019) in some years (e.g., >30°C; Appendix S1: Figure S1). Given that excessively high temperatures can postpone maturation (Dhillon & Fox, 2004; Miranda et al., 2013), a variable frequency of extreme temperatures between years can cause increased size at maturation for first-time spawners in some cohorts but not others. Ideally, experiments with controlled temperature treatments at different locations along the thermal curve, pursued over generations, should be carried out to test this. The observed warming-induced increase in maturation variation demonstrates the importance of applying back-calculated individual growth trajectories in PMRN analyses in general and of addressing warming impacts on not only means but also on variation within populations.

Interestingly, the decreased maturation size of perch in the heated area compared with that in the unheated area weakened at older ages within the five years of heating, and changed direction after multigenerational warming. This could result from the increased variation in maturation probability in the heated area. It might also be partly due to a decrease in perch maturation size at age four and five over time in the unheated area. Although the unheated area was chosen and paired with the heated area as a “control” for the increased temperature “treatment”, it is open to the surrounding sea. Therefore, perch may have been subjected to a range of different selection pressures, such as exposure to natural predators with different predation pressures, on which we lack data to compare between the areas. It is unlikely that responses in the control area are due to temperature increase induced by water exchange with the adjacent heated area, as the design of the enclosed bay ensures this exchange is small (Sandström et al., 1995; Appendix S1: Figure S1). Both areas have been subjected to climate change, however, the temperature increase between the two study periods is small (<1°C/decade in the Baltic region; HELCOM, 2013) and much smaller than the temperature difference imposed by the artificial heating (Appendix S1: Figure S1). We cannot offer a definite explanation for the changes observed in the unheated area, as our heating experiment at the ecosystem scale suffers from the fact that there is only one heated ecosystem and one control ecosystem. Factors other than water temperature may have contributed to the differences between the control and heated areas. However, for factors for which data were available and based on the same type of measurements in both areas, that is, perch population density (as indicated by catch per unit effort), fish community composition, and water quality (as indicated by secchi depth), the differences between the areas do not correlate with warming (see Appendix S1: Comparison of the areas: similarities). Furthermore, perch sampling took place at the same water depths and distances to shore in the heated and unheated areas (Appendix S1: Figure S1), both free of fishing pressure. More importantly, the temperature difference (>5°C) between the treatment area and the control area is uniquely large and persistent over multiple generations for a natural system, especially if compared with the less than 1°C temperature increase induced by climate change in the Baltic region over the study period (HELCOM, 2013). These all suggest that the difference in temperature is the key difference between the areas and that changes observed between the artificially heated and unheated areas and in the heated area over multiple generations were likely caused by the substantial (+5–10°C; Appendix S1: Figure S1) warming.

We have to interpret our results somewhat cautiously due to a few limitations in sampling. Our sample of the youngest and oldest ages in both areas contains somewhat fewer fish than what would be ideal according to the method used (Barot et al., 2004; Appendix S1: Table S1). This might have caused the low variance explained of the ogive models (Appendix S1: Table S2). Alternatively, the reason of "low fit" ogive models could be that we were unable to incorporate body condition (which impacts fish maturation ogives; Uusi-Heikkilä et al., 2011) in our models due to a lack of body weight data. Because warming has increased perch body growth in the heated area over time (Huss et al., 2019), they were larger than perch from the unheated area in the late period but not in the early period (Appendix S1: Figure S13). This can explain the GSI clustering (that there were no small perch with developing gonads in the heated area and no big perch with developing gonads in the control area), which may have limited our ability to find differences in GSI between the areas. We selected identical sampling weeks ("prespawning period") for both areas for the GSI analysis. Warming can however shift spawning phenology in fish (Miranda et al., 2013) and such shifts have been observed in our case (Appendix S1: Figure S2; Lukšienė et al., 2000), which means more perch were sampled closer to spawning in the heated area than in the unheated area. This may explain the larger GSI found in the heated area. However, due to the different sampling schedules in the areas, it is difficult to compare the temporal dynamic of gonad development over the entire reproductive cycle between the areas. While these aspects limit our ability to infer the actual mechanism of increased GSI due to warming, our main finding that warming increases the probability of maturation and reduces maturation size in young fish holds.

Increased maturation probability and smaller maturation size due to warming are likely to affect both ecological and evolutionary dynamics. A younger maturation age implies shortened generation time, which can accelerate the speed at which evolutionary processes occur (Roff, 1992). If the cause of the smaller maturation size is evolutionary, the directional selection caused by warming can make the population lose genetic variation. As the elevated temperature regime in the heated area corresponds to the projected increase of 2–4°C in the Baltic Sea surface temperature until the end of the century (HELCOM, 2013), our findings based on a whole-ecosystem heating experiment make the case for that climate change will impact fish maturation size. A warming-induced decrease in maturation sizes results in smaller mean adult sizes in the population, which potentially decreases recruitment capacity (Hutchings, 2002) and population biomass production (van Dorst et al., 2019). Decreased sizes can also cause changes in predator–prey interactions, affecting the overall food web and ecosystem functioning (Lindmark et al., 2019).

In conclusion, our study demonstrates multigenerational warming effects on maturation and reproductive investment on an unexploited, wild fish population based on a large sample size. We found a strong increase in maturation probability, that is, a decrease in maturation size, in response to warming over a five-year period. Interestingly, this decrease intensified after multiple generations of warming, suggesting evolutionary change. Parallel to a decrease in maturation size, we found that reproductive investment increased after five years of warming, however, this difference disappeared after multiple generations of warming. Our results emphasize that warming impacts on organism maturation can vary both ontogenetically and over time, involving potentially both phenotypic and genotypic responses, and also be linked to other life history traits. We call for future experimental studies looking into effects of increased temperature on ectotherm growth-independent maturation schedules over multiple generations, coupled with investigations of corresponding genomic changes.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Niu et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.7351524.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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