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Cite this article: Twardochleb LA, Zarnetske PL, Klausmeier CA. 2023 Life-history responses to temperature and seasonality mediate ectotherm consumer–resource dynamics under climate warming. *Proc. R. Soc. B* **290**: 20222377.
https://doi.org/10.1098/rspb.2022.2377

Received: 25 November 2022
Accepted: 27 March 2023

Subject Category:
Ecology

Subject Areas:
ecology, theoretical biology

Keywords:
climate change, life cycle, predator–prey, population dynamics, temperature, seasonality

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6534024.

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Life-history responses to temperature and seasonality mediate ectotherm consumer–resource dynamics under climate warming

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Climate warming is altering life cycles of ectotherms by advancing phenology and decreasing generation times. Theoretical models provide powerful tools to investigate these effects of climate warming on consumer–resource population dynamics. Yet, existing theory primarily considers organisms with simplified life histories in constant temperature environments, making it difficult to predict how warming will affect organisms with complex life cycles in seasonal environments. We develop a size-structured consumer–resource model with seasonal temperature dependence, parameterized for a freshwater insect consuming zooplankton. We simulate how climate warming in a seasonal environment could alter a key life-history trait of the consumer, number of generations per year, mediating responses of consumer–resource population sizes and consumer persistence. We find that, with warming, consumer population sizes increase through multiple mechanisms. First, warming decreases generation times by increasing rates of resource ingestion and growth and/or lengthening the growing season. Second, these life-history changes shorten the juvenile stage, increasing the number of emerging adults and population-level reproduction. Unstructured models with similar assumptions found that warming destabilized consumer–resource dynamics. By contrast, our size-structured model predicts stability and consumer persistence. Our study suggests that, in seasonal environments experiencing climate warming, life-history changes that lead to shorter generation times could delay population extinctions.

1. Introduction

An outstanding question of climate change research is how rising temperature will alter ecological communities through its effects on consumer–resource interactions. Over large temperature ranges, ectotherm biological rates, including feeding, show left-skewed unimodal responses to temperature [1,2]. Within the rising portion of the unimodal response, biological rates increase exponentially with temperature because of increasing metabolism [3–5]. Theoretical models provide powerful tools to investigate these potential effects of climate warming because they allow us to simulate population dynamics and changes in community structure. Yet, most theoretical models cannot simulate realistic community outcomes because they primarily consider interacting organisms with simplified life histories, living in constant temperature environments [6]. This contrasts with the reality that temperate species experience pronounced seasonal changes in temperature, and most ectotherms have structured populations with complex life cycles [7,8]. To improve our understanding of climate change effects on ecological communities, theory must therefore incorporate interactions among organisms with complex life cycles in seasonally fluctuating environments.

Theory about the effect of climate warming on communities has often focused on unstructured populations, where all individuals are assumed to be identical. Yet the predictions of unstructured models vary with different assumptions about consumer–resource thermal performance [6]. Many unstructured models predict that consumer biomass will *decrease* with warming as consumers experience lower energetic efficiency—the balance between growth from feeding and losses from metabolism [9]—and become more susceptible to starvation extinction. As a result of this decreased efficiency, these unstructured models predict that communities will become more stable with warming, decreasing their propensity for rapid, large-amplitude population cycles [10–13]. However, the same models with different assumptions about consumer–resource interactions predict that consumer biomass will *increase* with warming and destabilize communities [6,10]. These predictions depend, in part, on whether consumer feeding and metabolism change exponentially or unimodally with temperature, whether consumer metabolism or feeding increases more steeply with temperature, and whether resource carrying capacity varies with temperature [6].

Structured population models have revealed additional mechanisms by which temperature can affect population dynamics and communities [14]. Stage-structured models have shown that warming can alter population stage-structure [15] and decrease predator persistence, regardless of the assumed temperature scaling of feeding and metabolism or resource carrying capacity [14]. Stage-structured population models developed for insects yielded insights into how seasonal variation in temperature can alter life histories of organisms with complex life cycles, including how higher mean temperatures and longer growing seasons can lead to shorter generation times [16,17]. Simple, easily interpretable models that incorporate complex life histories are needed to accurately reflect community response to warming. Scranton & Amarasekare [18] developed a simple model of stage-structured insect populations with overlapping generations in seasonal environments. Yet many populations have synchronized reproduction where juveniles and adults live in distinct habitats, which is not accounted for by existing theory

Climate warming has altered life cycles of ectotherms by advancing phenology and decreasing generation times [19,20]. In general, studies show that higher environmental temperatures often result in faster rates of ectotherm metabolism, feeding and growth [3,4,21,22], which increase maturation rate into the adult stage [23–25]. Shorter generation times could influence population dynamics by decreasing the length of time juveniles are susceptible to mortality, thereby increasing their survival to the adult stage [26–29]. If shorter generation times contribute to higher survivorship, then these benefits of warming may offset the negative effects of increasing mortality and result in larger consumer population sizes [17,30]. Accounting for temperature effects on life cycles in consumer–resource models could modify the frequent prediction that rising temperatures increase consumer extinction risks owing to higher metabolism and mortality [6] and reveal new mechanisms by which warming alters population dynamics and communities.

Diverse ectotherms experience seasonally fluctuating temperatures that structure their life history, including annual timing of feeding and growth, transitions among life stages, and adult emergence and reproduction [31–35]. Moreover, climate warming can interact with seasonality to alter phenology and population dynamics [7,20,36]. For example, many insects in temperate environments have synchronized life cycles maintained by a period of winter diapause, triggered by photoperiod and temperature [20]. Increases in temperature have enabled insects to become active earlier in the season and produce more generations per year [23–25,37]. Yet, seasonal photoperiodic cues still induce winter diapause in many species, placing upper limits on changes in their phenology and generation times with warming [20]. The effects of warming in seasonal environments also depend on the organisms' thermal performance: warming can impact consumer population sizes by increasing summer temperatures above the thermal optimum for activity and growth and therefore cause mortality due to thermal stress [7,8,20,38,39]. The effects of warming may be most pronounced for organisms at high latitudes where warming is greater and seasonal fluctuations are more extreme [40].

Theoretical models have examined the effects of seasonality on populations to understand the evolution of thermal traits [41,42] and species coexistence [43,44]. In addition, life-cycle models have demonstrated the consequences of seasonality on life histories and phenology for ectotherms [45–47]. However, there are gaps in our understanding of how climate warming affects consumer–resource population dynamics for organisms with complex life cycles living in seasonal environments. We bridge this knowledge gap by developing a size-structured consumer–resource model for ectotherms with seasonal temperature variation. We use the framework of physiologically structured population models (PSPMs; [48]), in which population dynamics depend on metabolism, feeding, growth in size, and transitions among life stages of the consumer, in response to resource levels and seasonally fluctuating environmental temperature. We develop and parameterize our model for a freshwater insect, the damselfly *Enallagma annexum*, feeding on zooplankton, using field surveys that characterize its life history and experiments to quantify its feeding and growth rates. We use our model to simulate how climate warming in a seasonal environment could alter a key life-history trait of the consumer, the number of generations per year, and how changes in this trait mediate responses of consumer–resource population sizes and consumer persistence to increasing environmental temperature.

2. Methods

(a) Life history of *Enallagma annexum*

Damselflies have complex life cycles, spending most of their life in an aquatic juvenile stage and emerging to a short-lived, terrestrial adult stage for reproduction. Many species of damselflies have generation times that vary within and across latitudes because environmental temperatures directly influence growth rates [49]. For species of *Enallagma*, the number of generations per year increases from less than one to two from the northern to the southern limit of their range [49]. We investigated the life history and population dynamics of *E. annexum* in south-western Michigan, USA, where these damselflies have 11 juvenile stages requiring 10–11 months for development from egg to adult, and one generation per year with synchronized emergence to the adult stage that is maintained by a period

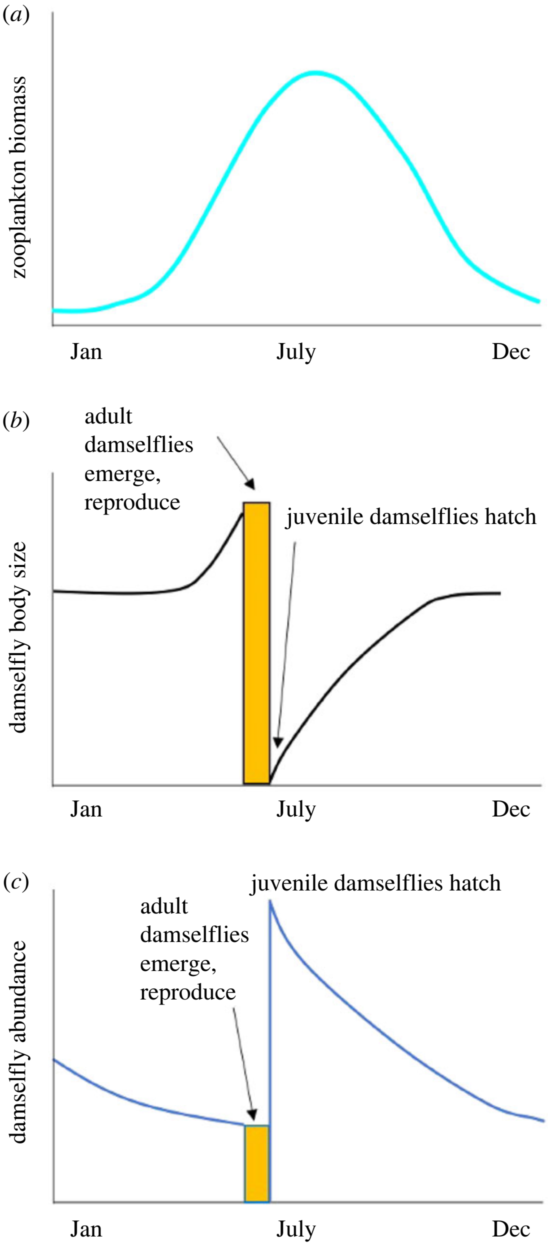

Figure 1. Idealized depiction of consumer–resource population dynamics in Michigan ponds, where damselflies have one generation per year. (*a*) Zooplankton biomass varies seasonally and peaks in mid-July. (*b*) Damselfly body size is at its minimum after juvenile damselflies hatch in early summer. Juvenile damselflies grow (black lines) over the course of the year and overwinter in diapause. They resume growth the following spring and emerge to the adult stage. Adult damselflies spend approximately 30 days outside of ponds foraging and reproducing (orange bar depicts adult size and duration outside of ponds). (*c*) Juvenile damselfly abundance (blue lines) is high after they hatch in early summer and declines owing to mortality throughout the year. In spring of the following year, damselflies emerge to the adult stage (orange bar depicts adult abundance and duration spent outside of the pond) and reproduce. Juvenile abundance is high in ponds after juvenile damselflies hatch.

of winter diapause as juveniles (figure 1, electronic supplementary material, figure S1) [50]. Adults live one to four weeks [51], during which they feed on terrestrial insects and breed, depositing their eggs in aquatic plants (figure 1; electronic supplementary material, figure S1) [52]. See electronic supplementary materials for detailed methodology and results of surveys of population dynamics of *E. annexum* and zooplankton prey in ponds.

(b) Size-structured consumer–resource population model (Standard Model)

We developed a size-structured consumer–resource population model, hereafter, the ‘Standard Model’ (figure 2). We based our model on the biomass-based model of [53], which we modified to incorporate the complex life history of a damselfly (figure 1; electronic supplementary material, figure S1). In addition, we incorporated features from other stage- or size-structured models as described and referenced below. Using a system of periodically forced ordinary differential equations, we model changes throughout the growing season in zooplankton (resource) biomass (Z), juvenile damselfly (consumer) body size (S) and damselfly abundance (C) (figure 2). We define the growing season [54,55] as the period when pond temperature exceeds 10°C (electronic supplementary material, figure S1), since below 10°C damselfly and zooplankton activity levels are low [56,57]. We track emergence from the damselfly juvenile to adult stage during the growing season as discrete events within this continuous-time system. We project within-season dynamics to inter-annual dynamics by modeling abundance and biomass at the beginning of each growing season as a function of the abundance and biomass at the end of the previous years’ growing season (a stroboscopic map).

We assume the resource (zooplankton) Z grows logistically in the absence of the consumer (damselflies), with maximum growth rate r and carrying capacity K (figure 2); we add a small immigration term i to account for refugia and to prevent unrealistically large population cycles. Juvenile damselflies increase their body size S by ingesting zooplankton following a saturating type-II functional response [56], minus loss in growth potential owing to maintenance μ. Rates of resource consumption and maintenance increase linearly with juvenile body size. Changes in the abundance of juvenile damselflies C are controlled by density-independent background mortality d and density-dependent interference mortality α, because cannibalism is an important source of mortality in damselflies [50]. The abundance of adult damselflies C_a is zero when juveniles are present. Together, these assumptions result in the following equations for within-pond dynamics:

$$\frac{\mathrm{d}Z}{\mathrm{d}t} = i + r(T)Z\left(1 - \frac{Z}{K}\right) - a(T)\frac{Z}{1 + h(T)a(T)Z}CS, \tag{2.1}$$

$$\frac{\mathrm{d}S}{\mathrm{d}t} = e_c a(T)\frac{Z}{1 + h(T)a(T)Z}S - \mu(T)S, \tag{2.2}$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = -d(T)C - \alpha C^2 \tag{2.3}$$

$$\text{and}\quad C_a = 0. \tag{2.4}$$

Here, a and h are the consumer attack rate and handling time on the resource, and e_c is the conversion efficiency of the resource into growth in juvenile body size. Assuming that the temperature remains below the optimum, the rates r, a, h, μ and d are modelled as functions of temperature T (Kelvin) using the Arrhenius equation [3,56]

$$Y = Y_0 e^{E_a/k(1/T_0 - 1/T)}. \tag{2.5}$$

Here, Y is the biological rate, Y_0 is the biological rate at the reference temperature $T_0 = 288.15$ K, E_a is the activation energy (eV) describing the strength of the temperature response and k is Boltzmann’s constant (8.617×10^{-5} eV). Parameter values are given in electronic supplementary material, table S1.

Our assumptions match observations that rates of resource ingestion and maintenance increase with damselfly body size, and ingestion is converted into growth in size, as in other PSPMs. Juveniles do not reproduce but use energy for growth and development to the adult stage, and adults reproduce but do not grow [48]. Our assumptions differ from most PSPMs in that

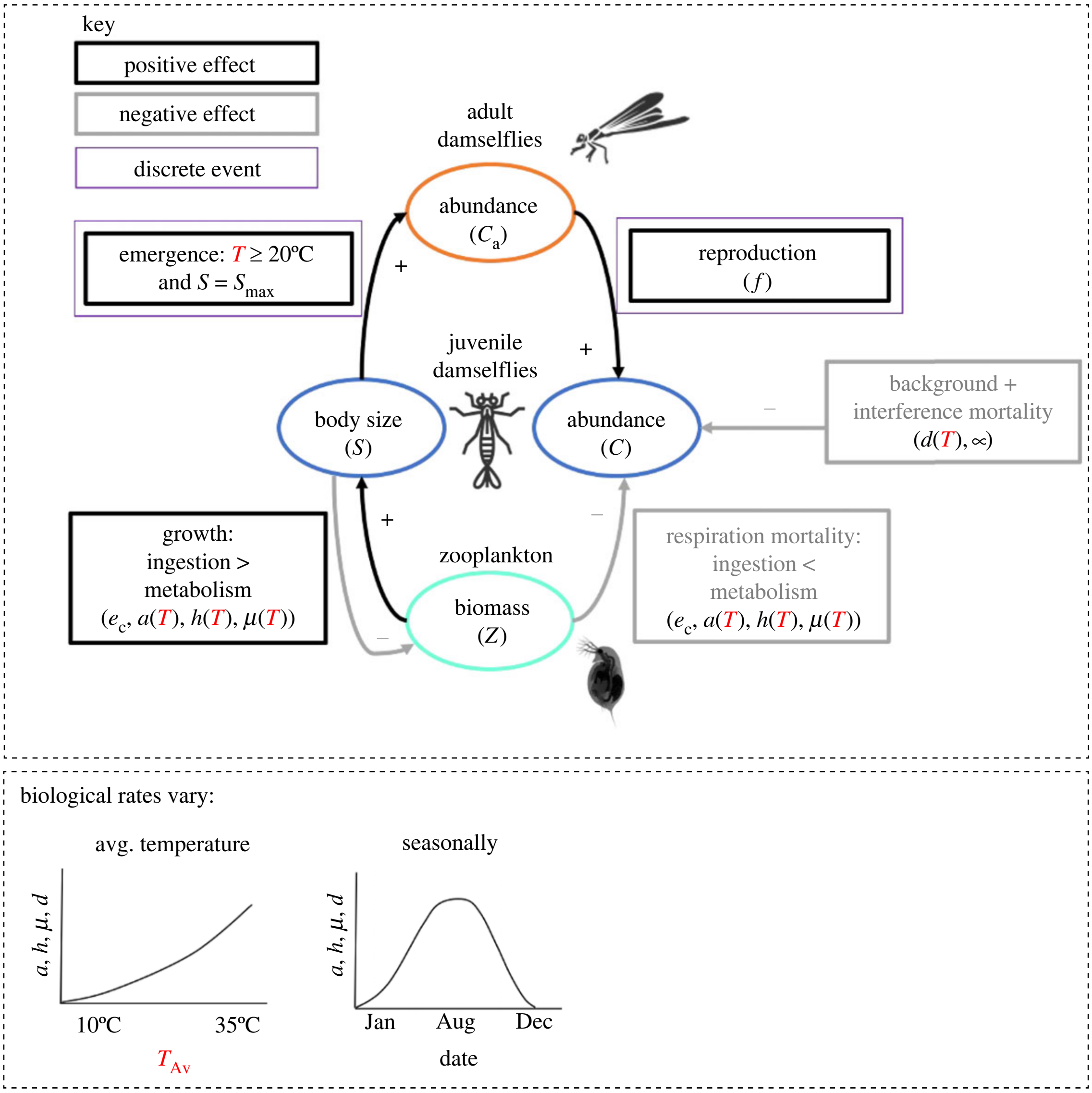

Figure 2. Conceptual diagram of the size-structured consumer–resource model. Top panel: within a growing season, juvenile damselflies grow when their ingestion of zooplankton exceeds metabolism, which reduces zooplankton biomass. Juvenile damselfly abundance is reduced through background and interference mortality and starvation when metabolism exceeds ingestion. Damselflies emerge to the adult stage when their body size is equal to S_{max} and temperature exceeds 20°C, which is represented by a discrete event within otherwise continuous dynamics. In a second discrete event, reproduction by adult damselflies produces the following cohort of damselflies. State variables are shown in ovals, biological events affecting state variables are enclosed in rectangles, and biological rates affecting each event are in parentheses. Arrows depict connections between state variables via biological rates described in parentheses. Temperature-dependent parameters are shown with T in parentheses. Bottom panel: biological rates vary in our model with both average temperature and seasonal changes in temperature.

we do not model energy storage or resource consumption by adults, which are terrestrial and rely on different resources. Instead, we assume that adult damselfly abundance is equivalent to the total juvenile abundance in a pond prior to emergence, and the number of new juveniles produced by adults is the number of adults at emergence multiplied by their fecundity. These assumptions are reasonable because the juvenile stage comprises most of the damselfly lifespan (figure 1; electronic supplementary material, figure S1; [51]).

Juvenile damselflies are born at an initial body size S_{min}, develop synchronously as a cohort, and emerge to the adult stage when individual body size has reached the threshold size S_{max} (figure 2). To emerge to the adult stage, the temperature in ponds must also exceed 20°C (*emergence window*, [58]). If these emergence conditions are not met, then the population remains in the juvenile stage until the next emergence window [16]. Adult emergence is modelled using discrete events that are triggered by emergence conditions. Specifically, a discrete change occurs in the damselflies as all juveniles emerge from the pond and spend $t_a = 30$ days in the adult stage (*emergence period*), converting juvenile abundance into adult abundance. During the emergence period, damselflies are absent from the pond, enabling zooplankton biomass to recover. The discrete changes in the system at the time of emergence (t_e) are described by

$$S(t_e^+) = S_{max}, \tag{2.6}$$

$$C(t_e^+) = 0 \tag{2.7}$$

$$\text{and} \quad C_a(t_e^+) = C(t_e^-), \tag{2.8}$$

where t_e^- is the time just before emergence, and t_e^+ is the time just after. While the damselflies are in the terrestrial, adult life stage, the zooplankton recover from predation following:

$$\frac{dZ}{dt} = i + rZ\left(1 - \frac{Z}{K}\right). \tag{2.9}$$

Adults reproduce t_a days after emergence, with adult abundance converted into new juveniles with initial size S_{min} according to the density-independent fecundity f (which incorporates adult mortality). Thus, after t_a days, the discrete changes in the system are described by

$$S(t_e + t_a) = S_{\min}, \tag{2.10}$$

$$C(t_e + t_a) = f \times C_a(t_e) \tag{2.11}$$

$$\text{and} \quad C_a(t_e + t_a) = 0. \tag{2.12}$$

If juvenile size reaches $S_{\max}$ before the emergence window, juveniles continue to ingest zooplankton, but no longer increase in size (in which case, excess energy is wasted). In addition, at low prey densities, maintenance may exceed resource consumption and assimilation, leading to starvation mortality for juveniles. To account for these conditions, we assume that growth in body size equals zero either when maintenance exceeds resource consumption and assimilation, or $S = S_{\max}$, in equation (2.2). We model starvation mortality [48] as an extra term in equation (2.3) equal to the difference between maintenance and feeding. Thus, juveniles are restricted to positive growth in body size as described by the piecewise equations

$$\frac{dS}{dt} = \begin{cases} e_c a(T) \dfrac{Z}{1 + h(T)a(T)Z} S - \mu(T)S, & \text{if} \quad \dfrac{e_c a(T)Z}{1 + a(T)h(T)Z} > \mu(T) \ \text{ and } S < S_{\max}, \\ 0, & \text{if} \quad \dfrac{e_c a(T)Z}{1 + a(T)h(T)Z} < \mu(T) \ \text{ or } S = S_{\max} \end{cases} \tag{2.13}$$

$$\frac{dC}{dt} = \begin{cases} -d(T)C - \alpha C^2, & \text{if} \quad \dfrac{e_c a(T)Z}{1 + a(T)h(T)Z} > \mu(T), \\ \left(-d(T) + e_c a(T) \dfrac{Z}{1 + h(T)a(T)Z} - \mu(T)\right) C - \alpha C^2, & \text{if} \quad \dfrac{e_c a(T)Z}{1 + a(T)h(T)Z} < \mu(T). \end{cases} \tag{2.14}$$

Temperature seasonality influences the length of the growing season, the timing and width of the emergence window, and consumer biological rates. We vary temperature seasonally according to a sinusoidal function,

$$T(t) = T_{av} + T_{amp} \left(\frac{\sin 2\pi(t - \phi)}{365} \right), \tag{2.15}$$

where T_{av} is average yearly temperature, T_{amp} is the amplitude, t is the day of the year and ϕ controls the phase. Increasing T_{av} leads to a longer growing season ($T(t) > 10$) and a larger emergence window ($T(t) > 20$).

(c) Model parameterization

We estimated minimum and maximum damselfly body sizes $S_{\min}$ and $S_{\max}$, and zooplankton carrying capacity K from field data (see electronic supplementary material). We assume that K is equivalent to the maximum zooplankton biomass in ponds during summer. Other biological rates were determined from the primary literature or set as needed to capture population dynamics observed in ponds (electronic supplementary material, table S1). We quantified parameter values of the temperature forcing function by fitting equation (2.15) to hourly pond temperature data from field surveys (see electronic supplementary material) using maximum likelihood estimation in R v. 3.6.1 [59]. We parameterized the temperature dependence of biological rates a, h and μ by fitting equation (2.5) to experimental data (electronic supplementary material, table S1; [56]). There is no clear evidence that conversion efficiency e_c or carrying capacity K vary with temperature [6]. In the absence of experimental data from our system, we assumed that zooplankton growth rate r increases with temperature, following the predictions of the metabolic theory of ecology [4], and that density-dependent interference mortality is temperature-independent.

(d) Analysis

We analysed our model in four forms: the Standard Model described above, and three Alternative Models in which we fixed the values of parameters to disentangle the mechanisms driving the results. In Alternative Model 1, we restricted the consumer generation time to at least 1 year, to demonstrate the effects of varying average temperature T_{av} (and therefore varying biological rates) in the absence of life-history changes in the consumer. In Alternative Model 2, we allowed growing season length and the width of the emergence window to vary with T_{av}, but fixed temperature-dependent biological rates in equations (2.1)–(2.4) to $T_{av} = 13°C$ (*reference temperature*, or current average temperature in ponds, see electronic supplementary material). Rates still varied seasonally but did not increase with T_{av}. In Alternative Model 3, we allowed biological rates to increase with T_{av}, but restricted the growing season length and the width of the emergence window to their values at $T_{av} = 13°C$. Together, Alternative Models 2 and 3 demonstrate how changing season length versus biological rates mediates consumer life-history and population responses to T_{av}.

To illustrate dynamics (figure 3), we simulated the model for 200 years to reach the long-term attractors. To generate bifurcation diagrams (figures 4 and 5), we varied T_{av}, increasing from 7.5 to 30°C by steps of 0.01°C. Using the final conditions of the previous step as initial conditions, we simulated the dynamics for 40 years to reach the new attractor (the small step size ensured convergence to the new attractor). We then recorded densities for the next 20 years, which we plot in our diagrams (time averages of Z and C across the growing season and unique values of C_a during the year). We also generated these bifurcation diagrams in the reverse direction (from 30 to 7.5°C) to check for alternative attractors, which we never found (see electronic supplementary material, figure S2). All model simulations were run in Mathematica v. 13.2 [60].

3. Results

Our model exhibits qualitatively similar within-year dynamics at the reference temperature $T_{av} = 13°C$ (figure 3*b*) to those we observed in the field (data shown in electronic supplementary material, figure S1 and idealized in figure 1). Each year, damselflies reach the emergence size shortly after the start of the emergence window. When adult damselflies leave the pond, the zooplankton resource has a chance to recover from predation. When juvenile damselflies hatch, they grow in size but decrease in abundance owing to mortality. At the end of the season, they overwinter as large juveniles and the annual cycle repeats.

The average temperature, T_{av}, has a complex effect on population abundance and dynamics in the Standard Model (figure 4). Damselflies went extinct for T_{av} less than 7.5°C, because the emergence window was too short to permit emergence and reproduction. Increasing T_{av} increased damselfly rates of prey ingestion and growth, which enabled shorter damselfly generation times, and lengthened the growing season and increased the width of the emergence window. Together, these effects enabled a shift in damselfly life history, from a biennial life history at low T_{av} (figure 3*a*), to an annual life history at intermediate T_{av} (including our reference temperature $T_{av} = 13°C$; figure 3*b*), to a bivoltine life history at high T_{av} (figure 3*c*). Between these temperatures, the model produced complex dynamics, which resulted in damselflies having irregular numbers of generations per year (figure 4).

Simulations of the Standard Model revealed that within a damselfly life-history strategy (for example, one generation per year), the adult and average juvenile abundance decreased with increasing temperature (figure 4) owing to increased

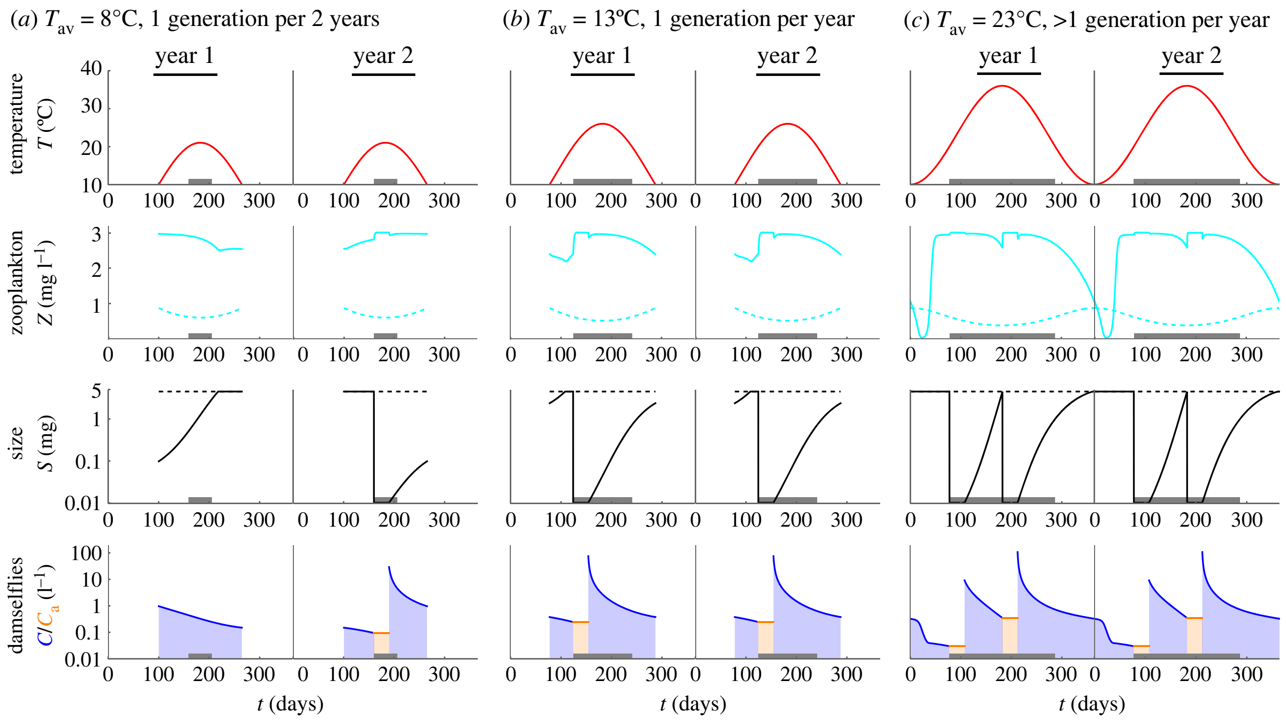

Figure 3. Modelled within season dynamics for (*a*) average temperature $T_{\mathrm{av}} = 8$°C, damselflies have one generation every other year; (*b*) $T_{\mathrm{av}} = 13$°C (reference temperature), one generation per year; and (*c*) $T_{\mathrm{av}} = 23$°C, two generations per year. From top to bottom: solid lines represent temperature (red), zooplankton biomass (cyan), damselfly body size (black), and damselfly abundance (blue/orange) during one growing season. Dashed lines on plots of zooplankton biomass indicate the minimum zooplankton biomass required for damselflies to avoid starvation mortality. Dashed lines on plots of damselfly body size indicate S_{max}, the threshold size for emergence to the adult stage. Blue fill on plots of damselfly abundance gives the juvenile abundance, and orange fill gives the adult abundance. Grey horizontal bars at the bottom of plots indicate the emergence window (temperature $T \geq 20$°C).

maintenance and mortality. However, damselfly population sizes increased abruptly when they underwent a warming-induced change in life history, for example, when transitioning from one to more than one generation per year or from two to more than two generations per year at higher temperatures. Thus, the life-history shifts were adaptive. Across the full temperature range of T_{av} from 7.5 to 30°C, and across all life-history strategies, the damselfly population size was above the persistence level and increased overall with warming (figure 4). Because individual damselflies consumed more resources at higher temperatures, we found a slight decrease in zooplankton population biomass with warming (figure 4). At major life-history transitions in the consumer, resource biomass increased as damselflies spent more time outside of ponds in the adult stage (e.g. damselflies transitioned from spending one 30-day period in the adult stage every year to alternating between one and two 30-day periods), during which the resource population recovered (figure 4).

There are multiple pathways by which increased temperatures can affect consumer dynamics and persistence (figure 2): longer growing seasons and emergence windows and more-rapid growth allow more generations per year, resulting in positive effects on the consumer, but increased maintenance and mortality have negative effects on the consumer. Our Alternative Models break these pathways, letting us disentangle their net effects (electronic supplementary material and figure 5). Alternative Model 1 forces the consumer to have at most one generation per year over the entire temperature range, which prevents it from taking advantage of the longer growing seasons, resulting in a steep decline in abundance with warming, and extinction around $T_{\mathrm{av}} = 26$°C (figure 5*a*). This result demonstrates that life-history transitions are key to the consumer's persistence under warming.

Alternative Model 2 fixes the temperature-dependent biological rates, which alleviates the direct negative effects of increased maintenance and mortality, but prevents juveniles from more rapidly maturing. This leads to an overall flat effect of warming (i.e. a small change in population size over the full temperature range) on consumer populations (figure 5*b*) and suggests that varying season length alone can facilitate consumer persistence under climate warming. By contrast, Alternative Model 3 fixes the season length, so that multiple generations per year are possible only at the highest average temperatures, resulting in substantial population declines with warming as the consumer is forced to maintain one generation per year over a large temperature range (figure 5*c*). Results of Alternative Models 2 and 3 indicate that varying season length and biological rates together are necessary to realize the full range of life-history strategies and overall increase in consumer population size with warming in the Standard Model (figure 4). Together, these Alternative Models show the importance of adaptive shifts in life history in promoting persistence of the consumer.

4. Discussion

With our size-structured consumer–resource model, we demonstrate that although there are ranges where populations decline with warming, across the entire temperature range warming results in a larger consumer population, owing to increased rates of prey ingestion and growth,

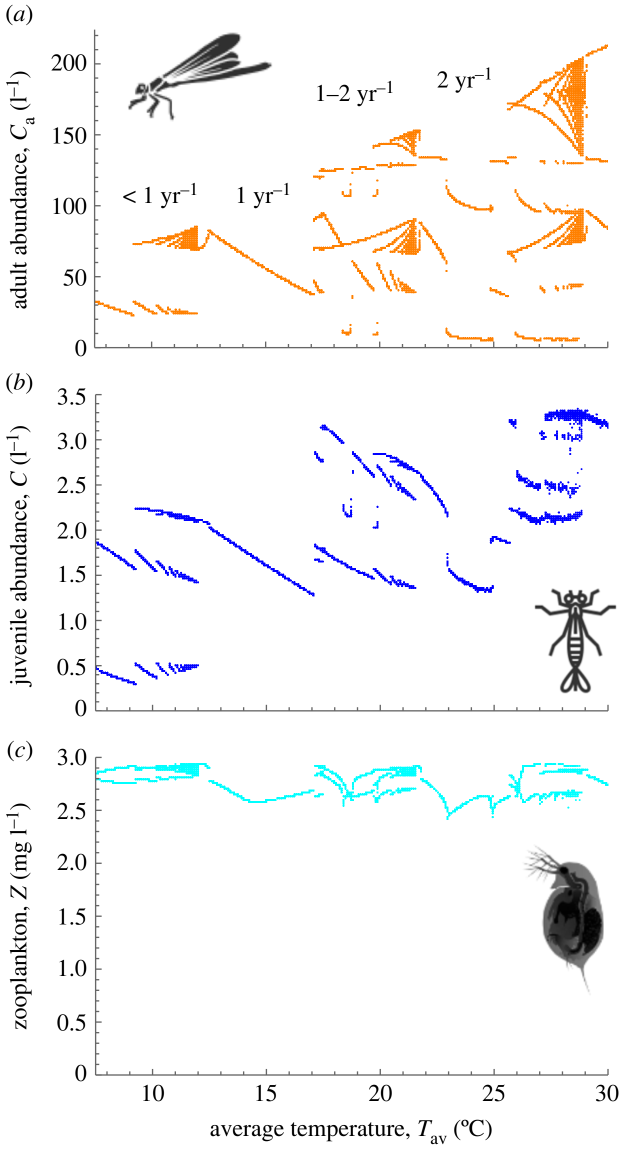

Figure 4. Bifurcation diagram demonstrating effects of average temperature in the Standard Model. Yearly average zooplankton biomass, Z (*c*), juvenile damselfly abundance, C (*b*), and the number of emerging adult damselflies,C_a (*a*). Annotations at the top label the damselflies' qualitative life-history dynamics. As temperature increases, damselflies transition from fewer than one generation per year (less than 1 yr^{-1}, to one generation per year (1 yr^{-1}, to one or two generations per year (1–2 yr^{-1}, to two generations per year (2 yr^{-1}, to more than two generations per year (greater than 2 yr^{-1}. Multiple population abundances and trajectories are possible (depicted by multiple coloured lines) within the following life-history strategies: 'less than 1 yr^{-1}', '1–2 yr^{-1}' and 'greater than 2 yr^{-1}'. Within these regions, the damselfly population has different numbers of cohorts in each year of the model simulation (e.g. within the 1–2 yr^{-1} strategy with T_{av} between 13 and 23°C, one cohort is produced in some years and two cohorts are produced in other years). This results in different initial abundances and trajectories over the year. For the life-history strategies of one (1 yr^{-1}) or two generations per year 2 yr^{-1} the same number of cohorts and abundances are produced in every model simulation at a given temperature, resulting in a single population trajectory for that strategy.

a longer growing season, and a larger emergence window, which altogether shorten consumer generation times. This life-history change in the consumer can offset warming-induced population declines that influence resource population biomass. In fact, high temperatures enabled damselflies to transition to more than one generation per year, resulting in larger damselfly population sizes and enhanced population persistence. As a result, the larger damselfly population exerted stronger predation pressure, decreasing zooplankton biomass overall across the temperature range. Increasing the growing season length and consumer biological rates with temperature both contributed to decreasing generation times in the consumer. In simulations of our Alternative Models, the damselfly population went extinct at higher temperatures when they were forced to maintain the same life-history strategy of one generation per year (figure 5*a*). Therefore, accounting for life-cycle complexity and temperature seasonality reversed the prediction of many theoretical models that climate warming decreases consumer persistence or destabilizes communities owing to direct effects of temperature on biological rates.

(a) Warming induces changes in consumer life history

We found that warming decreased damselfly generation time through two mechanisms: increasing biological rates and season length. First, warming increased damselfly rates of resource ingestion and growth, advancing their emergence to the adult stage (figure 3). Second, warming lengthened the growing season and increased the width of the emergence window, which enabled damselflies to emerge a second time in some years after reaching the emergence size. Restricting changes in resource ingestion rates or seasonality delayed life-history transitions in Alternative Models 2 and 3, in which damselflies did not transition to two generations per year at $T_{av} \leq 30$°C (figure 5*b*,*c*). If damselflies cannot ingest more resources and grow faster by increasing their attack and handling rates, a relatively longer season is necessary to permit multiple emergence events per year. Alternatively, if season length does not vary, the damselfly growth rate must be sufficiently high to reach the emergence size twice per year. However, allowing either biological rates or season length to vary with temperature was sufficient to prevent population extinction at higher temperatures (figure 5), and previous research suggests that each mechanism contributes to changes in life history. Experimental warming increases growth rates and advances emergence in dragonflies and damselflies [61–63], and their life histories vary latitudinally with changes in season length, where these insects have fewer than one generation per year at high latitudes and multiple generations per year at low latitudes [49,58].

(b) Changes in consumer life-history and temperature seasonality affect consumer persistence

Life-history transitions are necessary to offset warming-induced population declines and delay extinction in our system. Restricting damselflies to one generation or fewer per year (Alternative Model 1) resulted in damselfly population declines at higher temperatures owing to longer exposure to higher rates of background and maintenance mortality with a longer growing season (figure 5*a*). The key to escaping increased mortality at higher temperatures is decreasing the 'the window of vulnerability', by translating increased rates of resource ingestion and growth into higher rates of survival to the adult stage and earlier adult emergence [26], thereby increasing population-level reproduction. Although our model does not explore the effects of faster maturation

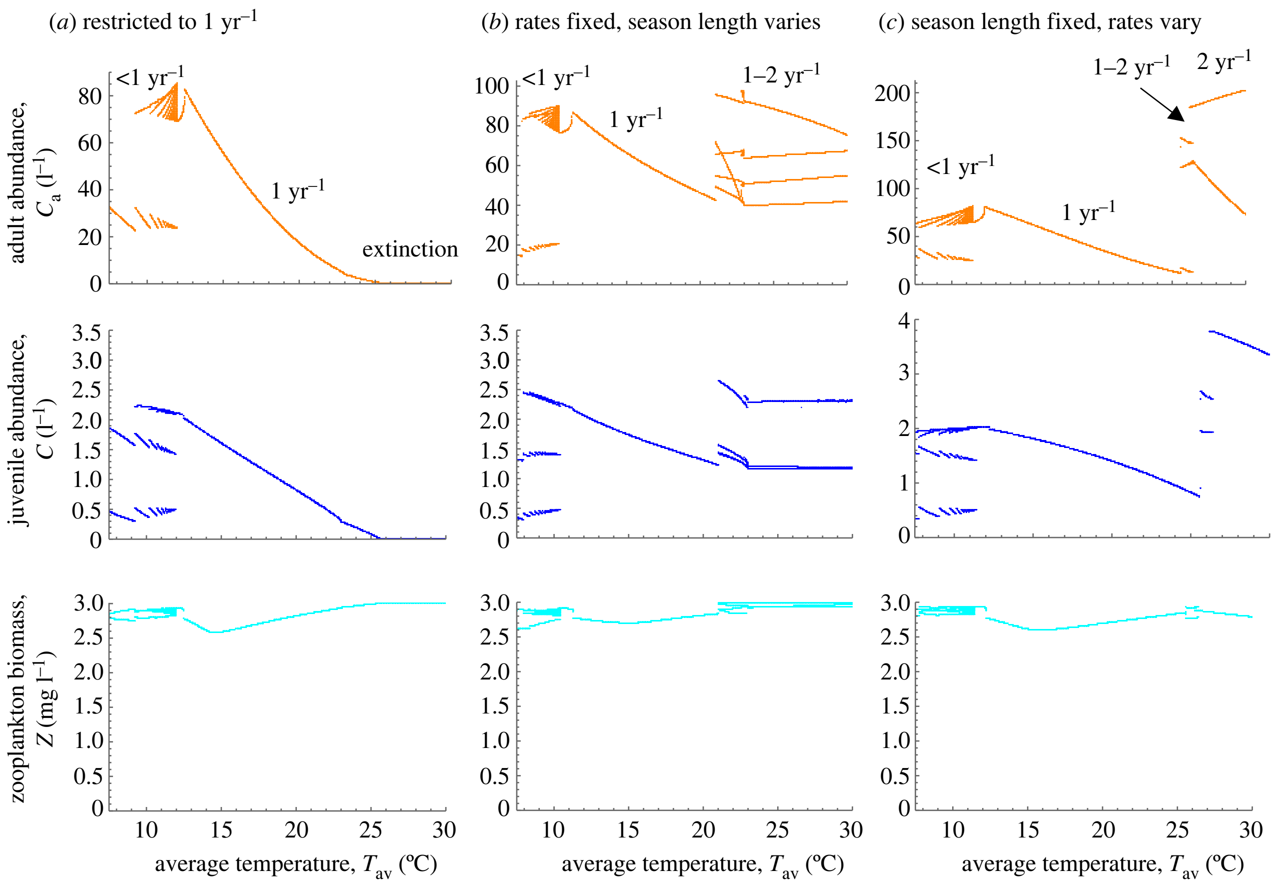

Figure 5. Bifurcation diagrams demonstrating effects of temperature in our Alternative Models. (*a*) Alternative Model 1, (*b*) Alternative Model 2, (*c*) Alternative Model 3. Yearly average zooplankton biomass (*Z*, bottom panel), juvenile damselfly abundance (*C*, middle panel), and the number of emerging adult damselflies (C_a, top panel). Annotations at the top divide the diagram according to the damselflies' qualitative life-history dynamics. As temperature increases damselflies transition from fewer than one generation per year (less than 1 yr^{-1}) to more than one generation per year (1–2 yr^{-1}), except in (*a*), where damselflies go extinct at high temperatures. Multiple trajectories shown within the 'less than 1 yr^{-1} and '1–2 yr^{-1}' strategies are as described for figure 4.

on individual reproductive rates, which could affect population-level reproduction, these results may still apply to ectotherms with vulnerable juvenile stages. In fact, the benefits of faster transitions from juvenile to adult stages for offsetting higher mortality with warming have been demonstrated for diverse ectotherms ranging from insects to anurans to fish [27–29,64]. However, more research is needed to assess the generality of these results for consumers with spatially and temporally overlapping juvenile and adult stages that may compete for resources, using models that account for life-cycle complexity and seasonality to simulate effects of climate warming (however, see [18]).

(c) Effects of life-history transitions on resource biomass and community structure

Damselflies more effectively suppressed resource biomass with warming because their rate of resource ingestion increased with temperature through their attack rates and handling times, and their population size increased as they transitioned to shorter generation times (figure 4). Therefore, our Standard Model predicted a top-heavy community at warmer temperatures relative to our Alternative Models restricting changes in consumer life history (figure 5). Our prediction of increasing consumer to resource population size is consistent with experiments [65,66] and the unstructured population model of [10] assuming that consumer biomass gains from ingestion increase more rapidly with warming than losses from maintenance, and that prey carrying capacity does not vary with temperature (also equivalent to 'scenario a' of [6], their fig. 4). Vasseur & McCann [10] predicted that this scenario would increase consumer persistence and destabilize community dynamics. Our model does not predict the destabilization of community dynamics because damselflies did not overexploit their prey. Three mechanisms likely explain this difference. First, when damselflies emerged from ponds as adults, the zooplankton biomass recovered to carrying capacity as adult damselflies switched to consuming terrestrial resources (figure 3). Second, interference mortality prevented the damselfly population from becoming too large and depleting the prey (see also [16]). Third, our assumption of immigration of zooplankton is known to prevent large-amplitude predator–prey cycles in unstructured population models. All of these mechanisms should help prevent predator–prey cycles resulting from over-exploitation of resources [67,68]. Therefore, incorporating life-cycle complexity, temperature seasonality and other components of biological realism predicts alternative outcomes for consumer–resource dynamics under warming compared with simpler, unstructured models.

(d) Model assumptions

Although our model improves ecological realism through added complexity, it has simplifying assumptions that may have affected the outcome of increasing temperature on population dynamics. Notably, we did not include temperature dependence of the resource carrying capacity or the intraspecific competition of consumers owing to lack of information. We modelled increases in resource ingestion rates using the Arrhenius equation, though it is now recognized that unimodal temperature functions are more appropriate for describing changes in the attack rate and maximum ingestion rate over a large temperature range [2,6]. We used the Arrhenius equation because it provided a better fit to our experimental data than a unimodal function for temperatures at or below 35°C [56], and we restricted model simulations to $T_{\mathrm{av}} \le 30$°C. This formulation already represents an increase of 17°C above the current average in southwestern Michigan ponds, well beyond the projected increase of 3 to 5°C by 2100 for the high emissions scenario RCP 8.5 [69]. Therefore, the Arrhenius equation is appropriate for modelling population responses to warming at or beyond temperatures that are realistic for our study system. The inclusion of a unimodal temperature function for resource attack and handling rates could reduce the consumer population size or cause extinction at high temperatures [6]. Temperature dependence of the zooplankton carrying capacity would be unlikely to change the qualitative outcomes of our simulations, because damselflies never depleted their resources enough to induce starvation mortality, except at high temperatures (figure 3*c*). Simulations in which we varied the value of the carrying capacity, *K*, from just above 0 to 100 at different temperatures showed that it had no qualitative effect on consumer–resource dynamics (see electronic supplementary material, figure S3).

We also made simplifying assumptions about damselfly life-history to demonstrate temperature effects on populations. For example, we omitted the effects of photoperiod when defining the growing season and emergence window, despite its importance for regulating the damselfly life cycle [70,71]. We also assumed a linear increase in biological rates with body size, although the effects of temperature can vary considerably with size and life stage [7]. To update our model, more research is needed to quantify biological rates across a range of temperatures and damselfly body sizes. Despite these simplifying assumptions, our Standard Model at the reference temperature accurately reflects the dynamics of damselfly populations in southwestern Michigan ponds (compare with figure 3*b*; electronic supplementary material, figure S1). In addition, our model captures many of the same dynamics in the more complex damselfly population model of [16], including stable cycles of yearly emergence within a life-history strategy and smaller average population sizes at lower temperatures (figures 3 and 4). That model was not designed to simulate climate change effects on populations, and it also differs in its depiction of transitions between life-history strategies (i.e. between one emergence every other year and one every year) by capturing ‘cohort-splitting’, or sub-populations that emerge in different years [58]. Although our model cannot demonstrate the effects of temperature in producing sub-populations, it effectively captures the qualitative changes in life-history already observed in dragonflies and damselflies [49,63,72] and other ectotherms in response to climate change or latitude [23–25,37].

5. Conclusion

We demonstrate the role of life history in mediating responses to warming by incorporating life-cycle complexity and temperature seasonality in our size-structured consumer–resource model. Using our model, we show that changes in consumer life history can alter the predicted outcomes of warming on populations compared with unstructured models parameterized for constant-temperature environments. We further show that warming can induce changes in ectotherm generation times by increasing rates of resource ingestion and growth or lengthening the growing season. Moreover, life-history changes can prevent consumer population declines with warming by shortening the duration of the juvenile stage and the window of vulnerability to mortality, increasing the number of emerging adults and population-level reproduction. We find increased stability of consumer–resource populations with increased predator persistence compared with unstructured models with similar assumptions. Our study reveals mechanisms by which climate change and latitude can affect ectotherm life histories and populations. Overall, our study suggests that life-history transitions to shorter generation times could delay population extinctions with warming. Life-cycle complexity and temperature seasonality should therefore be incorporated into research investigating the impacts of climate warming on diverse ectotherm consumer–resource populations in seasonal environments.

Data accessibility. Data used to parameterize the model was published previously [56]. Mathematica code and data are provided in the electronic supplementary material [73].

Authors’ contributions. L.A.T.: conceptualization, funding acquisition, investigation, visualization, writing—original draft; P.L.Z.: conceptualization, funding acquisition, writing—review and editing; C.A.K.: conceptualization, funding acquisition, investigation, software, supervision, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Funding was provided to L.A.T. by Michigan State University Department of Fisheries and Wildlife and Environmental Science and Policy Program, Kellogg Biological Station, Society for Freshwater Science. Funding for P.L.Z. and L.A.T. was also provided by NASA grant 80NSSC17K0395. C.A.K. was supported by NSF grants OCE-1638834 and DEB-1754250. This is W. K. Kellogg Biological Station contribution 2346.

Acknowledgements. We would like to thank Colin Love, Arpita Nayak, Faith Slubowski, Tyler Treakle, Jessie Ventzke and Jacob Wahl for assistance in the laboratory and field, Kate Boersma, Adam Siepielski, and the Mittelbach, Litchman–Klausmeier and Zarnetske Labs for many fruitful discussions about this research. Thanks also to Kellogg Biological Station staff.

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