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Disentangling the drivers of decadal body size decline in an insect population

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Abstract

While climate warming is widely predicted to reduce body size of ectotherms, evidence for this trend is mixed. Body size depends not only on temperature but also on other factors, such as food quality and intraspecific competition. Because temperature trends or other long-term environmental factors may affect population size and food sources, attributing trends in average body size to temperature requires the separation of potentially confounding effects. We evaluated trends in the body size of the midge *Tanytarsus gracilentus* and potential drivers (water temperature, population size, and food quality) between 1977 and 2015 at Lake Mývatn, Iceland. Although temperatures increased at Mývatn over this period, there was only a slight (non-significant) decrease in midge adult body size, contrary to theoretical expectations. Using a state-space model including multiple predictors, body size was negatively associated with both water temperature and midge population abundance, and it was positively associated with ^{13}C enrichment of midges (an indicator of favorable food conditions). The magnitude of these effects were similar, such that simultaneous changes in temperature, abundance, and carbon stable isotopic signature could counteract each other in the long-term body size trend. Our results illustrate how multiple factors, all of which could be influenced by global change, interact to affect average ectotherm body size.

KEYWORDS
body size, climate change, ectotherms, *Tanytarsus gracilentus*, temperature-size rule

1 | INTRODUCTION

The size of an organism plays an important role in determining its metabolic rates, fecundity, and interactions with other organisms (Bolnick et al., 2011; Brose et al., 2006; Brown et al., 2004; Kaiser-Bunbury et al., 2014; Kingsolver & Huey, 2008; Woodward et al., 2005). Temperature affects the body size of insects and other ectotherms, with warmer temperatures resulting in smaller individuals at maturity (i.e., the temperature-size rule; Atkinson, 1994; Daufresne et al., 2009;

Kingsolver & Huey, 2008; Sheridan & Bickford, 2011). Accordingly, there has been increasing interest in the effects of recent climate change on ectotherm body sizes (Daufresne et al., 2009; Scaven & Rafferty, 2013; Sheridan & Bickford, 2011). Several lines of evidence support the predictions of the temperature-size rule, including controlled warming experiments (Büyükyilmaz & Tseng, 2022; Culler et al., 2015; Frouz et al., 2002; McCauley et al., 2015; Wonglersak et al., 2021), biogeographic comparisons of body size across latitudes (Baranov et al., 2022; Hassall, 2013; but see Shelomi, 2012), and

comparisons between cohorts of multivoltine insects emerging at different times of the year (Horne et al., 2017). A meta-analysis of warming experiments shows that one degree of warming can result in up to a 2.6% decrease in arthropod body size, although most changes are between 0.2% and 1.5% (Klok & Harrison, 2013). While the physiological mechanisms underlying this pattern remain an active area of research, both differential effects of temperature on growth and development rates (Angilletta et al., 2004; Ghosh et al., 2013) and temperature-imposed physiological constraints on growth (Brown et al., 2004; Verberk et al., 2021; Von Bertalanffy, 1960) may be involved. Despite the plethora of support for the temperature-size rule, observational evidence for decreasing insect body sizes from time series concurrent with warming temperatures is mixed. Previous work identifies increasing (Davies, 2019), decreasing (Babin-Fenske et al., 2008; Bowden et al., 2015; Polidori et al., 2020; Wu et al., 2019), species-specific changes (Gérard et al., 2021; Tseng et al., 2018), and no change (Baar et al., 2018) in insect body sizes over time in warming regions.

The mismatch between theoretical expectations for decreasing insect body sizes and empirical evidence for long-term body size trends may be attributable to other factors that can also show temporal trends due to environmental change (Gardner et al., 2011; Musolin & Saulich, 2012). For example, nutrition is also a key factor determining body size (Chown & Gaston, 2010), with increasing food quantity and quality generally resulting in larger adults, unless associated with changes to other life history traits, such as reductions in development time (Blanckenhorn, 1999; Frost & Elser, 2002; Nijhout et al., 2010; Nylin & Gotthard, 1998; Teder et al., 2014). In addition to the direct effects of warming on body sizes, warming can indirectly influence the quantity and quality of food through differential increases to ectotherm consumption rates and the growth rates of their resource species (Gilbert et al., 2014; West & Post, 2016). Environmental change is also associated with systematic alterations to the quantity and quality of available food through shifts in the composition, distribution, and timing of interacting species (Bartley et al., 2019; Cleland et al., 2007; Kerr et al., 2020; Parmesan, 2006; Twining et al., 2022; Yang & Rudolf, 2010). Despite the importance of nutrition for insect body sizes and evidence that resources often change alongside warming, most previous studies evaluating trends in insect body sizes lack the necessary data on food quantity and quality to disentangle the causes of long-term change in insect size.

The interplay between climate warming and nutrition in shaping long-term patterns of insect body sizes may be especially pronounced for species like the nonbiting midge *Tanytarsus gracilentus* Holmgren (Diptera: Chironomidae). At Lake Mývatn in Iceland, *T. gracilentus* populations undergo large amplitude fluctuations (over five orders of magnitude) in abundance (Gardarsson et al., 2004). The leading hypothesis for these fluctuations is consumer–resource interactions between midges and the epipelic algae they consume as larvae (Einarsson et al., 2002, 2016; Ives et al., 2008; McCormick, Phillips, Botsch, Einarsson, et al., 2022). In fact, using wing length as a correlate of food availability, Einarsson et al. (2002) found statistical evidence for consumer-resource cycles in midge population size between 1979 and 1999: periods when midges were abundant were followed

by declines in average wing length, and generations with larger than average midges preceded increases in abundance. Evidence of consumer–resource dynamics is also supported by the carbon stable isotope signatures of the midge carcasses (McCormick, Phillips, Botsch, Einarsson, et al., 2022), with midge population abundance increasing when $\delta^{13}C$ was high, and high midge populations preceding drops in $\delta^{13}C$. These consumer–resource dynamics suggest that resources likely play a central role in determining midge body sizes in addition to abiotic conditions. Aquatic ectotherms like midges are also expected to have stronger responses to climate warming than terrestrial insects because dissolved oxygen availability decreases as water warms (Daufresne et al., 2009; Forster et al., 2012).

Given the potential complexities underpinning insect body sizes, understanding what contributes to trends in midge body sizes likely requires multiple data sources. Here, we use monitoring data on midge populations (including carbon stable isotope signatures) and associated abiotic variables collected at Mývatn to analyze the effects of multiple factors driving decadal-scale changes in *T. gracilentus* body size. We first show that the Mývatn region has experienced increasing air temperatures, like many other high latitude regions (Overland et al., 2014). We then analyze the individual time series for midge wing length, midge abundance, water temperature (as these are the relevant temperatures for midge development), and midge $\delta^{13}C$ to determine whether there is statistical evidence for linear trends in each variable over time. Finally, we combine all data in a time-series analysis to determine how midge abundance, water temperature, and midge $\delta^{13}C$ in combination explain the long-term changes in midge adult body size.

2 | METHODS

2.1 | Study system

Mývatn is a large (37 km²) shallow (mean depth ~2.5 m) lake situated in northeastern Iceland (65°40′ N, 17°00′ W, 277 m a.s.l.). The lake is fed by springs along its western edge and has short residence time (~27 days; Ólafsson, 1979a). The springs vary dramatically in temperature, but outside of their immediate vicinity, temperatures are fairly similar across the lake's surface and there is little vertical variation in water temperatures, because the lake does not stratify in the summer (Ólafsson, 1979a). The springs are nutrient rich (Ólafsson, 1979b). As a result, the lake supports high primary production and is considered naturally eutrophic (Einarsson et al., 2004). Because Mývatn is shallow, most of the primary production occurs in the benthos by epipelic algae (Einarsson et al., 2004). These epipelic algae support large midge populations (Einarsson et al., 2004; Ingvason et al., 2004; Lindegaard & Jónasson, 1979) for which the lake is named; Mývatn translates to "midge lake" in Icelandic. Mývatn historically remained ice-covered for an average of 190 days a year (Rist, 1979), although this may have changed as air temperatures have warmed. The lake is in a rural area where direct human impacts are minor, and little

land-use change has occurred in the last 50 years. However, diatomite was mined by dredging part of the benthos in the northern basin of the lake from 1967 to 2004 (Gardarsson, 2006), which substantially altered the bathymetry of the north basin (Einarsson et al., 2004). Because of the habitat requirements of *T. gracilentus*, it was not directly impacted by the mining operation.

2.2 | Midge data

Between 1977 and 2015, the adult midge populations at Mývatn were monitored at two locations along the lakeshore using passive window traps (Einarsson et al., 2004; Jónsson et al., 1986). One location (KS) is located in the south-east corner of the south basin, and the second (SN) is located on the peninsula separating the lake's south and north basins. In 1999, five additional traps were added around the lakeshore. Adult midges were collected every 7–12 days during the ice-free period when they emerge from Mývatn (May–September). To estimate abundance, midges were identified to species and counted, using subsampling during periods of high abundance.

While Mývatn is home to over 30 midge species (Lindegaard, 1979), our study focuses on a single species, *T. gracilentus*, which is by far the numerically dominant species in the lake (Lindegaard & Jónasson, 1979; Anthony R. Ives, unpublished data). *T. gracilentus* is generally bivoltine, with emergences occurring in early June and early August. Thus, our study period comprises 78 midge generations. Adult midges were grouped into overwintering and summer cohorts using July 15–20 as the separator (Gardarsson et al., 2004). In recent monitoring of the larval populations, we documented a partial summer emergence of *T. gracilentus* in 2015 in which a portion of the summer cohort delayed emergence until the following spring. Although we do not know whether similar partial emergences occurred earlier in the monitoring period, they appear to be rare events, so we treat the two cohorts as distinct. *T. gracilentus* larvae consume epipelic algae and associated autochthonous detritus (Ingvason et al., 2004), while adults appear not to feed. Larvae overwinter in a state of diapause (Ingvason et al., 2006). We use the raw count of *T. gracilentus* individuals averaged between the two main traps (KS and SN) as our metric of abundance (Einarsson et al., 2002). Because higher population sizes are associated with reduced per capita resource availability (Murdoch, 1994; Than et al., 2020), generations with high midge densities may be smaller on average.

We treat the $\delta^{13}C$ of adult *T. gracilentus* as a metric associated with food quality. The $\delta^{13}C$ signature of midges reflects the isotopic signature of the resources they consumed as larvae (Peterson & Fry, 1987). Reductions in $\delta^{13}C$ could reflect either a shift in the midge resource base from algae to a heavier reliance on detritus and associated bacteria (Fiskal et al., 2021) or a decrease in the productivity of the epipelic algal community on which they are feeding (Devlin et al., 2013; Finlay, 2001; McCormick, Phillips, Botsch, Einarsson, et al., 2022). In either case, high $\delta^{13}C$ is associated with food conditions that are likely to be favorable for *T. gracilentus* (high rates of primary production or higher reliance on algae). Higher rates of primary productivity are associated with higher midge survival and growth (Botsch, 2023; Phillips et al., 2021a, 2021b; Wetzel et al., 2021) and higher rates of primary production are associated with higher $\delta^{13}C$ for benthic algae at Mývatn (appendix S3, McCormick, Phillips, Botsch, Einarsson, et al., 2022) and elsewhere (Devlin et al., 2013). Similarly, *T. gracilentus* appears to select for higher $\delta^{13}C$ resources, as they are enriched relative to the surface of the surrounding sediment by a higher degree than would be expected by fractionation alone (McCormick, Phillips, Botsch, Ólafsson, et al., 2022). For this reason, we treat $\delta^{13}C$ as a metric associated with food quality for *T. gracilentus*, despite uncertainty in the exact mechanism causing variation in $\delta^{13}C$ signatures.

We measured the $\delta^{13}C$ from archived midges collected in the SN window trap (more details in McCormick, Phillips, Botsch, Einarsson, et al., 2022). Briefly, a target of 60 individuals was pooled from each generation of archived midges, although not all generations could be sampled due to low abundances. Individuals from each generation were combined, rinsed with deionized water, dried, homogenized, and analyzed at the University of California Davis Stable Isotope Laboratory (Davis, CA, USA). We report isotope signatures relative to the Vienna PeeDee Belemite standard, where $\delta = \left[\left(R_{sample} - R_{standard} \right) / R_{standard} \right] \times 1000$ and $R = {}^{13}C/{}^{12}C$.

We used wing length as a proxy for body size. This metric is commonly used for midges (Baranov et al., 2022; Einarsson et al., 2002; Wonglersak et al., 2021) and is highly correlated with body size and fecundity (McLachlan, 1985; Xue & Ali, 1994). We collected wings of up to 20 male *T. gracilentus* for each generation from archived samples between 1977 and 2015, primarily from the SN trap. However, some years did not have sufficient abundance of *T. gracilentus* in the archived samples at SN. Therefore, we used individuals from KS and HG (one of the traps added in 1999, located on the western side of the main basin) during periods of low abundance. For several generations, adequate numbers of individuals could not be collected from any combination of window traps, and thus data are missing. A single observer, ANZ, measured midge wings from the tip to the arculus using an ocular micrometer. Einarsson et al. (2002) also measured the wing lengths of individual adult midges collected from SN and KS between 1977 and 1999 using the same method; their estimates for the mean wing lengths are highly correlated with our data for the period over which there is overlap ($R^2 = .73$; Figure S1), although for consistency we analyze only our data.

2.3 | Water temperature data

Since 1972, daily water temperature has been measured with a thermocouple in the lake's outlet (Olafsson, 1999). Data are missing during some periods due to instrument failure. We filled in missing water temperature data using a linear regression that we fit to air temperature data collected at the Mývatn weather station (Icelandic Meteorological Office, 2022) and daily water temperature from the thermocouple (Figure S2; $R^2 = .672$). We restricted this regression to

periods where air temperature was greater than 0°C, because air and water temperatures are decoupled while the lake is ice-covered (Crisp & Howson, 1982). Furthermore, we assumed that the relevant water temperature for midges was only during this ice-free period because that is when larval midges are growing (not in diapause). We estimated dates of ice-off and ice-on to be the first and last day, respectively, at which the median water temperature over a 3-week rolling window exceeded 4°C, which is has been previously used to mark the beginning and end of winter phases in lake studies (Yang et al., 2020).

To pair water temperature to midge generations, we used the average water temperature during the ice-free periods corresponding to each generation. Although emergence timing is variable, no long-term observations of midge emergence exist at a fine enough temporal resolution to estimate changes in midge phenology across the entire dataset, and the lag in the timing between emergence and sampling by window traps is unknown. Therefore, we assumed that the relevant window for water temperature corresponding to the summer cohort was between 1 June and 1 August (Lindegaard & Jónasson, 1979). The remainder of the ice-free period (e.g., 2 August to ice-on and ice-off to 31 May) was assumed to be the development period for the overwintering cohort. We averaged the water temperature during these two periods to estimate the water temperature for each midge generation over the study period (Figure S3). Finally, for each generation, we subtracted these generation-scale water temperatures from the long-term cohort average temperature to aid in comparing the effects of temperature between generations.

2.4 | Air temperature data

Because the Mývatn weather station was not in operation until 1996, we used air temperature for the Grimsstaðir weather station (station 495, WMO number 4073) to evaluate whether air temperatures have warmed during the study period. The Grimsstaðir weather station sits approximately 30 km away from Mývatn (65°39′ N, 16°07′ W, 385 m a.s.l.). However, the average annual and monthly temperature at Grimsstaðir closely match those at Mývatn for the time period where we have both ($R^2 = .97$ and $R^2 = .996$, respectively). We accessed long-term average annual and monthly air temperature data collected by the Icelandic Meteorological Office (https://www.vedur.is/Medaltalstoflur-txt/Stod_495_Grimsstadir.ArsMedal.txt and https://www.vedur.is/Medaltalstoflur-txt/Stod_495_Grimsstadir.ManMedal.txt, respectively; Figure 1). We averaged the monthly air temperature at Grimsstaðir between May and September, which represent the months where Mývatn is typically ice-free for a given year, based on the method described above. This produced a dataset containing the average annual air temperature during a roughly equivalent period to the water temperature data (which we refer to as "ice-free air temperature") in order to assess whether the relevant air temperatures had increased.
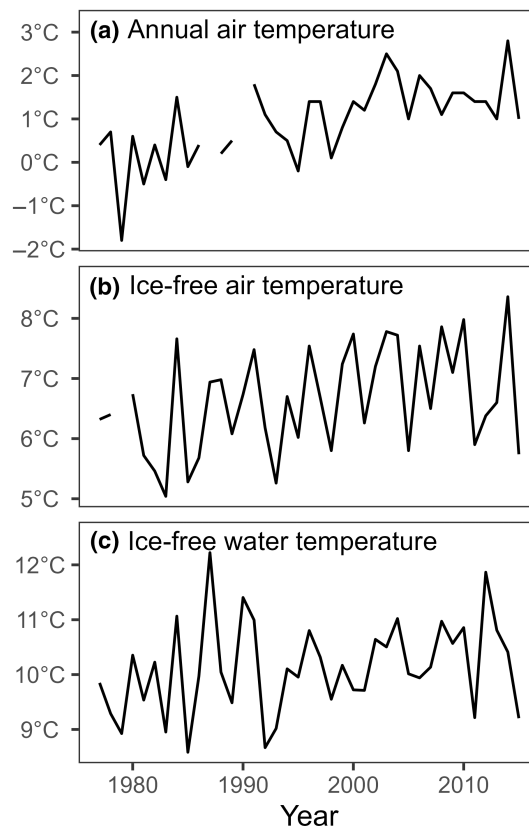

FIGURE 1 Average annual air temperature at Grimsstaðir (a), air temperature at Grimsstaðir during the period when the lake is ice-free (b), and ice-free water temperature in the outlet of Lake Mývatn (c).

2.5 | Statistical analysis

We used a state-space modeling (SSM) framework (Auger-Méthé et al., 2021; Harvey, 1989) to evaluate the drivers of midge wing length and to test for statistical evidence of trends in midge size, midge abundance, midge $\delta^{13}C$, air temperature, and water temperature over time. We chose SSMs because they account for temporal autocorrelation and can deal with missing observations in our time series. SSMs consist of two equations, the first describing the biological process of the system and the second describing the measurement of observations. The process equations have the form

$$z_t = \beta_0 + \mathbf{X}_t\boldsymbol{\beta} + \sum_{j=1}^{p} \phi_j\left(z_{t-j} - \beta_0\right) + \varepsilon_t; \varepsilon_t \sim N\left(0, \sigma_{\text{proc}}^2\right) \quad (1)$$

where z_t is the response variable (e.g., wing length) at time t, β_0 is the intercept, $\mathbf{X}_t$ is a row vector containing observed predictor variables at time t, and $\boldsymbol{\beta}$ is a column vector of estimated regression coefficients describing the effects of predictor variables $\mathbf{X}_t$ on z_t. The models include ϕ_j, which give the temporal autocorrelation of order j ($j = 1, ..., p$). The error term ε_t is normally distributed around 0 with a variance of σ_{proc}^2. The measurement equations have the form

$$y_t = z_t + \eta_t; \eta_t \sim N\left(0, \sigma_{obs,t}^2\right) \qquad (2)$$

where y_t is the observed value of the response variable at time t. This is measured imperfectly, with measurement error η_t given by a time-independent normal random variable with mean 0 and variance $\sigma_{obs,t}^2$ which can vary among time points t.

To evaluate the presence of trends in the data, we fit separate SSMs with linear time trends for the following response variables: air temperature (both the full year and ice-free), water temperature, midge size, midge $\delta^{13}C$, and midge abundance. Air temperature, ice-free air temperature, and ice-free water temperature described annual averages and were therefore iterated over an annual timestep, resulting in 39 time points. For both air and water temperature, we present results for the SSM with lag-1 autocorrelation ($p=1$) because allowing higher p did not increase the fit of the models (results not presented). The data for midge size, $\delta^{13}C$, and abundance have 78 time points for the 78 midge generations, and the SSMs were iterated accordingly. In comparison to the overwintering cohort, the summer cohort systematically differed in average body size, abundance, and $\delta^{13}C$ (Einarsson et al., 2002; McCormick, Phillips, Botsch, Ólafsson, et al., 2022). Therefore, we included a categorical covariate for cohort (0 and 1 for the overwintering and summer cohorts, respectively). Time was included as the number of generations since 1979 in decades (a sequence from 0 to 3.9 by increments of 0.05). The midge data (abundance, $\delta^{13}C$, and wing length) showed second-order autocorrelation (Einarsson et al., 2002; McCormick, Phillips, Botsch, Einarsson, et al., 2022), so we set $p=2$. Midge abundance was $\log_{10}$ transformed to match the exponential nature of population growth, but air and water temperature, wing length, and $\delta^{13}C$ were not transformed. Because we have replicate measurements of wing length for each generation, we computed $\sigma_{obs,t}^2$ (Equation 2) for each time point from the replicates. For ice-free air temperature, water temperature, abundance, and $\delta^{13}C$ we assumed that $\sigma_{obs,t}^2$ did not vary through time (the variance was homoscedastic) and estimated σ_{obs}^2 as a parameter in the SSM. For average annual air temperature, σ_{obs}^2 and σ_{proc}^2 could not be statistically separated, so we set $\sigma_{obs}^2 = 0$.

To investigate the multiple factors that could explain changes in midge wing lengths, we fit two SSMs. In the first, we regressed wing length against water temperature and a time trend, which mimics a scenario where we lack additional data, while including cohort as a categorical variable. In the second, we regressed wing length on water temperature, midge abundance ($\log_{10}$ transformed), midge $\delta^{13}C$, a time trend, and cohort as a categorical variable. We Z-transformed (subtracted means and divided by the standard deviation) abundance, $\delta^{13}C$, and water temperature to compare the magnitude of the effect sizes. We included a time trend to account for other unmeasured variables that might affect changes in wing length through time.

For hypothesis testing (obtaining p-values for the model parameters), we performed bootstrapped likelihood ratio tests (LRTs) (Ives, 2018; McLachlan, 1987). This was necessary, because the standard LRT relies on the deviance between log likelihood of full and reduced models being chi-square distributed, which is only guaranteed asymptotically (Wilks, 1938). Briefly, we fit SSMs to the data dropping the term of interest. We then used the estimated parameters from this reduced model to simulate 2000 time series of y_t (Equation 2) including all gaps and observation error present in the original data. For each simulated dataset, we fit the full and reduced SSMs, and from these constructed a bootstrap distribution of the log LRT which we used to assess the significance of the observed log LRT. In all cases, the results of the bootstrapped LRTs were more conservative (gave higher p-values) than standard LRTs (Tables S1 and S2).

We conducted all analyses in R v. 4.1.2 (R Core Team, 2022). We fit the SSMs using maximum likelihood estimation and the Kalman filter with code modified from Ives and Dakos (2012).

3 | RESULTS

3.1 | Time trends

The trends in our data were consistent with expectations of climate warming (Figures 1 and 2; fitted parameters in Table S1), although several trends were not statistically significant (Table 1). Annual air temperature increased by 0.67°C decade^{-1} ($p<.005$). The air temperature during the ice-free period increased by 0.40 decade^{-1} ($p=.013$). Our estimates of the length of the ice-free period on Lake Mývatn was 136 days, with no evidence for a trend in ice-cover duration (Figure S4). On average, annual ice-free water temperature increased 0.24°C per decade ($p=.09$). The log abundance of midges, $\delta^{13}C$, and wing lengths decreased [by 0.45 $\log_{10}$(individuals), 0.11 $\delta^{13}C$, and 0.038 mm decade^{-1}, respectively], but only the decline in midge abundance was significant ($p=.021$, Table 1).

3.2 | Drivers of midge size

We assessed the drivers of midge wing length by comparing a model containing abundance and $\delta^{13}C$ to a model without these drivers (Table 2). In the model without abundance and $\delta^{13}C$, the effect of water temperature on wing length was not significant ($p=.106$) but including abundance and $\delta^{13}C$ showed a significant effect of temperature ($p=.01$). Therefore, including abundance and $\delta^{13}C$ absorbed some of the unexplained variation in the model without drivers, revealing the effect of temperature.

The complete model shows that the effect magnitudes of the three drivers on wing length were similar (−0.056 for water temperature; −0.066 for abundance; 0.052 for $\delta^{13}C$), and all were statistically significant (Table 2). The strongest determinant of wing length was cohort, with the summer cohort being roughly 10% smaller than the winter cohort. When including water temperature, abundance, and $\delta^{13}C$, there was an additional declining trend in wing length that suggests additional unmeasured drivers may have also contributed decreased wing lengths, although this time
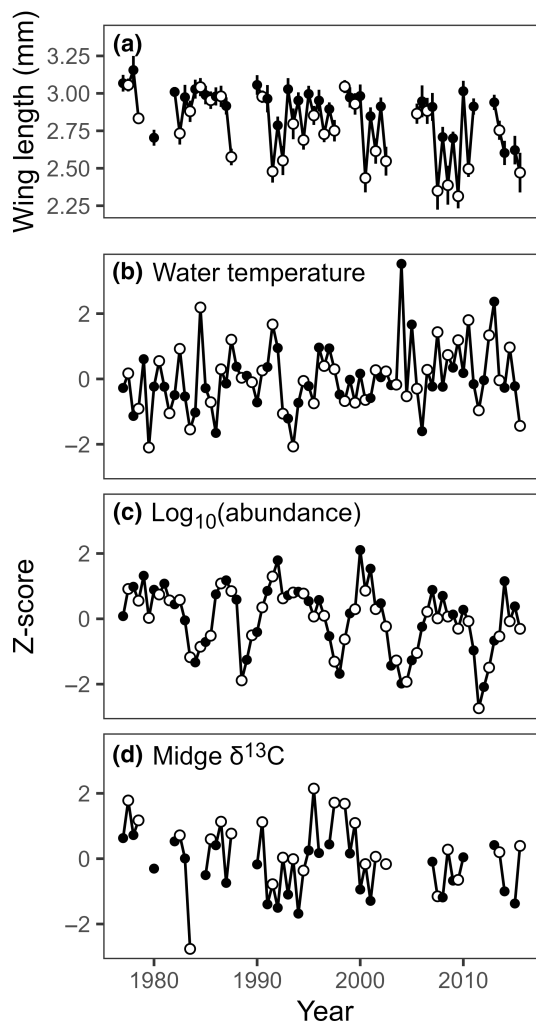
FIGURE 2 Time series of the data used in the analyses. Points are colored by generation. (a) Wing length was not transformed, and error bars show ±2 SE. (b) Cohort-scale water temperature, (c) log$_{10}$(midge abundance), and (d) midge δ^{13}C are plotted as Z-scores. Lines connect estimates over time, with gaps for missing data.

trend was only marginally significant with the bootstrapped LRT ($p = .078$).

4 | DISCUSSION

Given the increase in average annual air temperatures that we observed at Mývatn 1977–2015, we expected that *T. gracilentus* body size would decrease over the course of the time series. We found that midge body sizes decreased by about 1.3% on average per decade. Although we did not find strong statistical support for this trend, it is of a similar magnitude to those observed in other studies measuring insect body sizes through time (Babin-Fenske et al., 2008; Tseng et al., 2018). The trend would likely have been stronger if not for a slower rate of warming by the lake, which was not statistically significant in our analyses, relative to air temperatures in the Mývatn

TABLE 1 Estimates of linear trends over time for air temperature, ice-free water temperature, population abundance, midge δ^{13}C, and wing length.

	Time trend	Bootstrapped p-value
Annual air temperature[a]	0.67	<.0005[b]
Ice-free air temperature	0.40	.013
Water temperature	0.24	.090
Log$_{10}$ abundance	−0.45	.021
δ^{13}C	−0.11	.715
Wing length[c]	−0.038	.075

Note: Trends are reported in original units (°C for temperature, log$_{10}$ abundance, δ^{13}C, and mm for wing length). The *p*-values are given for the bootstrap LRTs. Full model results and *p*-values from standard LRTs are in Table S1.

Abbreviation: LRT, likelihood ratio test.

[a]Average annual air temperature was fit with $\sigma^2_{\text{obs},t} = 0$ (Equation 2).

[b]None of the 2000 bootstrap LRTs exceeded those from the original model fits.

[c]For wing lengths, we estimated $\sigma^2_{\text{obs},t}$ for each timepoint using measured variation in wing length.

region, which did show a statistically significant warming trend. Nonetheless, a time-series model that included water temperature and the abundance and isotopic signature of midges revealed a negative effect of water temperature on the intergenerational fluctuations in wing lengths that was not statistically significant in the absence of data on abundance and δ^{13}C. Therefore, the effects of water temperature were only apparent after accounting for patterns caused by other drivers of body size. Furthermore, the midge population declined significantly over the study period. Given that the effect sizes of population size and temperature were similar, this increase in per capita resource availability likely further weakened the negative trend associated with warming temperatures. Overall, our results show that the effects of temperature on *T. gracilentus* body size can only be understood by also accounting for the additional effects of abundance and food quality.

Environmental change is altering the life history of ectotherms in many ways simultaneously (Parmesan, 2006). These environmental changes can interact with each other, thereby obscuring expected trends in ectotherm traits from simple time-series analyses (Davies, 2019; Musolin & Saulich, 2012; Todgham & Stillman, 2013). Our result that the well-described effect of temperature on insect body size (Atkinson, 1994) can be obscured by coincident shifts in abundance and food quality is likely to be widespread for other species, because changes in abundance and food quality are common responses to environmental change (Twining et al., 2022; Wagner et al., 2021). In our study, the causal mechanisms driving intergenerational variation in midge abundance and stable isotope signature are unknown and likely integrate multiple factors, such as temperature, fluctuations in predator populations (Gudbergsson, 2004; Phillips et al., 2022, 2023), cyanobacterial blooms (McCormick et al., 2021), and changes in nutrient dynamics (K. Riley Book, unpublished data;

TABLE 2 Effects of changes in cohort-to-cohort mean wing length.

Term	Meaning	With drivers		Without drivers	
		Estimate	Bootstrapped *p*-value	Estimate	Bootstrapped *p*-value
β_0	Intercept	3.14	-	3.11	-
Φ_1	AR(1) term	−0.036	-	0.23	-
Φ_2	AR(2) term	0.300	-	0.08	-
σ_{proc}	Process error	0.108	-	0.14	-
β_{Cohort}	Cohort	−0.24	.004	−0.26	.0005
$\beta_{WaterTemp}$	Water temp.	−0.056	.010	−0.043	.106
$\beta_{Abundance}$	Abundance	−0.066	.007	-	-
$\beta_{\delta^{13}C}$	$\delta^{13}C$	0.052	.013	-	-
β_{Time}	Trend	−0.032	.078	−0.038	.152

Note: Predictors (temperature, abundance, and $\delta^{13}C$) are Z-transformed so that estimates are effects sizes. The time trend is linear time in decades. *p*-Values bootstrap LRTs are given, with *p*-values from standard LRTs given in Table S2. The models with and without drivers are identical (Equations 1 and 2) except the model without drivers excludes abundance and $\delta^{13}C$. A comparison between wing length and predictors for each timepoint can be seen in Figure S5.

Abbreviation: LRT, likelihood ratio test.

Wetzel et al., 2021). Our study included only male midges because species-level identifications based on morphology are difficult or impossible for many species of chironomids (Baranov et al., 2022; Ekrem et al., 2010). While different sexes of the same species may differ in the rate at which warming reduces body sizes (Frouz et al., 2002; McCauley et al., 2015), most studies report no difference (Atkinson, 1994; Wonglersak et al., 2021; Xi et al., 2016). Furthermore, our study and most other studies on insect body sizes do not consider possible differences in the sex ratio of individuals surviving to adulthood or fecundity, both of which can respond to temperature alongside body size and may feed back into population dynamics (Edmands, 2021; Kingsolver et al., 2011). Knowledge of the specific mechanisms underlying intraspecific variation in body size and their interactions are often lacking, which complicates understanding the true impact of climate change on body size.

Despite large-scale climatic changes, the local conditions experienced by organisms may not reflect these changes (Bartley et al., 2019; Pincebourde & Woods, 2020; Youngsteadt et al., 2022). Unlike Mývatn, lakes generally show warming trends of a similar magnitude to air temperatures, potentially generating large effects on aquatic ecosystems and ectotherms (Winder & Schindler, 2004; Woolway et al., 2020; Zohary et al., 2021). However, geophysical conditions may cause lakes to warm either faster or slower than local air temperatures (O'Reilly et al., 2015). The springs that feed Lake Mývatn, which are largely constant in temperature over time (Ólafsson, 1979a), may buffer the effects of warming air temperatures (Lusardi et al., 2021), despite the positive correlation between intra-annual variation in air and water air temperatures at Lake Mývatn (Olafsson, 1999). The weaker warming trend in water temperature than air temperature at Mývatn is accompanied by uneven climate warming across seasons, with faster warming occurring during winter when the lake is covered in ice and the midges are in diapause. Relatively faster winter warming is also observed in other

regions (Liu & Chen, 2000; Schwartz et al., 2006; Vicente-Serrano et al., 2018). Consequently, other lakes may show evidence of warming water temperatures only for certain parts of the year (Niedrist et al., 2018). Despite a weaker trend during the ice-free period, we still observed a statistical signal of warming air temperatures during the ice-free period that was not reflected in the lake temperatures, suggesting that these seasonal warming patterns are not the only factor in Mývatn's slower warming trend.

Predicting the effects of environmental change on the life history, physiology, and population size of organisms is an important challenge (Bellard et al., 2012). However, the many factors that can contribute to the physiology of a species results in complex responses to environmental change. Our analysis of midge body sizes at Mývatn suggests that the isotopic signature of their resources, conspecific population density, and temperature all have effects of a similar magnitude on midge body sizes. We further found strong statistical evidence that abundances have decreased over time. Therefore, body size reductions from warming temperatures may be offset by decreases in population abundances, increases in food quality, or both. Disentangling the effects of recent climate change on a population is complex and requires multiple types of data and knowledge of a species' natural history.

AUTHOR CONTRIBUTIONS

Jamieson C. Botsch: Conceptualization; data curation; formal analysis; funding acquisition; methodology; visualization; writing – original draft; writing – review and editing. **Aayush N. Zaveri:** Data curation; investigation; writing – review and editing. **Lucas A. Nell:** Data curation; investigation; writing – review and editing. **Amanda R. McCormick:** Data curation; investigation; writing – review and editing. **K. Riley Book:** Data curation; investigation; writing – review and editing. **Joseph S. Phillips:** Data curation; investigation; writing – review and editing. **Árni Einarsson:** Data curation; funding acquisition; investigation; methodology; writing – review and editing.

Anthony R. Ives: Conceptualization; formal analysis; funding acquisition; supervision; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All code and data associated with this manuscript are available on Dryad at http://doi.org/10.5061/dryad.79cnp5j2m.

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SUPPORTING INFORMATION

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