# Impacts of warming revealed by linking resource growth rates with consumer functional responses

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## Summary

**1.** Warming global temperatures are driving changes in species distributions, growth and timing, but much uncertainty remains regarding how climate change will alter species interactions.

**2.** Consumer–Resource interactions in particular can be strongly impacted by changes to the relative performance of interacting species. While consumers generally gain an advantage over their resources with increasing temperatures, nonlinearities can change this relation near temperature extremes.

**3.** We use an experimental approach to determine how temperature changes between 5 and 30 °C will alter the growth of the algae *Scenedesmus obliquus* and the functional responses of the small-bodied *Daphnia ambigua* and the larger *Daphnia pulicaria*.

**4.** The impact of warming generally followed expectations, making both *Daphnia* species more effective grazers, with the increase in feeding rates outpacing the increases in algal growth rate. At the extremes of our temperature range, however, warming resulted in a decrease in *Daphnia* grazing effectiveness. Between 25 and 30 °C, both species of *Daphnia* experienced a precipitous drop in feeding rates, while algal growth rates remained high, increasing the likelihood of algal blooms in warming summer temperatures.

**5.** *Daphnia pulicaria* performed significantly better at cold temperatures than *D. ambigua*, but by 20 °C, there was no significant difference between the two species, and at 25 °C, *D. ambigua* outperformed *D. pulicaria*. Warming summer temperatures will favour the smaller *D. ambigua,* but only over a narrow temperature range, and warming beyond 25 °C could open *D. ambigua* to invasion from tropical species.

**6.** By fitting our results to temperature-dependent functions, we develop a temperature- and density-dependent model, which produces a metric of grazing effectiveness, quantifying the grazer density necessary to halt algal growth. This approach should prove useful for tracking the transient dynamics of other density-dependent consumer–resource interactions, such as agricultural pests and biological-control agents.

**Key-words:** climate change, consumer–resource dynamics, *Daphnia*, growth rate, phytoplankton, temperature

## Introduction

Warming temperatures brought on by global climate change have well-documented impacts on species distributions and phenology (Parmesan 2006). The impacts of warming on species interactions, however, are more difficult to predict, with warming altering the outcome of competition and changing the flow of energy through food webs (Tylianakis *et al.* 2008; Gilman *et al.* 2010; O'Con-

nor *et al.* 2012). Species interactions can both counter and exacerbate the direct effects of climate change (Suttle, Thomsen & Power 2007; Post & Pedersen 2008; Harley 2011). Instances where species interactions exacerbate the direct effects of climate change are of particular concern, especially in the outbreak of pests and parasites (Harvell *et al.* 2002). Consumer–resource interactions, which are of importance to ecosystem function and stability (McCann, Hastings & Huxel 1998), may be especially vulnerable to shifts in temperature because they are strongly impacted by changes in thermal means and extremes (Petchey *et al.* 1999; Hoekman 2010; Gilbert *et al.* 2014).

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Consumers generally benefit from warming more than their prey (Rose & Caron 2007). In the absence of consumers, growth rates of organisms typically increase with temperature due to the speeding of biological processes (Fig. 1, arrow 1) (Savage *et al.* 2004). If resources are allowed to grow to high densities, however, this effect may reverse, because the maximum density that populations can attain (the carrying capacity) has been hypothesized to decrease with temperature due to increases in metabolic costs (Fig. 1, arrow 2) (Allen, Brown & Gillooly 2002; Fussmann *et al.* 2014). Consumers gain an advantage at warmer temperatures because of the combined effects of an increase in attack rates (Fig. 1, arrow 3) and an increase in the maximum feeding rate (Fig. 1, arrow 4). The increase in attack rates is the result of an increase in activity rates of the consumer and/or the resource, while the increase in maximum feeding rate is due to the speeding of digestion rates with a rise in temperature (Dell, Pawar & Savage 2014).

The relationship between temperature and the biological rates of consumers and resources has been established within the so-called 'biologically relevant' temperature range, which corresponds to temperatures in which organisms achieve positive growth, but before rates begin to decline at high temperatures (Savage *et al.* 2004). Differences in thermal optima have the potential to drive large changes to our general predictions at temperature extremes (Sentis, Hemptinne & Brodeur 2012; Dell, Pawar & Savage 2014). The performance of organisms at extreme temperatures will become increasingly important as global climate change extends the range of temperatures that organisms are exposed to (IPCC 2013). When temperatures exceed the thermal maxima for consumers, prey with a greater thermal maximum will outperform their predators, allowing prey to escape predation,
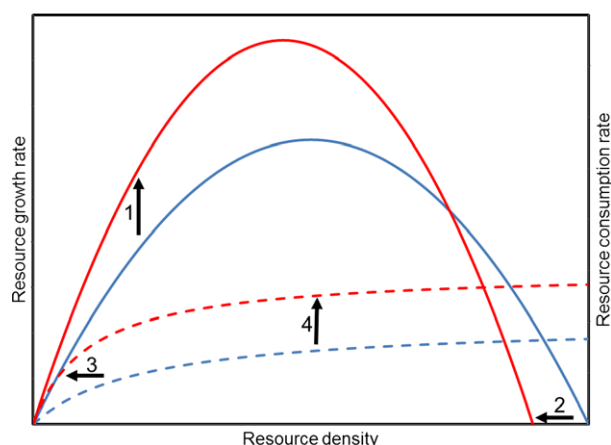
potentially becoming a nuisance species (Porter, Parry & Carter 1991).

The direct effects of temperature on growth and feeding can lead to complex outcomes of consumer–resource interactions because growth and feeding are nonlinear, density-dependent processes (Wilmers & Post 2006). The growth of small, fast-growing primary producers and the functional responses of herbivores feeding upon them can be characterized by saturating functions (Fig. 1). Temperature-driven shifts to initial rates of increase or saturating densities will alter consumer–resource interactions differently depending on the relative size of the responses and the density of the resource. For example, increases in consumer attack rates with temperature (Fig. 1, arrow 3) will have the most impact on the resource at low densities and will be especially important if they are of a different magnitude than the increase in initial resource growth rates (Fig. 1, arrow 1).

Recent work on consumer–resource interactions has improved our understanding of how the vital rates and feeding patterns scale with temperature (Fig. 1), allowing researchers to parameterize dynamic models to analyse the stability and dynamics of consumer–resource interactions (Fussmann *et al.* 2014; Gilbert *et al.* 2014). While the generality of this work is appealing, to understand the dynamics of individual interactions, it is necessary to measure the vital rates for the interacting species of interest. Additionally, the dynamic nature of seasonal temperature change in temperate systems presents a shifting landscape, limiting the ability of the system to reach an equilibrium and making transient population dynamics important (Hastings 2004). Here, we study the dynamics of specific consumer–resource pairs across a temperature gradient, capturing how relative changes in the vital rates of the two species will change the nature of their interaction. Rather than examining the long-term stability of an equilibrium, which may or may not be reached, we focus on the conditions that result in zero net population growth (ZNPG) of the resource, which is a turning point in the transient dynamic.

We use temperate lake plankton to study how changes in temperature and prey density alter the interaction strength of this consumer–resource interaction. Organisms in temperate lakes naturally experience a wide range of temperatures, ranging from winter temperatures near freezing to 30 °C in summer. Climate change is unlikely to affect the low end of the temperature extremes in most temperate lakes, as they will still reach temperatures at or near freezing even with substantial warming in winter months. Warming is impacting temperate lakes by advancing the timing of key spring events such as the onset of stratification and start of the growing season (when water temperature reaches ~5 °C), as well as increasing the maximum temperatures experienced in lakes in summer (Shatwell, Kohler & Nicklisch 2008).

The coupling of phytoplankton and zooplankton grazers is particularly important to lake food webs. Grazer



**Fig. 1.** Expectations for how resource growth rate (solid lines) and consumption rate (dashed) will change with temperature (cold – blue, warm – red). With an increase in temperature, we expect (1) an increase in the resource intrinsic growth rate, (2) a decrease in resource carrying capacity, (3) an increase in the consumer attack rate and (4) an increase in maximum consumption rate.

control of production is common in lakes, especially during the spring when the populations of both phytoplankton and their crustacean zooplankton grazers are growing rapidly (Sommer *et al.* 2012). *Daphnia* sp. are particularly effective herbivorous crustaceans, which often play a dominant role in the grazer community (Shapiro & Wright 1984), making them an important link between phytoplankton and fish in aquatic food webs (Mittelbach *et al.* 1995). Changes to the strength of the interaction between *Daphnia* and the phytoplankton resource have the potential to alter the timing and magnitude of the spring bloom and the biomass of *Daphnia* available to move up the food web through the growing season (Winder & Schindler 2004; Kratina *et al.* 2012).

In this study, we measure the growth rates of the freshwater green algae *Scenedesmus obliquus* across the range of temperatures found in temperate lakes and characterize the functional response of two *Daphnia* species feeding upon the algae across the same temperature range. Both daphnids are widely distributed in north temperate lakes and can be a dominant force in the spring grazer community, but they differ in body size and evolutionary history. *Daphnia pulicaria* is a larger cold-adapted species, while *Daphnia ambigua* is smaller, widespread, and thought to be of subtropical origin (Hebert, Witt & Adamowicz 2003). Our study design allows us to measure the impact of temperature upon algal growth and the functional response. By combining algal growth rates and the consumption of algae by *Daphnia,* we obtain a metric of grazing effectiveness, which shows how this consumer–resource interaction changes with temperature.

## Materials and methods

### ALGAL GROWTH RATE

We measured the growth rate of the algae *S. obliquus* at five-degree intervals from 5 to 30 °C. Algae were cultured at their destined temperature regime for 3 days prior to the experiment. A starting density of <0·5 mg L$^{-1}$ was added to 150 mL of COMBO growth media (Kilham *et al.* 1998) in 250-mL Erlenmeyer flasks. All cultures were maintained in triplicate and were grown in front of a Philips F15/T8 Plant and Aquarium fluorescent light in an otherwise dark incubator. Cultures were vigorously swirled daily and density was quantified using a laser particle counter (Spectrex PC-2200, Redwood City, CA, USA). We initially quantified algal densities daily, but reduced the frequency to twice weekly as growth rates slowed.

We converted cell counts to biomass by estimating the dry mass of three samples from a healthy culture maintained at 20 °C. For each sample, we simultaneously counted cells with the particle counter and filtered the sample onto pre-weighed glass fibre filters. These filters were dried at 60 °C for 24 h and reweighed. This resulted in a dry mass of 1 mg L$^{-1}$ per $2 \cdot 16 \times 10^4$ ($\pm 0 \cdot 07 \times 10^4$) counts mL$^{-1}$ of *S. obliquus*. The particle counter showed that the size of *S. obliquus* was variable through time; however, this variability was primarily driven by algal density, not temperature. Counter to the pattern found in

the 'temperature-size rule' (Forster, Hirst & Atkinson 2012) for the last two dates at each temperature, when the algae were close to carrying capacity, the estimated spherical diameter (ESD) measured by the particle counter was largest at the warmest temperature. As found in previous experiments, much of the variation in *S. obliquus* ESD is probably due to changes in the length: width ratio (Margalef 1954). All results are given as dry mass.

To estimate the algal growth rate at each temperature, we calculated the exponential growth rate before density dependence slowed the growth rate. To do this, we inspected the log-transformed plot of time and density, and identified the density at which the curve began to plateau as 9·5 mg L$^{-1}$. For each temperature, data from day one until the day at which a culture reached this density were pooled across replicates and the slope of the log-transformed biomass density vs. time was determined using linear regression.

We fit a function to the full time series of *S. obliquus* to quantify the growth rate at different algal densities. The commonly used logistic growth curve did not fit the time series of *S. obliquus* growth well because the logistic features a linear decline in the mass-specific growth rate, while the density dependence of *S. obliquus* was strongly nonlinear with a concave shape, which results in a very poor fit to the logistic function (Smith 1963). Following the approach of Paine *et al.* (2012), we tested the suite of saturating models recommended in their study as well as the theta-logistic model to match the form of density dependence found in the data. Logistic models proved to be the best fit to our data set (Table S1, Supporting information). The pattern of density dependence we observed, which was strongly nonlinear, was best fit by the theta-logistic model:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left[1 - \left(\frac{N}{K}\right)^{\theta}\right] \qquad \text{eqn 1}$$

where $K$ is the saturating density, $r$ is the initial instantaneous growth rate and $\theta$ is a constant, which alters the form of density dependence. When $\theta$ is equal to 1, the equation simplifies to the familiar logistic equation with a linear relationship between per-capita growth rate and density. When $\theta$ is >1, the graph of per-capita growth rate and density becomes convex, and when it is <1, it becomes concave. Integrating and simplifying this equation gives the abundance ($N_t$) at any time ($t$) as:

$$N_t = [k^{-\theta} + (N_0^{-\theta} - K^{-\theta})e^{(-r\theta t)}]^{\frac{-1}{\theta}} \qquad \text{eqn 2}$$

where $N_0$ is the initial density, and $e$ is the exponential function. To fit the data, we used nonlinear least squares regression, using the nls function in R (R Development Core Team 2013). The theta-logistic function is difficult to fit to data because $r$ and $\theta$ are highly correlated (Clark *et al.* 2010). We were able to overcome this by fixing $r$ to the value from the initial phase of algal growth, which allowed us to obtain reasonable fits for $\theta$ and $K$.

### DAPHNIA FEEDING EXPERIMENT

We estimated the functional response of *Daphnia pulicaria* and *Daphnia ambigua* feeding upon *S. obliquus*, again at five-degree intervals from 5 to 30 °C. The same approach was used for both daphnids, although modifications were necessary for *D. ambigua* at low temperatures due to their low feeding rate. For all treatments, *Daphnia* were raised in their target temperature for their

entire lifetime. Gravid females that had not yet released their first clutch were used in all experiments. If a full clutch was released during the course of a feeding trial, the replicate was discarded. If one to three neonates were released, it did not seem to affect the feeding rate measurements and these replicates were included.

In recognition that intraspecific variation in the *Daphnia* response to temperature exists between clones, we used five clones of each species for the experiments. Measuring the different response of each clone was beyond the scope of this study, so one individual from each clone went into each replicate of the feeding experiment to better measure the mean of the species response to warming. *Daphnia* were kept at high food density until the start of the experiment. The five *Daphnia* were added to 80 mL of COMBO media into each of seven initial algal densities between 0·45 and 17·5 mg L$^{-1}$. Five replicates of each algal density were used. Additionally, three algal cultures at each density were left free of *Daphnia* as controls. Jars were placed at the appropriate treatment temperature and left in the dark to minimize algal growth. After 8 h, the *S. obliquus* were quantified using the laser particle counter. The quantity of algae consumed was calculated by subtracting the algae remaining after 8 h from the density of the controls.

*Daphnia ambigua* had very low feeding rates at low temperatures. As a result, we were not able to obtain estimates for 5 °C and we increased the number of *D. ambigua* to 15 in each replicate at 10 and 15 °C. As the mass of *D. ambigua* is approximately one-third of *D. pulicaria* (*D. pulicaria* 67·4 μg dry mass, *D. ambigua* 20·5 μg dry mass), we do not expect the increase in *Daphnia* density to increase density-related foraging interference beyond that experienced by *D. pulicaria*. Furthermore, at 10 °C, we found it necessary to starve the *D. ambigua* for 24 h prior to the start of the experiment to observe depletion of algae. Thus, the 10 °C consumption rates for *D. ambigua* are an overestimate of consumption in comparison with the other treatment and provided only for reference.

### FITTING THE FUNCTIONAL RESPONSE

Saturation in the functional response was apparent at all temperatures. To test whether a Holling type II or III curve was most appropriate, we used logistic regression (Holling 1959; Juliano 2001). For the majority of temperatures for both species, a type II curve proved to be the best fit, so we present those results here. The Holling type II curve is a mechanistic model with the form

$$N_e = \frac{atN}{1 + ahN} \qquad \text{eqn 3}$$

where $N_e$ is the number of prey eaten per consumer, $a$ is the attack rate (1 per mg *Daphnia* h), $t$ is time, $N$ is the number of prey available and $h$ is the handling time (mg *Daphnia* h per mg algae). To account for prey depletion, we use the Rogers Random Predator function (Rogers 1972).

$$N_e = N(1 - e^{-a(t - hN_e)}) \qquad \text{eqn 4}$$

As a mechanistic model, the Holling type II curve allows us to examine how temperature affects the two parameters of the functional response, attack rate ($a$) and handing time ($h$). Using a maximum likelihood approach resulted in a poor fit, especially at

high algal densities, so the curves were fit with nonlinear least squares using the lambert *w* function to solve the Rogers Random Predator Equation in R (Bolker 2008).

To compare the functional response across temperatures and between species, we used pairwise sum of squares reduction and an *F*-test. We constrained the model so that the parameters $a$ and $h$ were the same for both pairs (model 1) and compared this with the full model with the two factors fit separately (model 2). We then compared fits with an *F*-test;

$$F = \frac{((\text{RSS}_1 - \text{RSS}_2)/(p_2 - p_1))}{(\text{RSS}_2/(n - p_2))} \qquad \text{eqn 5}$$

where $\text{RSS}_i$ are the residual sums of squares for model $i$, $p_i$ are the number of parameters in model $i$ and $n$ is the number of data points. Significant differences between the full and reduced models from an *F*-distribution (with $p_2–p_1$, $n–p_2$ degrees of freedom) show that the functional response is different for the temperatures or species considered. We carried out this comparison for each temperature pairing within a species (10 comparisons for *D. ambigua,* 15 for *D. pulicaria*) and for each matched temperature between species (4 comparisons – 10 °C was excluded) using a Bonferroni-corrected α for multiple comparisons (α = 0·005 for *D. ambigua,* α = 0·0033 for *D. pulicaria* and α = 0·013 for the between-species comparison).

### TEMPERATURE DEPENDENCE OF GRAZING EFFECTIVENESS

By combining the functions for the growth rate of *S. obliquus* and the consumption of *S. obliquus* by *Daphnia,* we are able to construct a model for algal growth in the presence of either daphnid (Z).

$$\frac{dN}{dt} = rN\left[1 - \left(\frac{N}{K}\right)^\theta\right] - \frac{aNZ}{1 + ahN} \qquad \text{eqn 6}$$

To incorporate temperature into our model, we fit each parameter ($r$, $K$, θ for algal growth, $a$ and $h$ for each *Daphnia* species) to a temperature-dependent function. All vital rates for algal growth and *Daphnia* consumption were first fit at their individual temperatures as detailed above. We then fit the Arrhenius model to the results

$$Y = ce^{E_a(-1/k(T+273\cdot15))} \qquad \text{eqn 7}$$

where $Y$ is the parameter of interest, $c$ is a constant and $E_a$ is the activation energy in eV, $k$ is Boltzmann's constant ($8\cdot617 \times 10^{-5}$ eV°Kelvin$^{-1}$) and $T$ is the temperature in °C. This model has received extensive study in investigating the temperature dependence of various biological rates (Gillooly *et al.* 2001; Englund *et al.* 2011). While it has been successful in revealing patterns within the 'biologically relevant' temperature range, it results in poor fits when a thermal optimum is present. In such cases, a quadratic model may be preferable (Englund *et al.* 2011):

$$Y = ce^{b(-1/k(T+273\cdot15)) + q(-1/k(T+273\cdot15))^2} \qquad \text{eqn 8}$$

where $c$, $b$ (eV) and $q$ (eV$^2$) are fitted parameters, which determine the shape of the temperature dependence (Englund *et al.*

2011). In this case, the parameter '*b*' can no longer be interpreted as the activation energy.

We used a weighted regression with the values of the parameters from the individual regression fits at each temperature for algal growth and the functional response as the data, and the inverse of the standard error of the parameter estimates as weights. To select between the Arrhenius model and the Arrhenius quadratic model, we compared the Akaike information criteria (AIC) for the regression fits of each parameter to eqns 7 and 8 and chose the model with the lower AIC. We omit the 10 °C treatment of *D. ambigua* because the differences in methodology do not allow for a reasonable comparison to other treatments.

Using the temperature-dependent functions, we determined the density of *Daphnia* (Z) necessary to reach ZNPG of *S. obliquus* by setting d*N*/d*t* in eqn 5 to zero and solving for Z. To facilitate comparison between the two *Daphnia* species, we transform the per-capita consumption to a per-gram basis. The biomass of *Daphnia* necessary for ZNPG is a useful measure of grazing effectiveness because it measures the ability of *Daphnia* to consume algae relative to the algal growth rate. A higher grazing effectiveness translates to a lower biomass of *Daphnia* necessary for ZNPG of algae. Grazing effectiveness increases with an increase in feeding rate or a decrease in algal growth rate, but can decrease even with an increase in feeding rate if algal growth rate increases more quickly.
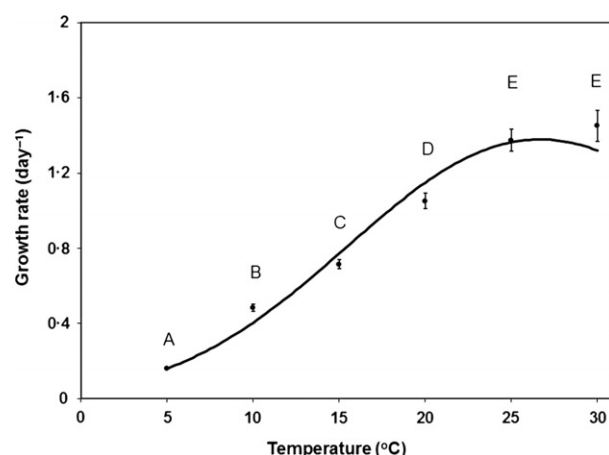


**Fig. 2.** *Scenedesmus obliquus* intrinsic growth rate, estimated by the slope of the log-transformed time series up to a density of 9·5 mg L$^{-1}$. Error bars indicate one standard error around the slope, letters indicate rates that are statistically different from each other (ANCOVA, $P < 0·01$). The line is the fit to the quadratic temperature-dependent model; see Table 2 for parameters.

By combining our measurements of *Daphnia* feeding with our observations on *Daphnia* survival, metabolic theory and values from the literature, we were able to construct a model for *Daphnia* growth across temperature (eqn S1). Combining the model for algal growth with the model for *Daphnia* growth enables us to simulate the transient dynamics of the *Daphnia*–algae system.

## Results

At low densities, algal growth rates increased with an increase in temperature up to 25 °C (ANCOVA $P < 0·001$ for all pairwise contrasts), but there was no significant difference in the intrinsic growth rate between 25 and 30 °C (ANCOVA, $F_{1,15} = 0·586$, $P = 0·46$) (Fig. 2). Using the theta-logistic growth model, we obtained good fits to the algal growth at all temperatures from 5 to 30 °C (Table 1). Algal growth did not saturate until exceeding 420 mg L$^{-1}$ at 30 °C, with higher densities at saturation at cooler temperatures, saturating at over 1000 mg L$^{-1}$ at 5 and 10 °C (Table 1). The quadratic temperature-dependent model was a better fit for the algal growth rate and density dependence terms (*r* and θ), while the carrying capacity best fit with the Arrhenius model (Table 2). The quadratic model indicated that algal growth rate (*r*) peaked at 26·6 °C, while the density dependence term (θ) reached a minimum at 24·8 °C.

*Daphnia* feeding rates generally increased up to 25 °C and decreased significantly between 25 and 30 °C for both *D. ambigua* and *D. pulicaria* (Fig. 3). For *D. ambigua*, there was a significant difference in the functional response between every temperature (*F*-tests, $P < 0·001$) except between 15 and 30 °C ($F_{2,58} = 1·065$, $P = 0·35$). For *D. pulicaria,* feeding rates increased significantly between 5 and 10 °C and between 10 and 15 °C (*F*-tests, $P < 0·001$), but there was no significant difference in the functional response between 15, 20 and 25 °C (15 and 20 °C: $F_{2,61} = 0·726$, $P = 0·49$, 20 and 25 °C: $F_{2,64} = 0·83$, $P = 0·44$, 15 and 25 °C: $F_{2,57} = 5·68$, $P = 0·006$). At 30 °C, the functional response for *D. pulicaria* was significantly different from all other temperatures (*F*-tests, $P < 0·001$).

At warmer temperatures, the smaller *D. ambigua* gained an advantage in feeding over *D. pulicaria*. Below 10 °C, we were unable to record depletion of algae for *D. ambigua* using the same methods as *D. pulicaria,* indicating

**Table 1.** Fits of algal growth time series to the theta-logistic growth model. Parameter *r* is the initial growth rate from a separate regression (see Materials and methods). The remaining parameters are fit using nonlinear least squares regression: K is the saturating density (carrying capacity), θ is the exponent that determines the shape of density dependence and $N_0$ is the fit for the initial density

| Temperature (°C) | *r* (h$^{-1}$) ± SE | $N_0$(mg L$^{-1}$) ± SE | K (mg L$^{-1}$) ± SE | θ ± SE |
|---|---|---|---|---|
| 5 | 0·0067 ± 0·0002 | 0·37 ± 0·12 | 1079 ± 70 | 0·461 ± 0·056 |
| 10 | 0·0202 ± 0·0008 | 3·53 ± 0·80 | 1123 ± 27 | 0·106 ± 0·004 |
| 15 | 0·0298 ± 0·0010 | 3·38 ± 0·67 | 731 ± 90 | 0·084 ± 0·011 |
| 20 | 0·0438 ± 0·0017 | 2·05 ± 0·67 | 573 ± 17 | 0·081 ± 0·005 |
| 25 | 0·0573 ± 0·0024 | 4·61 ± 1·05 | 557 ± 14 | 0·059 ± 0·003 |
| 30 | 0·0605 ± 0·0035 | 3·43 ± 1·49 | 421 ± 13 | 0·070 ± 0·006 |

**Table 2.** Temperature dependence of *Scenedesmus obliquus* growth and *Daphnia* functional response parameter values, as fit to Arrhenius (eqn 5) or Arrhenius quadratic (eqn 6) models. Units for $\ln(c)$ depend upon the parameter, and are listed with the parameter of interest

| Parameter | $\ln(c) \pm$ SE | $b$ (eV) $\pm$ SE | $q$ (eV$^2$) $\pm$ SE | $R^2$ |
|---|---|---|---|---|
| $r$ (day$^{-1}$) | $-354.64 \pm 79.24$ | $-18.3393 \pm 3.92697$ | $-0.23688 \pm 0.04862$ | 0.9909 |
| $K$ (mg L$^{-1}$) | $-5.79 \pm 1.62$ | $-0.30939 \pm 0.04103$ | n/a $\pm$ n/a | 0.9343 |
| $\theta$ | $235.87 \pm 166.98$ | $12.2534 \pm 8.404$ | $0.1573 \pm 0.1057$ | 0.7769 |
| $a_{ambigua}$ (1 per mg Daph h) | $-1968.12 \pm 638.42$ | $-100.3089 \pm 32.5058$ | $-1.2789 \pm 0.4136$ | 0.9185 |
| $h_{ambigua}$ (mg Daph h per mg algae) | $1178.65 \pm 1560.84$ | $60.233 \pm 79.5631$ | $0.7709 \pm 1.0137$ | 0.4266 |
| $a_{pulicaria}$ (1 per mg Daph h) | $-781.41 \pm 135.99$ | $-39.5555 \pm 6.77161$ | $-0.50128 \pm 0.08421$ | 0.9808 |
| $h_{pulicara}$ (mg Daph h per mg algae) | $616.75 \pm 253.97$ | $31.0988 \pm 12.801$ | $0.3936 \pm 0.1613$ | 0.6953 |
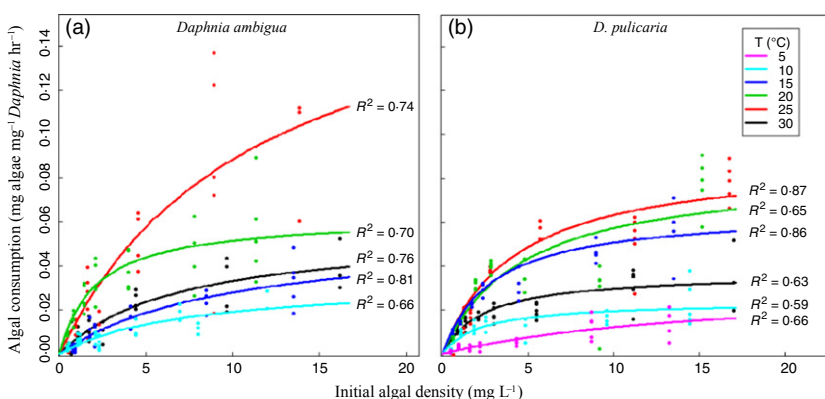


**Fig. 3.** The Holling type II functional response for *Daphnia ambigua* (a) and *D. pulicaria* (b). Dots show the algal consumption for each replicate at each temperature and initial algal density during that trial.

that *D. pulicaria* outperformed *D. ambigua* at these temperatures. At 15 °C, *D. pulicaria* had a significantly higher feeding rate ($F_{2,57} = 21.5$, $P < 0.001$); at 20 °C, there was no significant difference between the functional responses ($F_{2,65} = 1.14$, $P = 0.33$); and at 25 °C, *D. ambigua* had a significantly higher feeding rate ($F_{2,59} = 9.36$, $P < 0.001$). After both species lost function at 30 °C, there was again no significant difference between the functional responses ($F_{2,57} = 1.87$, $P = 0.16$).

The increase in feeding rate with temperature was caused by both an increase in the attack rate and a decrease in the handling time (Fig. 4). The Arrhenius quadratic temperature-dependent model was a best fit for both attack rate and handling time for *D. pulicaria* and for attack rate for *D. ambigua*. Although the AIC slightly prefers the Arrhenius model for handling time of *D. ambigua* (Table S2), neither model was a good fit. We have elected to use the Arrhenius quadratic model for this parameter as well, based on the consensus from the other functional response parameters. The quadratic model showed that for *D. pulicaria*, attack rate reached a maximum at 21·0 °C and handling time reached a minimum at 20·6 °C. For *D. ambigua*, the temperature dependence was shifted to warmer temperatures, 22·8 °C for attack rate and 23·9 °C for handling time.

We combined our results for the effects of temperature on algal growth and *Daphnia* grazing to produce a response surface showing how the density of *Daphnia* necessary to produce ZNPG of algae changes with algal density and temperature (Fig. 5). Grazing effectiveness of *D. pulicaria* was maximized at 19 °C, while grazing effectiveness of *D. ambigua* did not peak until 23 °C.

## Discussion

Our experiments revealed that a warming of 5 °C could increase, decrease or have little effect on the consumer–resource interaction depending on the starting temperature, the resource density and the species identity. We expected to see an increase in grazing effectiveness with warming as the attack rate increased and handling time decreased more rapidly than algal growth increased. Between 5 and 25 °C, *Scenedesmus obliquus* growth, as well as *Daphnia ambigua* and *D. pulicaria* feeding, generally followed this pattern. Within this temperature range, algal growth rates and *Daphnia* feeding rates increased with temperature (Figs 2 and 3). Increases in temperature had a stronger effect on *Daphnia* feeding rates than algal growth between 10 and 25 °C, as indicated by a lower density of *Daphnia* necessary to balance algal growth (Fig. 5).

Above 25 °C, however, we saw departures from our expectations. A dramatic decrease in *Daphnia* grazing effectiveness between 25 and 30 °C (Fig. 5) highlights one of the most troubling impacts of climate change on species interactions (Porter, Parry & Carter 1991). As temperature increased from 25 to 30 °C, algal growth rates remained high (Fig. 2); however, *Daphnia* grazing rates began to fall. For both species of *Daphnia*, this reduction in performance was largely due to an increase in handling time (Fig. 4), indicating that *Daphnia* may be entering an
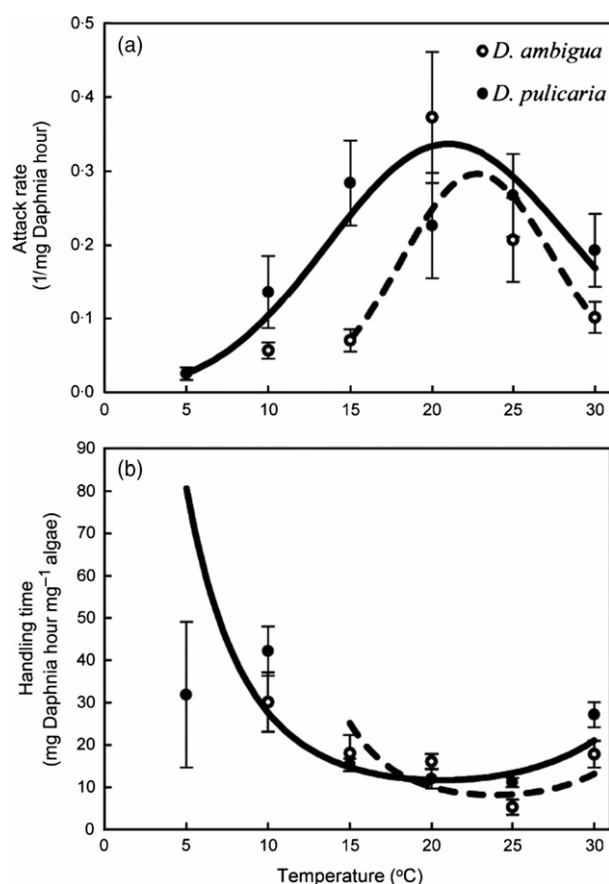
**Fig. 4.** The (a) attack rate, and (b) handling time parameters for the Holling type II functional response of *D. ambigua* (open circles) and *Daphnia pulicaria* (solid circles) across a range of temperatures. The lines are the fit to the quadratic temperature-dependent model for *D. ambigua* (dashed) and *D. pulicaria* (solid); see Table 2 for parameters.

anaerobic condition at 30 °C (Portner & Farrell 2008). For the consumer–resource pair of *Daphnia* and *Scenedesmus*, pushing the system to these warmest temperatures

would enable algae to escape control by grazers, allowing them to reach high densities associated with nuisance algal blooms (Carpenter *et al.* 1995).

Changes in algal density have an impact on grazing effectiveness that is similar in magnitude to changes in temperature (Fig. 5). Although the per-capita growth of algae slows with increases in algal density, the population growth rate of the algae increases with density up to ~1/3 of carrying capacity (Fig. S2) so the population growth rate increases across all densities we consider in Fig. 5. As algal density increases, the overall consumption rate of *Daphnia* increases; however, the saturating nature of the type II functional response slows this affect, and results in the per-algal mortality rate decreasing with increasing algal density. As a result, the ability of *Daphnia* to control the algal resource in spring is greatly aided by temperatures warming rapidly so that consumption rates increase while algal populations remain low (D. C. West and D. M. Post, in preparation).

Our results suggest that caution is needed in applying temperature-dependent models near temperature extremes where the models may not fit the performance of specific species well. While the fits of the functional response parameters to the quadratic temperature-dependent model were generally good (Fig. 4, Table 2), at the coldest temperature analysed for each daphnid, the temperature-dependent model estimates much higher handling times than the functional response model fit to the raw data (Fig. 4b). The temperature-dependent model fits are not unreasonable, as they pass within the observed data points (Fig. S4) and the standard errors for the handling time fits at these cold temperatures were the highest of any of the temperatures considered. Nonetheless, the large increase in handling time for *D. pulicaria* at 5 °C changes the conclusions of our investigation of grazing effectiveness both quantitatively and qualitatively. Analysing the independently fit functional responses, we find that the increase in feeding rate between 5 and 10 °C was not
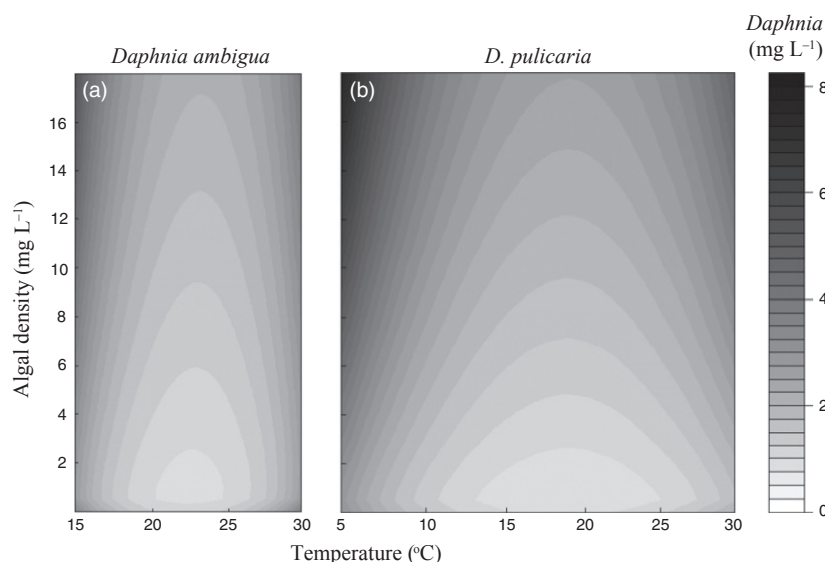


**Fig. 5.** The biomass of *Daphnia ambigua* (a) and *D. pulicaria* (b) required to result in zero net population growth of algae from the temperature-dependent function fits.

rapid enough to outpace the increase in algal growth rate at high algal densities (Fig. S5), causing *D. pulicaria* grazing effectiveness to decline. The cause for the poor fit of handling time at cold temperatures in this study is not clear. Selecting a different functional shape for temperature dependence could decrease the discrepancies, but near temperature extremes, organismal adaptations or changes in behaviour (Heinrich 1974; Jayatilaka *et al.* 2011) could result in systematic biases in temperature-dependent models.

The *Daphnia* biomass necessary to reach ZNPG of algae provides a useful measure of grazing effectiveness, but is also an important metric in itself. When this value is reached in spring in temperate lakes, it marks the maximum extent of the spring bloom, after which the algal population declines and the *Daphnia* population crashes. The specific values that we produce in this study are unlikely to be widely generalizable, as differences in nutrient content and light intensity will alter algal growth rates. Additionally, as the temperature dependence is nonlinear and there are spatial and temporal variations in water temperature, this can become a difficult calculation in complex systems. Nonetheless, in stable lake environments, managers concerned with limiting algal growth to prescribed limits may be able to estimate algal growth *in situ* and use this with the feeding parameters developed here to estimate grazer densities necessary to halt algal growth in their systems. Similarly, this approach should be useful for managing pest populations, allowing managers of greenhouses or agricultural fields to determine the density of predators necessary for biological control of pest outbreaks.

In summer, climate change is pushing maximum temperatures beyond where they reached historically (IPCC, 2013). As water warms beyond 25 °C, it will cause *D. ambigua* and *D. pulicaria* to lose grazing function, while *S. obliquus* is unaffected, allowing algae to proliferate. This could have a myriad of impacts upon freshwater or marine plankton ecosystems experiencing similar changes in species interactions. One troubling ecosystem-level change is the impact of algal blooms on oxygen dynamics. Although algae produce oxygen when photosynthesizing, they are net consumers of oxygen at night and when decomposing (Hallegraeff 1993). Increases in temperature exacerbate the oxygen use of both living and decomposing algal cells, resulting in greater drawdowns of oxygen at higher temperatures (Jewell & McCarty 1971; Lopez-Urrutia *et al.* 2006). The combined effects of an increase in summer algal biomass along with faster metabolism and decomposition from increased temperatures could lead to dramatic oxygen fluctuations.

The fall in algal carrying capacity (*K*) with temperature followed the expectation that the saturating density should decrease with temperature due to greater metabolic demands at high temperatures (Figs 1 and 2b). *K* was the only parameter we analysed that followed the Arrhenius model, showing a consistent impact of temperature, rather

than a hump-shaped relationship. The activation energy of $-0.31$ eV is slightly higher than the average of $-0.71$ eV found by Fussmann *et al.* (2014). Although their analysis consisted of only six studies, of which five were bacterial studies, this indicates that the carrying capacity of *S. obliquus* may be less affected by temperature change than other organisms.

Within the 'biologically relevant' temperature range, our results are generally consistent with the general finding from bioenergetics studies of growth rates (*r*) (Savage *et al.* 2004), carrying capacity (*K*) (Allen, Brown & Gillooly 2002), attack rate (*a*) (Dell, Pawar & Savage 2014) and handling time (*h*) (Fussmann *et al.* 2014). However, as the organisms we are studying regularly experience temperatures ranging from 5 to 30 °C, we extended our temperature-dependent model to this range, requiring a quadratic model to fit the data for all parameters except carrying capacity. By connecting the resource growth rate to the consumption rate, we are able to characterize the temperature and density dependence of the consumer–resource interaction in terms that are important to the population dynamics. Our results show that both differences in the strength of the response to temperature and differences in thermal optima are important for the *S. obliquus–Daphnia* interaction (Dell, Pawar & Savage 2014). Fussmann *et al.* (2014) identified 26 studies that measured the functional response of a consumer or parasite across multiple temperatures. Of these only Durbin & Durbin (1992) measure the growth rate of the resource and, in that case, it was only measured as a part of their methodology for measuring the functional response. Many of the studies note a drop in performance of consumers at high temperatures, but it is not clear how this influences the consumer–resource interaction if performance of the resource is not known.

Differences in thermal tolerances between grazer species will play an important role in determining the impact of warming on consumer–resource interactions and affect their ability to coexist in natural systems. In this study, *D. pulicaria* far outperforms *D. ambigua* at cold temperatures, while *D. ambigua* becomes a more effective consumer as temperatures warm beyond 20 °C. While seasonal variation in temperature may increase the ability of these grazers to coexist, warming that pushes temperate lakes out of cool winter temperatures more quickly and drives summer temperatures into the 25 °C range should favour *D. ambigua* over *D. pulicaria*. Interestingly, in southern North America, *D. ambigua* is facing competition from the invasive *D. lumholtzi*, which has been shown to tolerate temperatures in the 27–30 °C range where *D. ambigua* begins to lose function (Work & Gophen 1999). In Florida, USA, *D. ambigua* has remained the dominant daphnid in all but one of a set 15 lakes, which were recently surveyed (Havens *et al.* 2012), although *D. lumholtzi* has established populations in 10 of these systems. This area is part of what is known as the 'warming hole', which has experienced a slight cooling

over the past 50 years (Meehl, Arblaster & Branstator 2012), leaving open the possibility that *D. lumholtzi* will replace *D. ambigua* if the Southeastern USA begins to warm in coming years (Engel, Tollrian & Jeschke 2012).

Explicitly linking the growth rate of a resource with the functional response of a consumer feeding upon that resource across a range of temperatures is a powerful approach for studying the impact of temperature on consumer–resource dynamics. Detailed laboratory experiments such as this clearly cannot be performed for all consumer–resources pairs that will be impacted by global climate change; however, it would be valuable to conduct similar studies on strongly interacting species in other systems – in particular agricultural pests and their biological-control agents. Pairing the functional response with resource growth rates will allow further modelling work to anticipate the impacts of climate change as well as pinpoint the conditions when the resource is primed for growth or vulnerable to depletion.

Our study reinforces the notion that the impact of climate change upon species interactions will be complex (Angert, LaDeau & Ostfeld 2013), requiring careful study if we want to be able to predict the impact of warming on ecosystem dynamics. By extending our study to temperatures that are experienced by organisms but seldom studied in the laboratory, we revealed important alterations to the strength of interaction between algae and a keystone grazer in temperate lakes. Rather than focusing on equilibrium dynamics, which may not be reached, our approach of relating temperature- and density-dependent growth and consumption rates allows us to examine the transient dynamics, which are critical to the outbreaks of fast-growing populations. While caution must be used when applying temperature-dependent models near temperature extremes, there is tremendous potential for these models to both improve our understanding and increase our predictive power for consumer–resource interactions.

## Acknowledgements

## Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.h5j86 (West & Post 2016).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1**. The parameterization for a dynamic model of the *Daphnia–Scenedesmus* system with an analysis of the transient dynamics of the system.

**Table S1.** Corrected Akaike information criteria ($AIC_c$) for models of algal growth.

**Table S2.** Akaike information criteria (AIC) values for the temperature dependent model fits to the Arrhenius and Arrhenius quadratic models.

**Table S3.** Values of the mortality parameter ($m$) in eqn S1 of *Daphnia ambigua* and *D. pulicaria*.

**Table S4.** Sensitivity analysis of the *Daphnia - Scenedesmus obliquus* dynamic model.

**Fig. S1.** Plot of the possible values for *Daphnia* mortality at 30 °C against the minimum *S. obliquus* density necessary for *Daphnia* persistence.

**Fig. S2.** Phase plane diagram for *Daphnia ambigua* (a) and *D. pulicaria* (b) across temperature.

**Fig. S3.** Simulated maximum extent of algal growth for *Daphnia ambigua* (black) and *D. pulicaria* (red) when growing from a density of 4 mg $L^{-1}$ *S. obliquus* and 10 µg $L^{-1}$ *Daphnia*.

**Fig. S4.** The Holling type II functional response fits using the parameters from the quadratic temperature dependent model for *Daphnia ambigua* (a) and *D. pulicaria* (b).

**Fig. S5.** The biomass of *Daphnia ambigua* (a) and *D. pulicaria* (b) required to result in zero net population growth of algae.