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The temperature independence of interaction strength in a sit-and-wait predator

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Abstract. The strength of interactions between consumers and their resources has important implications for the overall structure and function of food webs. These interactions can change with warming, depending on the foraging mode of the predator. Theory predicts that warming increases foraging velocity in ectotherms, but in a sit-and-wait predator that has zero velocity when foraging, the interaction strength should be temperature independent. Using the protist *Urocentrum turbo* and the sit-and-wait copepod *Orthocyclops modestus*, we tested this prediction by measuring dynamic interaction strengths (effect of a predator on prey population growth rate) and by estimating the parameters of a functional response. Both of these metrics were consistent with the prediction that interaction strength is temperature independent in a sit-and-wait predator. Our results indicate that there may be considerable variability in how warming alters foraging interactions, and estimating the overall effects of climate change on food webs may require consideration of the distribution of foraging strategies and the potential asymmetries that arise with interactions that involve different strategies.

Key words: allometry; body size; climate change; interaction strength; *Orthocyclops modestus*; predator prey interactions; *Urocentrum turbo*.

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INTRODUCTION

The strength of interactions between consumers and their resources strongly influences the structure and function of food webs and the ecosystems in which they reside (Paine 1980, McCann et al. 1998). Interaction strengths are defined and measured in a variety of ways, from the relative effect of a consumer on the resource population abundance to parameters of the functional response (Wootton and Emmerson 2005, Novak and Wootton 2010, Gilbert et al. 2014). Although these different interaction strength metrics integrate different sets of the components that make up a consumer-resource interaction, they all strive to quantify just how

important the interaction is to the flux of energy and materials through a particular link in a food web.

Interaction strengths can be used to predict community properties such as stability and overall function (McCann et al. 1998, Vallina and Le Quéré 2011). Because of this, anything that influences interaction strengths can potentially influence food webs, and it has therefore become important to assess how various abiotic and biotic factors alter interaction strengths. In particular, expectations of increased mean environmental temperature associated with climate change has driven a growing interest in how temperature influences interaction strengths (O'Connor 2009, Rall et al. 2010, Gilbert et al.

2014).

Interaction strengths have at their heart some process that determines how much of a resource can be eaten by a consumer. This process can be described from the consumer's point of view, such as a functional response, or from the resource point of view, such as changes in population growth rate with and without consumers present. Either way, temperature has the ability to alter interaction strengths because of the kinetic effects of temperature on movement rates, at least for ectotherms (Kruse et al. 2008, Englund et al. 2011, Dell et al. 2013). In colder temperatures, organisms are prone to moving more slowly because metabolic processes inside the organism may be slower (Brown et al. 2004, Dell et al. 2011). With warming, biochemical reaction rates may increase, enabling faster movement through the environment and increasing contacts between a consumer and its resource. Not surprisingly then, interaction strengths often increase with warming (Jiang and Morin 2004, O'Connor 2009, Rall et al. 2010, Kratina et al. 2012).

The 'area of capture' parameter a in the functional response (also known as 'attack efficiency' or 'attack rate') typically responds positively to temperature as well, for both parasitoids and consumers, although there is considerable variation in how steeply a increases with temperature and whether it reaches a peak at intermediate temperatures (Ding-Xu et al. 2007, Kruse et al. 2008, Englund et al. 2011). Dell et al. (2013) provided a framework for the area of capture parameter that predicts how it responds to temperature. Building on existing expressions (Aljetlawi et al. 2004), Dell et al. decomposed a into the product of detection area A_d and the mean root square velocity of the consumer V_c and the resource V_r :

$$a = A_d \sqrt{V_c^2 + V_r^2}. \quad (1)$$

By making the velocities increasing functions of temperature, the mean root square velocity increases with temperature and therefore a does as well, depending on whether temperature influences the consumer, the resource, or both and what the foraging strategies are. Sit-and-wait predators have approximately zero velocity while searching for prey at any temperature

(Dell et al. 2013), although they do have a velocity when they relocate to new foraging sites. Thus, the temperature dependence of a should be driven primarily by the effect of temperature on the prey velocity and less so by the effect on predator velocity. If the prey also uses a sit-and-wait strategy, with movements that are primarily relocations between foraging sites, then interaction strengths should be close to temperature-independent. We are unaware of previous studies that have tested this prediction, but it is important to do so because the temperature dependence embedded in Eq. 1 has the potential to be very useful in assessing the effects of warming on food webs.

Eq. 1 also shows that body size may influence interaction strengths via the relationship between body size and movement rates. Area of capture is positively related to consumer body size for a range of organisms (Vucic-Pestic et al. 2010, DeLong and Vasseur 2012a, b), yet for a sit-and-wait predator, body size may have minimal impact unless size also influences detection area. Thus, although size and temperature may both influence interaction strengths, in a sit-and-wait predator we expect neither size nor temperature to have strong effects on the parameter a . In this study, we test the prediction of temperature- and body size-independent interaction strengths in a generalist aquatic predator. We use the sit-and-wait copepod *Orthocyclops modestus* (hereafter cyclops) preying on the 'sit-and-wait' filter feeding protist *Urocentrum turbo* (hereafter *Urocentrum*), both collected from the same pond. *Urocentrum* is approximately stationary when feeding, although it drifts with the water, which means that the cyclops and *Urocentrum* interact primarily when they relocate to find a new food source or when they drift into proximity. Assuming the relocation behaviors are not strongly temperature dependent, the interaction strength between these two species should be insensitive to temperature. Assessing interaction strengths with both functional responses and *Urocentrum* growth rates, we show that temperature and body size have only minor effects on the interaction strength between cyclops and *Urocentrum*.

MATERIALS AND METHODS

Experimental methods

We collected *Urocentrum* and cyclops from a pond at the Spring Creek Prairie Audubon Center near Lincoln, NE. Both species were repeatedly found in the same water sample and the cyclops was readily observed foraging on *Urocentrum* and other protists. We isolated and rinsed these individuals, and then cultured them at room temperature ($\sim 23^{\circ}\text{C}$) in separate dishes in a mixture of filtered water collected from the source pond and liquid protozoa media from Carolina Biological Supply (Burlington, NC, USA).

We initiated 36 replicate populations of *Urocentrum* in 50 mm diameter plastic Petri dishes. We started the populations with four *Urocentrum* collected in a 100 μL -draw from the stock cultures and placed in 5 mL of a media made of 80% 5- μm filtered pond water and 20% liquid protozoa media (1:9 liquid protozoa media to spring water, both from Carolina Biological Supply), inoculated with an assemblage of bacteria acquired from the source pond water. Each replicate population was randomly assigned to a temperature: 18°C , 22°C , or 26°C . We incubated the populations in the dark at their respective temperatures at 70% humidity.

Urocentrum showed a lag phase with little growth for about two days. Therefore, day three was considered the starting point for the experiment. We added one small cyclops randomly to half of the dishes in each temperature on the second day of the experiment (Fig. 1). Using only one predator with a long generation time relative to the prey allowed us to eliminate the effects of interference competition on per capita interaction strengths (DeLong and Vasseur 2011). Some of the populations failed to grow, so instead of six replicates in each predator by temperature combination, we had four replicates without a predator at 18°C and five replicates with and without a predator at 26°C .

Every Monday, Wednesday, and Friday, we counted the *Urocentrum* population under a stereoscopic microscope (Leica M165C). Depending on the population density, we counted cells in the whole dish, half of the dish, or a 0.2-mL sample, and used those counts to calculate the density of the whole dish (DeLong and Vasseur

2012c). These techniques helped us when the amount of *Urocentrum* in a dish was too numerous to count. For whole dish and half dish counts, we placed the dish over a transparent grid and systematically scanned along the grid, counting the *Urocentrum* within the lines as we passed them. The 0.2-mL samples appeared to be under-representing the number of *Urocentrum*, possibly due to behaviors that help them avoid being collected in the pipette, so we developed a regression ($R^2 = 0.87$) allowing us to more accurately estimate density from these smaller samples at the highest *Urocentrum* densities. We calculated this regression using 56 samples, counting both the 0.2-mL samples and the whole dish at the same time. We collected data for two weeks, at which point the populations of all the dishes approached zero and we stopped the experiment.

We also quantified the functional response for cyclops foraging on *Urocentrum*. We placed varying numbers of *Urocentrum* in a drop of media for one hour and a cyclops in another drop of media for two hours and allowed them to acclimate to their randomly assigned temperature (18°C , 22°C , or 26°C). After the two-hour period, cyclops individuals were added to the acclimated *Urocentrum* and allowed to forage at the experimental temperature in their respective incubators for ~ 10 minutes, which was long enough to observe numerous kills. We then counted the remaining number of *Urocentrum* in the dish, calculating the kill rate as the difference in the *Urocentrum* numbers between the start and end of the trial divided by the actual time for each dish. We conducted 24 trials at 18°C and 20 trials at 22°C and 26°C .

Each individual cyclops used in either the population growth or the functional response experiments was photographed with a digital camera (Leica IC80 HD) attached to the microscope. We measured the length of each individual and used the length-weight regression from Alcaraz and Strickler (1988) to convert the length to a mass ($\text{weight (mg)} = 0.055 \times \text{length (mm)}^{2.73}$). We measured individuals used in the functional response experiment prior to use and those used in the population growth experiment after use.

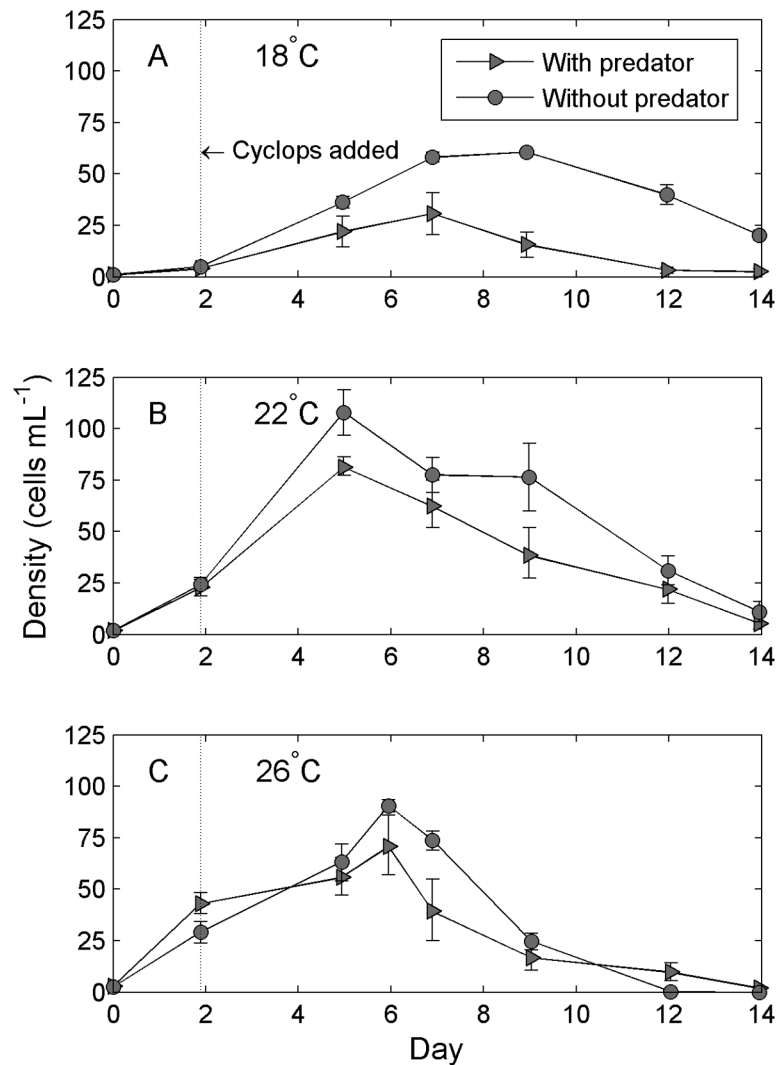


Fig. 1. Population dynamics of *Urocentrum* with and without predators (cyclops) at (A) 18°C, (B) 22°C, and (C) 26°C. Cyclops were added on day 2 (vertical gray line).

Analysis methods

We calculated the interaction strength between the predator and prey in two ways. First we used the dynamic interaction strength (DI_{growth}) described by Novak and Wootton (2010):

$$DI_{\text{growth}} = \frac{\ln\left(\frac{N_{+P,t+\Delta t}}{N_{+P,t}} / \frac{N_{-P,t+\Delta t}}{N_{-P,t}}\right)}{P\Delta t} \quad (2)$$

where N is the abundance of the prey (*Urocentrum*) and P is the abundance of the predator (=one cyclops in this case), t is the initial time, and Δt is the change in time between successive measurements. We calculated DI_{growth} for the

mean growth rates with and without predators at each temperature, but to get confidence intervals on the interaction strength, we used a Monte Carlo approach. We randomly chose individual replicates for a particular temperature with and without predators and calculated DI_{growth} for each pair. We repeated this process 1,000 times and used the 2.5 and 97.5 percentiles to determine the 95% confidence intervals on the interaction strength at each temperature.

We assessed the body-size dependence of DI_{growth} by calculating the difference between the growth rate of each replicate population with

a predator and the mean growth rate for all the replicates without a predator for each temperature. This procedure yielded a relative DI_{growth} metric that could be compared across predator replicates and temperatures. We then assessed whether the body size of the predator was correlated with DI_{growth} overall or within temperature using Pearson correlations.

We quantified a second type of interaction strength by estimating parameters of the functional response. Copepods often show a standard Type II (saturating) functional response relating the kill rate f to prey density N : $f = aN/(1 + ahN)$, where a is the area of capture and h is the handling time (Wickham 1995). Because of prey depletion during the course of the experiment, we used a modified version of the random predator equation to analyze consumption rates (Rogers 1972, Bolker 2011):

$$N_e = N_0 - \frac{W\left(ahN_0e^{-a(t-hN_0)}\right)}{ah} \quad (3)$$

where N_e is the number of resource items eaten in time t , N_0 is the initial density of resource, and W represents the Lambert W function. We used the *fit* routine in Matlab to fit Eq. 3 to our data and retrieve estimates of the parameters a and h (DeLong and Vasseur 2013). We assessed differences in the parameters across temperatures by comparing 95% confidence intervals. To investigate the body size dependence of the functional response, we set $a = a_0M^\alpha$, where a_0 is the intercept, M is the mass of the cyclops, and α is a scaling exponent (DeLong and Vasseur 2012a, b). We again used the *fit* routine in Matlab to fit Eq. 3 to both the prey density and body size data. All other analyses also were conducted in Matlab.

RESULTS

In the population growth experiment, all populations showed a boom-bust dynamic, consistent with our observations of *Urocentrum* at the collection site (J. P. DeLong, *personal observation*; Fig. 1). Cell densities increased for about 4–6 days and then decreased until the populations went extinct in both the predator and non-predator treatments. *Urocentrum* reached its highest densities at 22°C, followed by 26°C and then 18°C. Populations with predators typically were smaller and usually

grew more slowly in the presence of predators.

Before the cyclops were added, growth rates of *Urocentrum* were lowest at 18°C but were about the same at 22°C and 26°C (Fig. 2A). After the cyclops were added, growth rates declined with temperature and were generally lower in the presence of the predator (Fig. 2B). Most importantly, there was neither a significant difference in DI_{growth} among the temperatures or any suggestion that interaction strengths increased with temperature (Fig. 2C). There were no significant correlations between the relative DI_{growth} and body size within any temperature or for all observations combined (all $r > -0.71$ and $p > 0.11$).

The functional response experiment showed that the cyclops foraging rate increased with *Urocentrum* density, but it was very difficult to detect a saturation point (Table 1). This indicates handling times for the cyclops were very small, which is consistent with our observation that cyclops simply ingests *Urocentrum* whole, in one quick movement. There was no significant difference between the area of capture parameter (a) across the temperatures 18°C, 22°C, and 26°C (Fig. 3A, Table 1). In contrast to our results for DI_{growth} , however, a was significantly negatively related to body size with an exponent $\alpha = -0.24$ (Fig. 3B, Table 1). Because handling time was difficult to estimate, we were unable to make comparisons across temperature for this parameter.

DISCUSSION

We tested the recent theoretical prediction that interaction strengths of sit-and-wait predators should not increase with warming (Dell et al. 2013). We measured the interaction strength of the sit-and-wait predator cyclops foraging on the filter-feeding protist *Urocentrum* using dynamic changes in abundance and the functional response. Consistent with this theory, neither of these metrics varied with warming. This finding differs, however, from typical findings in both empirical and theoretical studies that find or propose that interaction strengths increase with temperature (Jiang and Morin 2004, Vasseur and McCann 2005, Ding-Xu et al. 2007, Kruse et al. 2008, O'Connor 2009, Rall et al. 2010, Englund et al. 2011, Kratina et al. 2012). Our results therefore

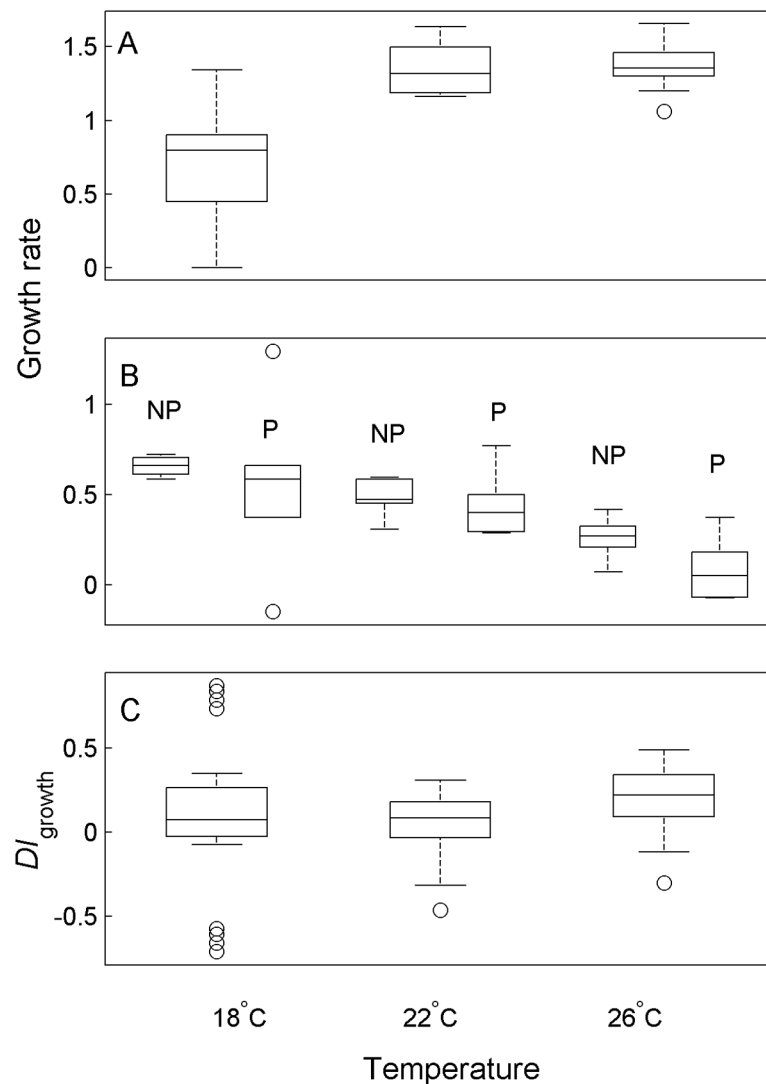


Fig. 2. Population growth rates and interaction strengths (DI_{growth}) between cyclops and *Urocentrum* at 18°C, 22°C, and 26°C. Population growth rates before the cyclops were added (A) were lower at 18°C than at 22°C and 26°C. After cyclops were added (B) growth rates declined and were generally lower in the presence of the predator (P) than with no predator (NP). Interaction strengths did not differ among temperatures (C).

point to the relevance of foraging mode and understanding the mechanisms underlying the temperature dependence of interaction strengths when attempting to forecast the effect of climate warming.

Interaction strengths may increase with body size (Vucic-Pestic et al. 2010, DeLong and Vasseur 2012a). We therefore assessed whether cyclops body size could account for some of the variation in interaction strengths independent of the effect of temperature. In the case of the

dynamic interaction strength (DI_{growth}), there was no clear effect of size. In contrast, we found that body size had a negative effect on the area of capture parameter (a) in the functional response (Fig. 3B). We speculate that this surprising outcome may be related to behavioral changes associated with maturation, perhaps inducing a slowing down of foraging intensity, although we have no measurements to confirm this possibility. Alternatively, *Urocentrum* may be less optimal as prey for larger cyclops, diminishing the rate of

Table 1. Parameter estimates for the functional response of cyclops on *Urocentrum*. Parameters are estimates with 95% confidence intervals in parentheses. At 22°C and 26°C, the fit was unable to converge on a handling time.

Functional response	Area of capture, a (mL pred ⁻¹ day ⁻¹)	Mass-dependent area of capture, a_0 (mL pred ⁻¹ day ⁻¹)	Scaling parameter for area of capture, b	Handling time, h (day)	R^2
By temperature					
18°C	0.030 (0.0012 to 0.058)			0.24 (-0.44 to 0.91)	0.51
22°C	0.036 (0.026 to 0.047)				0.53
26°C	0.036 (0.029 to 0.042)				0.79
By body size		0.011 (0.0016 to 0.019)	-0.24 (-0.41 to -0.058)		0.59

attacks (Vucic-Pestic et al. 2010). In either case, the role of body size in setting foraging rates in this species may be more complicated than classic allometric theory suggests (Yodzis and Innes 1992).

Peak *Urocentrum* densities were highest at the intermediate temperature (Fig. 1). This finding contradicts recent theory about the relationship between abundance and temperature. With a given resource supply, warming is expected to lower abundances because of increasing individual metabolic demand (Marquet et al. 2004, Brown et al. 2004). In many food webs, however, warming may alter the resource base as well. In this study, it is possible that the bacterial food base for *Urocentrum* was optimal at the intermediate temperatures, promoting a high abundance of *Urocentrum* even with a relatively high metabolic rate. In fact, it seems clear that the indirect effects of temperature on prey productivity were important for *Urocentrum*, as the temperature dependence of their population growth rate changed qualitatively after the first couple of days (Fig. 2A, B).

Our data show no sign of an effect of temperature on interaction strengths between *Cyclops* and *Urocentrum*, and this is consistent with recent theory (Dell et al. 2013). It is possible, however, that a wider range of temperatures would more thoroughly reveal the effects of temperature on the interaction strength in this predator-prey pair. Another potential limitation in our study is the level of precision in our measurements. *Cyclops* foraging rates can be quite variable (Fig. 3A), which would have generated error in our measurements of both

the dynamic interaction strength and the functional response parameters (Table 1). Despite this noise, however, there is no suggestion of an increase in interaction strength with temperature in either interaction strength metric, even though measurements span 8°C, which for other small crustaceans can cover almost the entire rising portion of a thermal performance curve (Fey and Cottingham 2012). In addition, R^2 values for the fits of Eq. 3 to foraging data were reasonably good (>0.5), and the data were sufficiently precise to detect a strong effect of body size in the functional response. Thus, we suggest that the lack of a temperature effect is unlikely to be due to insensitivity in our experiment but rather, as suggested by theory, due to the limited effect of temperature on the searching velocity of the *Cyclops* and the *Urocentrum*.

Temperature may alter the structure and function of food webs by altering interaction strengths between species in a food web (Rall et al. 2010). There is concern that climate warming will strengthen predator-prey interactions and therefore negatively alter food web stability and diversity (O'Connor et al. 2009). The mechanism by which temperature alters interactions, however, is crucial. Dell et al. (2013) suggest that the effect of temperature on velocities is the basis for changing the area of capture parameter of the functional response. This theory also suggests that sit-and-wait predators like cyclops should not experience strong increases in interaction strengths with warming unless their prey velocities also increase. Our results are consistent with this prediction and call attention to potential asymmetries in food web responses to tempera-

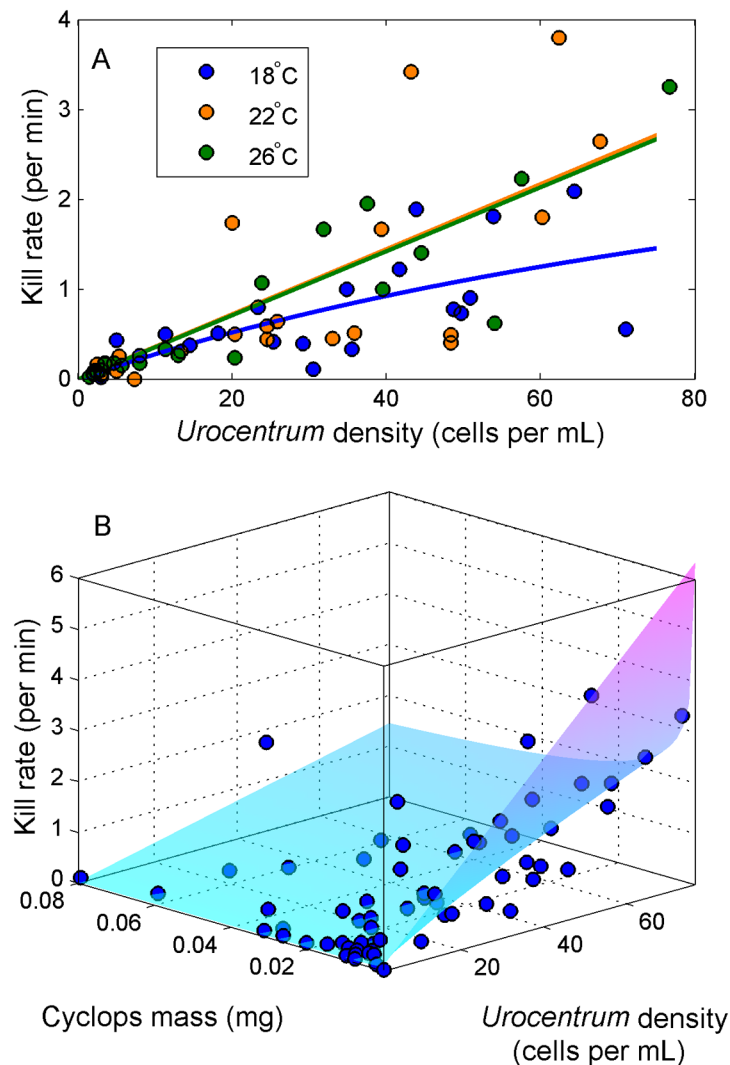


Fig. 3. Functional responses of cyclops foraging on *Urocentrum* at three temperatures. Functional response parameters did not differ by temperature (A), but foraging rates declined with body size (B). Notice that in panel A, the lower curve for 18°C was generated not by a difference in area of capture but in having a higher handling time.

ture. While some interactions may get stronger, others may not change, potentially changing the structure of the food web and ultimately its stability or diversity. Thus, understanding the distribution of foraging modes in a food web may be an important part of forecasting the effects of climate change on diversity.

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