RESEARCH ARTICLE

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Elevated temperatures drive the evolution of armour loss in the threespine stickleback *Gasterosteus aculeatus*

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Abstract

1. While there is evidence of genetic and phenotypic responses to climate change, few studies have demonstrated change in functional traits with a known genetic basis.
2. Here we present evidence for an evolutionary adaptive response to elevated temperatures in freshwater populations of the threespine stickleback *Gasterosteus aculeatus*.
3. Using a unique set of historical data and museum specimens, in combination with contemporary samples, we fitted a Bayesian spatial model to identify a population-level decline in the number of lateral bony plates, comprising anti-predator armour, in multiple populations of sticklebacks over the last 91 years in Poland.
4. Armor loss was predicted by elevated temperatures and is proposed to be a correlated response to selection for reduced body size.
5. This study demonstrates a change in a functional trait of known genetic basis in response to elevated temperature, and illustrates the utility of the threespine stickleback as a model for measuring the evolutionary and ecological impacts of environmental change across the northern hemisphere.

KEYWORDS
adaptation, body size, climate change, Gasterosteidae, intraspecific variation, scaling

1 | INTRODUCTION

The central assumption of evolutionary theory is that natural selection drives phenotypic adaptation of populations to local environmental conditions through changes in the genetic composition of the population. These adaptive changes arise from the differential reproductive success of individuals that vary genetically (Darwin, 1859; Fisher, 1930; Williams, 1966). In this context, the capacity of natural populations to respond to rapid climate change is contingent on adaptive change to phenotypic traits that have a genetic basis. While numerous studies demonstrate correlations between temperature and phenotypic traits, many traits are highly plastic and the adaptive value of these changes is unclear (reviewed by Crozier & Hutchings, 2014).

To unequivocally show an adaptive evolutionary response to climate change, it is necessary to demonstrate consistent and predicted alteration in a functional trait that is under genetic control. A suitable species is one with short generation time, subject to high or consistent selection pressure for a trait under simple genetic control and with standing genetic variation present in populations (Crozier & Hutchings, 2014). The threespine stickleback *Gasterosteus aculeatus* is a model vertebrate in behavioural and evolutionary biology that possesses these features and is widely distributed across the northern hemisphere. The species occupies

a wide range of environments and shows a high degree of phenotypic variability over small spatial scales (Bell & Foster, 1994; Des Roches et al., 2019; Smith et al., 2020a; Wootton, 1976, 1984, 2009). Marine populations of the threespine stickleback have repeatedly invaded freshwater habitats. These invasions are characterized by rapid reduction in the extent of anti-predator 'armour', comprising lateral bony plates, pelvic girdle and spines, and dorsal spines, as well as other aspects of their biology (Bell & Foster, 1994; Wootton, 1976, 2009).

Most freshwater populations of threespine sticklebacks converge on a *low* lateral plate ecomorph, with <10 lateral plates on each side of the anterior portion of the body, along with three dorsal spines, pelvic girdle and a pair of pelvic spines. The separate elements of the armour function in concert, with anterior lateral plates bracing the dorsal and pelvic spines, which thereby resist compression while also limiting ingestion by gape-limited vertebrate predators (Reimchen, 1994). Marine sticklebacks are almost exclusively represented by a *complete* ecomorph, with >30 lateral plates along the entire body. Posterior lateral plates appear to function in preventing skin puncture by toothed predators (Reimchen, 1994). A *partial* ecomorph also occurs, expressing an intermediate and variable number of lateral plates, and is typically encountered in brackish water (Wootton, 1976). Population-level change in the number of lateral plates can be rapid, with a reversal in plate ecomorph dominance in as few as 10 generations (e.g. Bell et al., 2004).

The accepted contemporary model for threespine stickleback lateral plate evolution involves the repeated, independent establishment of freshwater populations from ancestral, panmictic populations of fully plated marine fish. Multiple genomic regions have been associated with adaptation to fresh water (Jones et al., 2012), with the *ectodysplasin A* locus specifically implicated in lateral plate evolution. The heritability of plate number is high (Hansson et al., 2016), with 70% of variation in plate number associated with variation in *ectodysplasin A* (Colosimo et al., 2005; Cresko et al., 2004). Marine populations are assumed to possess a pool of standing genetic variation, with rare variants of the *ectodysplasin A* locus experiencing strong selection once fish enter fresh water, where they rapidly increase in frequency (Barrett, 2010).

A number of hypotheses have been proposed to explain the selective agent responsible for armour loss in freshwaters, including predation, calcium and phosphorus availability, water density, parasitism, competition, body size and swimming performance (Barrett, 2010; Myhre & Klepaker, 2009; Smith et al., 2020b; Wootton, 2009). At a large geographical scale, it is also apparent that temperature plays a role in driving variation in lateral plate number (Des Roches et al., 2019; Münzing, 1963; Smith et al., 2020b; Wootton, 1976, 1984), with well-developed armour associated with low winter temperatures and the converse at higher temperatures. A striking deviation from the typical pattern of lateral plate morph evolution is the widespread occurrence of fully plated sticklebacks in fresh waters in Eastern Europe and the east coast of North America, where they are associated with low winter temperatures (Hagen & Moodie, 1982; Wootton, 1976, 2009). The almost ubiquitous occurrence of *complete* ecomorph populations in Poland, in particular, has been the focus of research for many decades (e.g. Bańbura, 1989; Penczak, 1965; Piesik, 1937; Smith et al., 2020b).

The association between environmental temperature and variation in threespine stickleback lateral plate number provides an opportunity to investigate whether large-scale climate trends can drive phenotypic change in lateral plate number among stickleback populations. Their wide distribution, tolerance of a wide range of environmental conditions and striking phenotypic variability make the threespine stickleback an ideal model for investigating selective forces underpinning climate change.

In this study, we investigated temporal trends in lateral plate number over a 91-year period across Poland, using a spatially explicit Bayesian model. Given the association between lateral plate number and temperature, we predicted a decrease in the lateral plate number of threespine sticklebacks over the past nine decades, corresponding with increasing environmental temperatures while controlling for the effects of concomitant changes in body size and spatial dependency.

## 2 | MATERIALS AND METHODS

2.1 | Fish data

Samples of threespine sticklebacks were collected in 2017 and 2018 from 61 sites across Poland using electrofishing, dipnets and small Seine nets. Collected fish were killed with anaesthetic (benzocaine) and fixed in 4% buffered formalin. For each fish, a record was made of standard length (measured from the tip of the snout to the origin of the tail) and total number of lateral plates on the left flank of the body. An additional 15 samples were obtained from the archive of the Museum of the Institute of Zoology of the Polish Academy of Sciences in Warsaw. These samples were collected between 1927 and 1963. Specimens were measured for standard length and the total number of lateral plates on the left side of each fish was counted. Information on the date and location of collected specimens were available. Finally, we used previously published data from colleagues at the University of Łódź (Bańbura, 1988, 1994; Penczak, 1960, 1962), which included fish collections conducted between 1947 and 1987 for 78 populations. The locations of sampling sites are illustrated in Figure 1 and summarized in Table S1. Samples were restricted to adult fish >27 mm standard length to ensure lateral plate development was complete (Bańbura, 1989). Data were also limited to samples containing a minimum of 20 fish, collected between April and October. These limitations yielded a final sample size of 110 populations, spanning 91 years (1927–2018).

2.2 | Temperature data

Temperature data were compiled from 34 meteorological stations across Poland. Daily air temperature data were available from January 1881 until the present, though not for all weather stations. The mean

FIGURE 1 Collection sites of threespine stickleback samples (red dots) and weather stations (blue dots) in Poland. Note that one sample, in the top right of the figure, falls outside the current Polish border. When this sample was collected (September 1928), the collection site was on Polish territory (now in Lithuania)
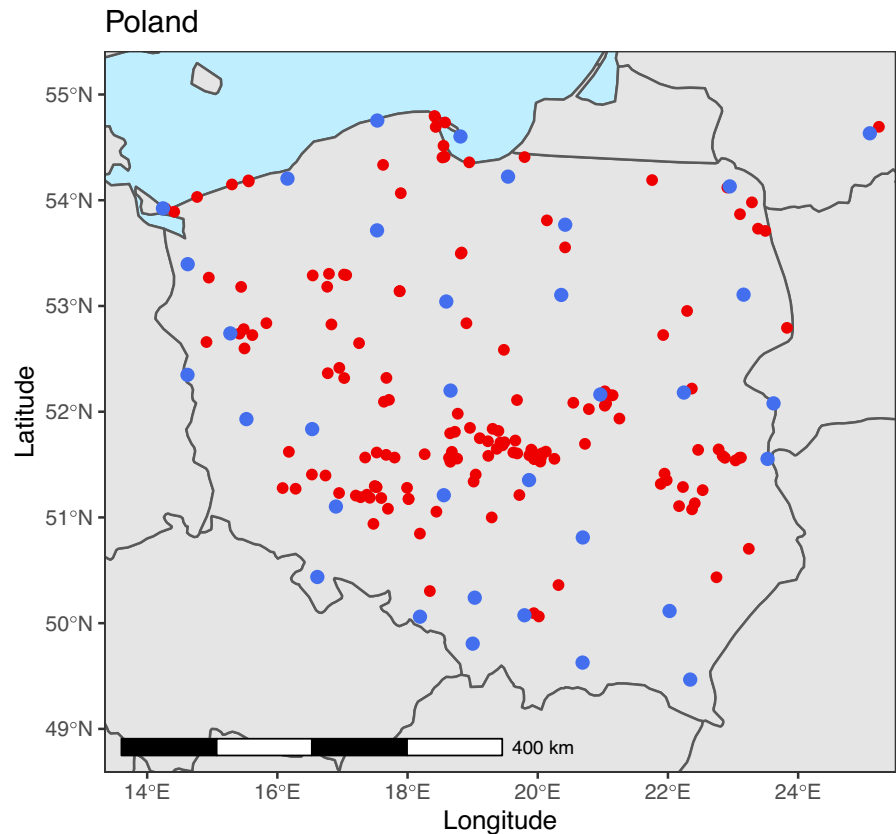
of the 10-year antecedent air temperatures (T_{10}) from the geographically nearest weather station with a complete time series of data was calculated for each stickleback sampling location. A period of 10 years was used because this is sufficient time for a change in threespine stickleback lateral plate phenotype to evolve following environmental change (Bell et al., 2004). For some sample locations, a complete 10-year time series of temperature data was not available (data collection was interrupted at some locations during WWII and in its immediate aftermath), in which case an incomplete time series was used. The spatial distribution of weather stations is shown in Figure 1. Summary data for every sample and the location of the nearest weather station are summarized in Tables S1 and S2, and mean stickleback population standard length among months in Figure S1.

2.3 | Data analysis

Data were modelled using R (version 4.0.2; R Development Core Team, 2020) with models fitted in a Bayesian framework using INLA (Integrated Nested Laplace Approximation) with the R-INLA package (Rue et al., 2017). To model the data at the population level, lateral plate count (Gaussian distribution) was regressed against historical near-surface air temperature data and body size. Data exploration suggested trends in plate number associated with changes in the 10-year antecedent near-surface air temperature anomaly over the last nine decades (Figure 2a) based on the CRUTEM4 dataset (Morice et al., 2012), particularly associated with a rapid rise in the European

surface air temperature over the last three decades (Figure 2b). These data included spatial patterns arising from variation in sample locations through time, in combination with spatial variation in surface air temperature among sample locations, resulting in residual spatial autocorrelation (Legendre, 1993). To accommodate this potentially confounding structure to the data, we used spatially explicit, Bayesian approximation methods to generate model parameter estimates. R-INLA includes functions to construct Gaussian Markovian random fields that permit parameter estimation in relation to spatial structure in the data (Lindgren et al., 2011). Gaussian Markovian random fields are estimated using Matérn correlation solved with a stochastic partial differential equation on a 'mesh', comprising small, non-overlapping triangles that encompass the sampling area (Zuur et al., 2017). Using this approach, we modelled threespine stickleback plate number as a function of standard length and T_{10} from the geographically nearest weather station to each sampling site while accommodating spatial dependency in the data. A mesh of 3,461 vertices was generated by constrained refined Delaunay triangulation to encompass all sampling sites in Poland (Figure 3). For this model, we predicted a negative relationship between plate number and T_{10} and a positive relationship with body size (Smith et al., 2020b).

Near-surface air temperatures are considered to provide one of the clearest signals of regional climate change (Morice et al., 2012). Surface air temperatures correlate closely with river temperatures (e.g. Marszelewski & Pius, 2018; Mohseni & Stefan, 1999; Pilgrim et al., 1998). Thus, while absolute temperatures experienced by sticklebacks across Poland may have differed from those used to
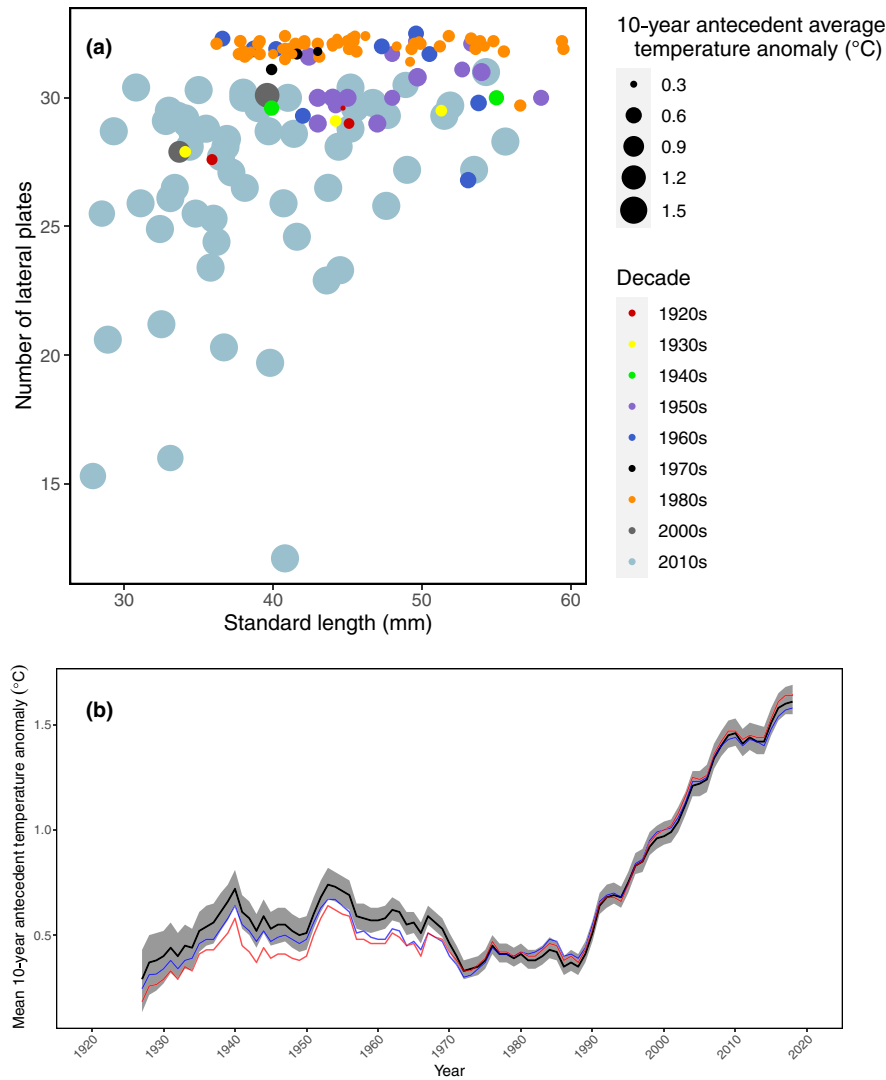
FIGURE 2 (a) Bubble plot of threespine stickleback lateral plate number against standard length (mm), with size of points relative to mean 10-year antecedent near-surface air temperature anomalies over land for Europe (°C) from the CRUTEM4 dataset compiled by the UK Met Office Hadley Centre (www.metoffice.gov.uk/hadobs/hadcrut4). Different coloured points represent different decades; (b) Plot of 10-year antecedent surface air temperature anomalies over land for Europe (°C) from the CRUTEM4 dataset by year from 1927 to 2018, the period over which threespine stickleback data were collected and compiled. The black line is the mean surface air temperature and shaded area is the 95% confidence interval. Data for the same period from the NASA Goddard Institute for Space Studies (blue line), and National Oceanic and Atmospheric Administration (red line) are included for comparison
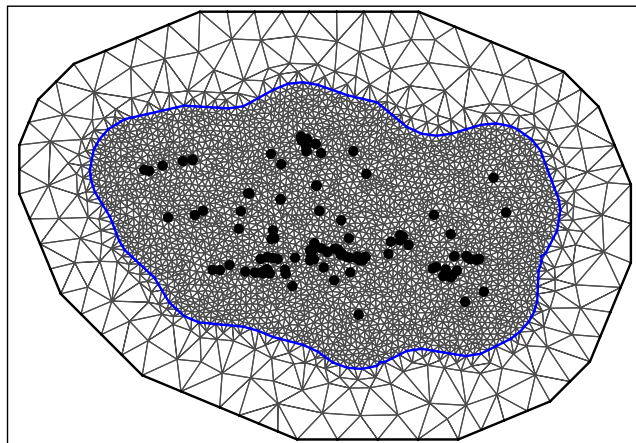

FIGURE 3 Mesh of 3,461 vertices generated by constrained refined Delaunay triangulation

model the relationship with body size and plate number, because the pattern of temperature variation showed consistent regional behaviour, local variations would not be expected to negatively affect the correlation between air and water temperatures (Marszelewski & Pius, 2018).

Seven models were fitted to the data, with standard length and T_{10} either included or removed, and with or without the inclusion of a spatially correlated random effect. A baseline model was also included, comprising an intercept and spatially correlated random effect only. Model selection was conducted using the deviance information criterion (Spiegelhalter et al., 2002) as a measure of goodness-of-fit, and the log-conditional predictive ordinate (Roos & Held, 2011) as a measure of model predictive quality. The best-fitting model, determined by deviance information criterion and log-conditional predictive ordinate, took the form:

$$\text{Plate}_i \sim N\left(\mu_i, \sigma^2\right),$$

$$E\left(\text{Plate}_i\right) = \mu_i \text{ and var}\left(\text{Plate}_i\right) = \sigma^2,$$

$$\mu_i = \beta_1 + \beta_2 \times \text{Length}_i + \beta_3 \times \text{Temperature}_i + u_i,$$

$$u_i \sim GF\left(0, \Sigma\right),$$

where Plate_i is the number of lateral plates for the stickleback population at sampling location i assuming a Gaussian distribution with mean μ_i and variance σ^2. The variable Length_i is a continuous covariate representing population mean standard length at sampling location i, and

Temperature$_i$ is a continuous covariate representing the mean 10-year antecedent air temperature at location i. The term u_i is a spatially correlated random effect at sampling location i for the Gaussian field (GF) with mean 0 and covariance matrix Σ.

3 | RESULTS

Average 10-year antecedent temperature anomalies over land across Europe have shown a rise over the last century, with an elevated rate of increase over the last three decades in particular (Figure 2b); the mean annual temperature over European land areas in the last decade was 1.4–1.6°C warmer than during the pre-industrial period. Almost identical patterns of temperature change were obtained with data from the NASA Goddard Institute for Space Studies (Lenssen et al., 2019), and National Oceanic and Atmospheric Administration (Karl et al., 2015) (Figure 2b). The spatial model was effective in removing residual spatial autocorrelation in the model; model comparison demonstrated that inclusion of a spatial random effect improved model goodness of fit (deviance information criterion) and predictive quality (log-conditional predictive ordinate) in comparison with the same models that did not accommodate spatial dependency (Table 1). Posterior mean values of the Gaussian field also showed clear spatial patterns (Figure 4a), as did variance in the posterior values (Figure 4b). The best-fitting model included fixed effects for standard length and T_{10} and a spatially correlated random effect (Table 1).

In the best-fitting model, both standard length and T_{10} were statistically important predictors of lateral plate number (Table 2; Figure 5a–c). As predicted, T_{10} showed a negative association with lateral plate number (Figure 6a) while standard length showed a positive association with lateral plate number (Figure 6b). Approximately 10% of variation in lateral plate number was explained in the spatial random field with the strongest effects in central Poland, which also showed elevated variance in the spatial field (Figure 4b). Spatial dependency in lateral plate number was important at a scale of 1 km (Table 2; Figure 5d).

4 | DISCUSSION

Based on the HadCRUT4 dataset (Morice et al., 2012), 10-year antecedent near-surface air temperature anomalies across Europe,

relative to a 'pre-industrial' period between 1850 and 1899, show a rise over the last century, with a notable increase over the last three decades (Figure 2b). Using a latent Gaussian model, we provide evidence that over multiple decades, and on a large spatial scale, variation in threespine stickleback lateral plate number is predicted by average antecedent air temperature at each collection site. This effect is associated with body size; elevated temperatures correlate negatively with body size in the threespine stickleback, and body size is negatively correlated with plate number (Figure S2; Figure 6b; Smith et al., 2020b).

The strongest effects in the spatial random field were observed in Central Poland. In this region, plate numbers were lowest (dark blue in Figure 4a), and with correspondingly low variance (red in Figure 4b), indicating the highest impact of elevated temperatures in this region. This finding contrasted with a region in north-west Poland (green in Figure 4a, yellow in Figure 4b), where plate number appeared to be buffered. In this region of north-west of Poland, the River Oder debouches into the Szczecin Lagoon and the Baltic Sea, permitting heavily plated *complete* ecomorph threespine sticklebacks to penetrate freshwater systems from the Baltic, reflected in a spatial signal of high plate number.

The findings of this study are significant in demonstrating that temporal change in average temperature is associated with a phenotypic trait with a known genetic basis. Many studies that show phenotypic responses to climate change represent modifications to highly plastic traits, such as fecundity, survival, timing of migration and reproductive phenology (Crozier & Hutchings, 2014). Growth is also a plastic trait in the threespine stickleback (e.g. Mccairns & Bernatchez, 2012; Wund et al., 2012), though plate number shows extremely limited plasticity (Barrett et al., 2008; Colosimo et al., 2005; Hansson et al., 2016; Marchinko, 2009). There is some evidence for epigenetic effects on plate number, with multiple differentially methylated genomic regions between individuals with contrasting plate numbers, several of which have a function in growth (Smith et al., 2015). Like other teleost fishes, sticklebacks express indeterminate growth. In Poland, in common with much of Europe, sticklebacks are essentially annual; approximately 95% of recruits die at the end of their first year, with the remainder surviving 2 years, and rarely 3 years (Bańbura, 1994; Wootton & Smith, 2000). Length–frequency plots for fish from the study support this life-history pattern and provide no evidence for a temporal change in age structure.

TABLE 1 Deviance information criterion and log-conditional predictive ordinates of fitted models to determine threespine stickleback lateral plate number. Length is stickleback standard length, T_{10} is the average 10-year antecedent air temperature. Models ranked by deviance information criterion and log-conditional predictive ordinate

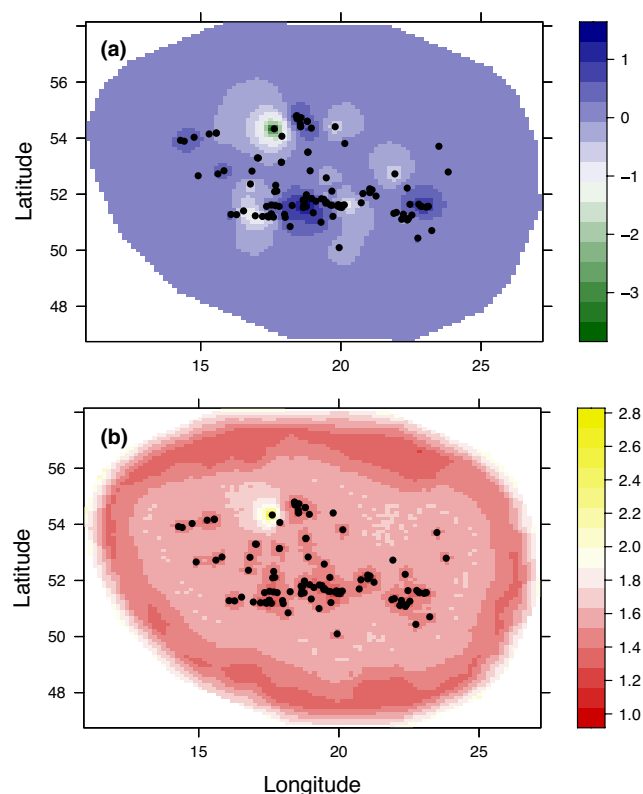| Rank	Model	Deviance information criterion	Log-conditional predictive ordinate
1	Spatial effect + Length + T_{10}	545	279
5	Spatial effect + Length	548	281
2	Length + T_{10}	552	279
6	Length	555	281
3	Spatial effect + T_{10}	557	286
7	Spatial effect only	559	287
4	T_{10}	569	287

FIGURE 4 (a) Posterior mean values of the random spatial field estimated for threespine stickleback plate number across Poland; (b) Variation (*SD*) of the random spatial field estimated for threespine stickleback plate number

TABLE 2 Fixed effects from the best-fitting model for threespine stickleback lateral plate number in Poland. Credible intervals are the 2.5% and 97.5% quantiles. Hyperparameters are: $\kappa_{spatial} = 4.60$, $\sigma_{spatial} = 1.51$; range = 0.99 km. Credible intervals that do not include zero indicate statistical importance

Term	Posterior mean	2.5% quantile	97.5% quantile
Intercept	29.80	28.83	30.65
Standard length	1.23	0.66	1.80
10-year antecedent temperature	−0.63	−1.25	−0.02

In a previous study with a different dataset (Smith et al., 2020b), we examined stickleback populations across the entire range of the species in Europe and showed that body size and average antecedent minimum winter temperature were the most important predictors of plate number. In that case, average antecedent minimum winter temperature showed higher variance than average antecedent temperature, though if average antecedent temperature was used in the analysis, the same qualitative outcome was obtained. In the present study, which was restricted to a smaller geographical region, if average antecedent minimum winter temperature was used in the model instead of average antecedent temperature, the statistically important effect of temperature disappeared, though not if the model did not include a term for spatial autocorrelation. This finding indicates that plate number was a function of minimum temperature only as a result of spatial variation in minimum temperatures across Poland. Because average antecedent temperature was a significant predictor of plate number, even after controlling for spatial autocorrelation in the data, the implication is that average (but not minimum) antecedent temperature has a direct effect on plate number, irrespective of any variance in plate number that is spatially correlated with average antecedent temperature.

The association between elevated temperature and lateral plate number demonstrated here represents a rare example of a phenotypic response to temperature change that is likely to be underpinned by genetic change. Importantly, the result does not simply represent variance in phenotype along a spatial climatic gradient, which can be a reflection of adaptation to contrasting environmental conditions. Instead, after controlling for spatial patterns in the data, we show a broad trend of declining plate number in response to a long-term increase in environmental temperature. A caveat to these inferences is that the data do not permit definitive conclusions to be drawn on whether temperature drives selection for body size or for lateral plates directly. Because we control for spatial autocorrelation in the data, we can tentatively conclude that these associations do not simply reflect other ecological responses to elevated temperatures with consequences for lateral plate number that also correlate with body size, such as predation. However, we believe the most parsimonious interpretation of the results are that (a) A decline in body size is associated with elevated average temperatures, which shows a temporal association (this study) and a spatial association (Smith et al., 2020b), and reflects a well-established ecological relationship between body size and temperature (Verberk et al., 2021). (b) Lateral plate number is strongly associated with body size in sticklebacks, which is associated with swimming efficiency (Bergstrom, 2002; Smith et al., 2020b).

An association between threespine stickleback lateral plate number and temperature has been recognized for several decades, though it has never been adequately explained (Hagen & Moodie, 1982; Heuts, 1947; Wootton, 2009). High numbers of lateral plates are particularly characteristic of fresh water populations exposed to low winter temperatures on the eastern and northern fringes of continents (Hagen & Moodie, 1982; Wootton, 1976). In contrast, low numbers of lateral plates are associated with mild winter temperatures in the south and west of the geographical range of the species (Smith et al., 2020b; Wootton, 2009). Despite this striking pattern, the association between plate number and temperature has not been a feature of discussions on other potential selective agents for the evolution of plate number in the threespine stickleback, at least until recently (Des Roches et al., 2019; Smith et al., 2020b).

Body size is a key attribute of an organism, with implications for fecundity, competition and predation (Hildrew et al., 2007; Schmidt-Nielsen, 1984). The temperature–size rule, whereby warmer conditions drive maturation at a smaller body size, has been recognized in over 80% of ectotherms that have been

FIGURE 5 Posterior (marginal) distributions for (a) model intercept; (b) standard length (mm); (c) average 10-year antecedent air temperature (°C); (d) Matérn correlation function
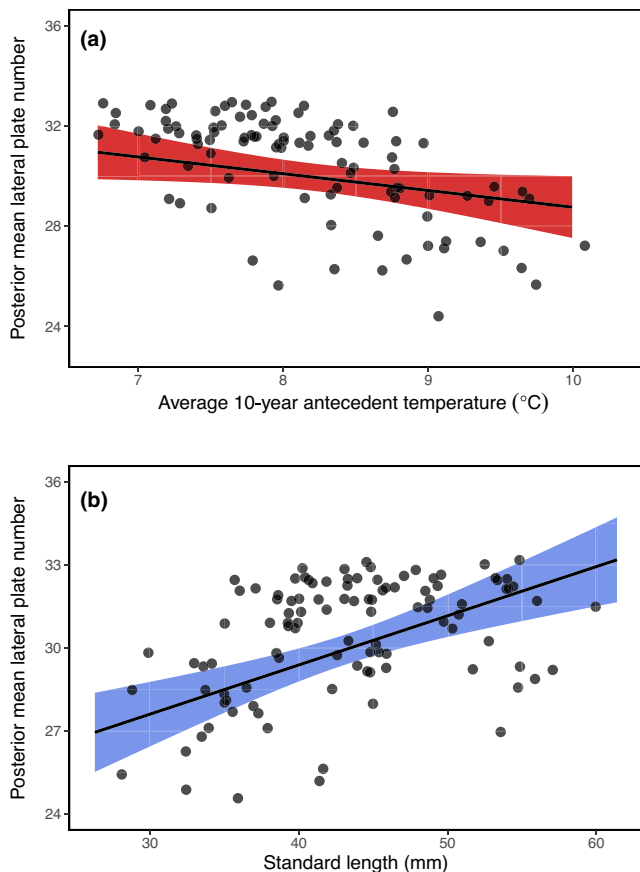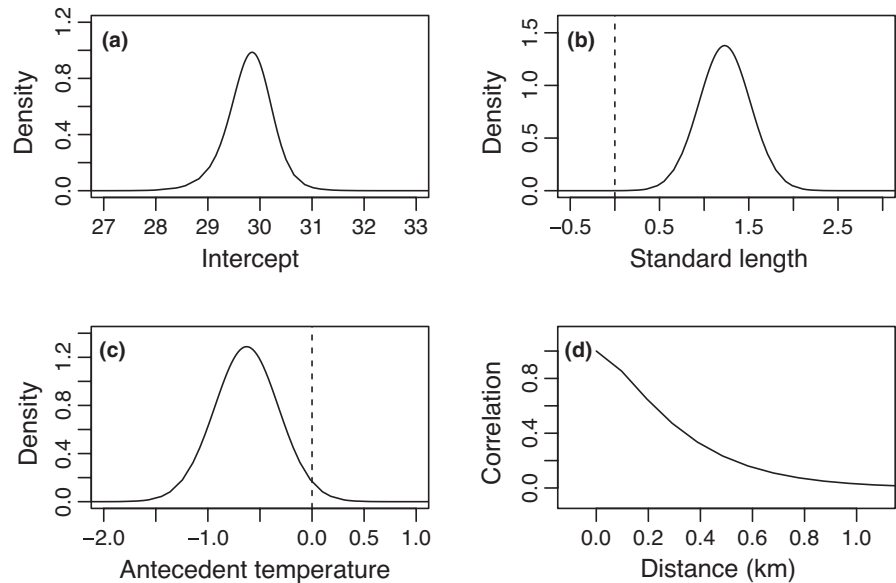

FIGURE 6 Posterior mean fitted estimates of lateral plate number for threespine sticklebacks as a function of: (a) average 10-year antecedent air temperature (°C); (b) mean population standard length (mm). Shaded areas are 95% credible intervals. Black points are observed data for stickleback populations

investigated (Verberk et al., 2021). So pervasive is this relationship that the effect is recognized as a universal response to environmental warming, along with range and phenological shifts

(Gardner et al., 2011). Bony fishes are no exception, and a wealth of empirical studies support the pattern in this group (reviewed by Verberk et al., 2021, though see Belk & Houston, 2002), including *G. aculeatus* (Des Roches et al., 2019; Morris et al., 2017; Smith et al., 2020b).

While an association between body size and plate number in threespine sticklebacks has been demonstrated in several studies, it has only recently been proposed as the potential mechanism for variation in plate number (Smith et al., 2020b). Rapid lateral plate evolution is typically accompanied by associated changes in body size. For example, a marine population of threespine sticklebacks that colonized Loberg Lake in Alaska in 1990 was shown by Bell et al., (2004) to decline from almost 100% completely plated to just 11% over a 12-year period, and showed a concomitant decline in body size. Conversely, a switch from 91% dominance by low-plated sticklebacks to dominance by completely plated fish in Lake Washington was associated with a 30% increase in mean fish length (Kitano et al., 2008).

Given the uncertainty of whether reduced plate number represents an adaptive response to elevated temperatures, or a correlated response to reduced body size, alternative mechanisms to explain observed variance in lateral plate number present themselves. If a reduction in plate number is mediated by a change in body size, an implication is that fewer lateral plates at elevated temperatures offers no adaptive advantage. Reduced body size as a response to higher temperatures reflects the temperature–size rule (Verberk et al., 2021). The causal explanation for this relationship is unclear, but applies across a range of endotherms and ectotherms, including fishes (Morris et al., 2017; Verberk et al., 2021). In the case of ectotherms, higher resting metabolic rates may incur higher energetic costs that compromise growth, or the association may arise from oxygen limitation, particularly for aquatic organisms (Verberk et al., 2021). Selection for large offspring body size at low temperatures may also play a role (Pettersen et al., 2019). Irrespective of the proximate explanations for the relationship, changes in body size in

response to temperature have important evolutionary outcomes for life-history evolution.

In the case of a correlated response between body size and lateral plate number, variation in lateral plate number as a function of body size potentially implies no Darwinian adaptive advantage and solely reflects a scaling relationship sensu Thompson (1917). Alternatively, natural selection may drive changes in body size in response to temperature, with plate number varying to optimize mechanical efficiency at a given body size (Bonner & Horn, 2000). In aquatic animals, scaling effects have consequences for hydrodynamic resistance to movement (Schmidt-Nielsen, 1984). Lateral plates increase drag in the threespine stickleback and correlate negatively with swimming velocity after correcting for body size (Bergstrom, 2002). An outcome is that selection on sticklebacks for armour loss will minimize drag (Bergstrom, 2002; Walker, 1997), and sticklebacks that experience selection for reduced body size at elevated temperatures are predicted to simultaneously experience selection for plate loss to avoid compromising hydrodynamic efficiency (Smith et al., 2020b). An outcome is a trade-off between the number of lateral plates and body size in sticklebacks, with the prediction, given the well-established negative relationship between body size and environmental temperature in ectotherms, for the potential for warming to drive lateral plate loss (Des Roches et al., 2019).

The threespine stickleback is common and widespread species across coastal regions of the northern hemisphere (Wootton, 1976). It is a vertebrate model in evolutionary, genomic, behavioural and ecological studies, and has been the subject of a broad range of research questions for over a century. Lateral plate phenotype offers a potential tool for monitoring environmental change in historical datasets and archived samples, and potentially also in the fossil record (Bell, 2009). This study demonstrates the potential utility of the threespine stickleback as a model species for measuring the evolutionary and ecological impacts of climate change across the northern hemisphere.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the design of the study and conducted data collection. C.S. analysed the data and led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.14074559.v1 (Smith, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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