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PRIMARY RESEARCH PAPER

Temperature and prey morphology influence attack rate and handling time in a predator–prey interaction

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Abstract Functional responses describe how the proportion of prey consumed by a predator changes as prey density changes. For predators consuming a single prey species, functional responses are determined by two parameters: attack rate and handling time. These parameters may be influenced by morphological and behavioral differences in prey stemming from interspecific or environmentally-driven processes. Here we investigate how interspecific morphological differences and changes in movement rate impact a predator's functional response. Using a flatworm predator (*Stenostomum virginianum*) consuming either *Paramecium aurelia* or *P. multimicronucleatum* we show that movement rate changes significantly with temperature, leading to changes in attack rate. We also show how body size affects the amount of time predators require to handle prey. We fit a mechanistic functional response model to demonstrate how changes in attack rate and handling time affect overall rates of predation. Our results demonstrate that *S. virginianum* attack rates are greater for *P. aurelia* than *P. multimicronucleatum*. In addition, higher temperature increases *S. virginianum* attack rates on both species, and reduces the time needed to handle *P. aurelia*. These differences in predation rate appear related to prey species' traits, and the temperature-mediated changes in these traits, highlighting the complex processes that underpin predator–prey interactions.

Keywords Functional responses · Predator prey interactions · Abiotic factors · Prey traits · Paramecium · Stenostomum

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Introduction

Consumptive interactions, such as predators ingesting prey, drive the structure of ecological communities and the functions they perform (Paine, 1976; Bertness & Ellison, 2016). The persistence of consumers, and therefore their populations, is dependent on their ability to find and handle food items (Jeschke et al., 2004; Haddaway et al., 2012). Given the importance of consumptive interactions, it is critical to understand how abiotic features of the environment, together with prey traits, influence predator ingestion rates. In many cases, factors such as sunlight (Jeschke et al., 2002; Chase & Knight, 2003) and chemical concentrations

(Chivers & Mirza, 2001; van Uitregt et al., 2012) impact the rates at which predators capture their prey. These differences in the rates at which predators consume prey can determine whether predators and prey can co-exist, or whether over-exploitation of prey by predators leads to the extinction of prey and the collapse of food webs (Hammill et al., 2010b). Understanding the factors that drive rates of prey consumption is therefore critical given their influence on food web stability.

The rate at which predators consume prey can be described using mechanistic models (Jeschke et al., 2002). These models use biologically relevant parameters to describe the processes that predict prey consumption. If a mechanistic model can be fit to data on a predator–prey interaction across a range of conditions (morphological characteristics, densities, and environmental conditions), it indicates that such a model is appropriate in describing the system. This is demonstrably true for Holling's Type II and Type III functional response models, through which prey consumption by predators is commonly described (Holling, 1959; Piersma et al., 1995; Jeschke et al., 2004; Englund et al., 2011). In many mechanistic models, attack rate (a) describes the frequency with which a predator encounters and begins consumption of a prey, while handling time (h) describes the time required by a predator to subdue and consume an individual. A Type III model indicates a variable rate of attack over increasing prey density, largely because predators are unable to successfully pursue prey at low densities due to prey refuge. The shape of the response is therefore sigmoidal (Hammill et al., 2010b). In contrast, a Type II model assumes constant attack rate across prey densities, meaning that prey face the greatest risk of consumption at their lowest densities. In both models, at high prey densities the number of prey consumed becomes constant as all a predator's time is spent handling prey, limiting overall consumption (Jeschke et al., 2002). Intuitively, attack rates and handling times are related to the size (related to detectability) and rate of movement (related to encounter rate) of the organisms involved. For gape-limited predators, changes in the size of prey has been shown to alter the handling time, as larger prey may take more time to consume or be more difficult to subdue (Hammill et al., 2015a).

Basic prey attributes, such as size and rate of movement, vary under different environmental conditions. For example, poikilothermic species experience reductions in the rate of movement and metabolic demand as temperature drops (Petchey et al., 1999). Similarly, predator traits related to prey consumption also vary with environmental conditions. For example, organisms under cold conditions may experience reduced metabolic rates, requiring more time to be able to consume and digest prey (Hylander et al., 2012), increasing handling times. Predator attack rate and handling time can also be heavily influenced by prey size (Hammill et al., 2010b) and movement rate (Beveridge et al., 2010), as well as fundamental aspects of the predator itself. Therefore, attack rate and handling time may vary with respect to environmental factors. The impact of changes in temperature has been shown to influence the shape of functional responses across a broad variety of taxa, with attack rates generally showing a hump-shaped response to increasing temperature, i.e. highest at intermediate levels (Uiterwaal & DeLong, 2020). In addition, prey size variability by temperature indicates that smaller organisms may be harder to find but require less time to subdue (Connell, 1961), while gape-limited species may be unable to consume some prey due to their size (Hammill et al., 2009).

While the role of temperature and morphology on the shape of functional responses has received substantial attention previously (Uiterwaal & DeLong, 2020), the way temperature alters predator and prey morphological traits and how these trait changes are related to the shape of the functional response has received considerably less attention. In previous investigations into the role of temperature in altering the functional response, comparisons between the magnitude of changes in species traits and values of a and h are often not explicitly made. Comparing the magnitude of species' trait changes to changes in a and h may increase our overall mechanistic understanding of the role of traits and temperature.

We used a predator–prey pair consisting of the flatworm *Stenostomum virginianum* Nuttycombe, 1931 consuming either *Paramecium aurelia* Ehrenberg, 1838 or *Paramecium multimicronucleatum* Powers & Mittchell, 1910. *Stenostomum virginianum* are small (< 1000 μm) microturbellarian flatworms and form part of a taxonomic group that are found in inland waters throughout the world (Damborenea et al., 2011; Dumont et al., 2014). The genus consumes a variety of unicellular organisms including bacteria

and ciliates, as well as small multicellular species such as rotifers and cladocerans (Nandini et al., 2011; Núñez-Ortiz et al., 2016). *Stenostomum virginianum* actively hunt for *Paramecium* spp. and act as dominant predators in the macrobenthos. Due to their wide diet breadth, *S. virginianum* play an important role in structuring the food webs in which they exist (Forbes & Hammill, 2013). *Stenostomum virginianum* feed by slowly moving through their environment and engulfing small prey (Nuttycombe & Waters, 1935). As the species relies on engulfing prey, it is gape limited, and unable to consume prey too large to be sucked into its pharynx (Nuttycombe & Waters, 1935; Núñez-Ortiz et al., 2016). Although *S. virginianum* are active hunters, they have no method of perceiving specific prey individuals from a distance. Therefore, they rely on random encounters to sense prey via sensory cells near the mouth (Nuttycombe & Waters, 1935). *Paramecium* spp. are single celled ciliate protists that consume bacteria and micro ciliates. They have a pan-global distribution (Komala & Pryzbos, 1984) and form an important component of aquatic biofilms (Weitere et al., 2018). It has been shown that *Paramecium* spp. are capable of sensing the presence of *S. virginianum* through the detection of predator-specific chemicals but are unable to sense specific predators until physical contact is made. *Paramecium* spp. species are readily consumed by *S. virginianum* with consumption rates often following a Type II functional response (Núñez-Ortiz et al., 2016), and may be driven to extinction by *S. virginianum* predation (Hammill et al., 2015b). *Paramecium aurelia* represents the smaller of the two species, a morphological characteristic that may make it more susceptible to predation by gape-limited *S. virginianum.*

Our goal was to investigate how components of the functional response, and therefore prey consumption rates, are influenced by changes to behavior and morphology. We fit a Type II functional response model that includes prey depletion (Real, 1977) to quantify attack rates and handling times under different temperature and prey size conditions. Changes to the values of the mechanistic parameters within the functional response model can then be compared to measured morphological and behavioral changes to determine the relationships between changes to traits and consumptive interactions.

Methods

Prior to being used in the experiments, all *Paramecium* spp. were cultured in 200 mL Mason^{TM} jars containing media produced by adding 1 gL^{-1} protist pellets (Carolina Biological Supply, Burlington NC) to Arrowhead^{TM} mineral water (San Bernardino, CA). *Stenostomum virginianum* were cultured in 100 mm petri dishes containing the same media and were sustained by adding *P. aurelia* and *P. multimicronucleatum* twice a week. All species had been cultured in the laboratory for over 12 months before use in experiments. *Stenostomum virginianum* were starved for 24 h before use.

The movement rate of both predators and prey was calculated using video analysis. For each video, the organisms were placed in a 100 mm petri dish and videoed from above using an Omano stereomicroscope (microscope.com) connected to a 1080p 60 fps digital camera (Amscope.com). Each species was recorded singly. For each video, organisms were introduced into the petri dish and allowed 30 s to settle prior to the start of recording. Two-minute videos were captured, and movement rate was calculated by tracking the distance travelled by individuals in ImageJ [Rasband, (n.d.)] and dividing the distance travelled by the time recorded. For each organism, we tracked the movement rate of eight to ten individuals at two temperatures (14°C and 19°C). These temperatures were selected as they are within the range of summer temperatures experienced by local water bodies from where the predators were collected. Populations of *Paramecium* spp. and *S. virginianum* are most abundant during the summer months (Hammill – *personal observation*), so we selected 14°C and 19°C as they spanned a reasonable range of temperature, but did not cause thermal stress or torpor in our study species.

Morphometric differences between species and within species at different temperatures were quantified using an Olympus BX40 inverted lens microscope attached to the same digital camera. Organisms were photographed, and body length was measured by digitizing the photographs using ImageJ. Differences in movement rate and body size were analyzed using a 2-way ANOVA and a post-hoc Tukey's test to look for significant differences among treatments.

We used a 2 × 2 factorial cross to quantify how changes to temperature and prey species affected the

predator's functional response. The four treatment level combinations were created by crossing temperature (14°C and 19°C) and prey species (*P. aurelia* and *P. multimicronucleatum*). Each experimental replicate was prepared by placing 260 µL of 0.1 gL^{-1} protist media into the well of a 24-well plate. We used a total of eight different prey densities (3, 5, 10, 15, 20, 30, 40, 80) which were decided upon following the results of pilot experiments that indicated the range was suitable to identify maximum consumption rates for all species, but also contained enough replicates at low densities to allow Type II or Type III functional responses to be distinguished. Each density:temperature:prey species combination was replicated five times. Additionally, we performed five predator-free control trials for each *Paramecium* spp. at each temperature to ensure that reproduction, mortality and counting errors were not large enough to affect results and that the collection and counting of the prey species was sufficiently accurate. We counted the number of individuals remaining at the end of the predator-free control runs and used an ANCOVA to test if there was a significant difference between the densities of individuals at the end of our control trials and the densities offered in the replicates containing predators. Within this ANCOVA, we used the number of *Paramecium* spp. we assumed we had introduced (i.e. our intended density) as a descriptive variable, and the number counted at the end as our response. We included a binary covariate to denote whether the replicate was a "control" or a "predator" trial. For the controls, the response was the actual number of *Paramecium* spp. counted at the end of the five control trials, for the predator trial we used the number we assumed we had introduced as the response (e.g. for trials with an intended density of 15, we used "15" as the response value). Through this method, we were able to quantify whether the amount we assumed we had introduced into the predator trials was significantly different from what we had actually introduced if the covariate was significant.

Using a microscope and pipette, the appropriate number of *Paramecium* spp. were collected and placed in each well, and then extra media was added to fill each well to 500 µL. After five minutes settling time, a single *S. virginianum* in 20 µL was added to each well. The plates were then incubated at either 14°C or 19°C for four hours, giving sufficient time for consumption to take place but avoiding excessive time that would cause reproduction in *Paramecium* spp., or the induction of anti-predator morphological changes (Hammill et al., 2010a). At the end of the experiment Lugol's solution was used to kill all organisms. Using a microscope, the number of *Paramecium* of the given species that were not consumed were counted and recorded.

We used our empirical data to parameterize the following functional response equation (Holling, 1959) for the *Paramecium* spp. at the two different temperatures:

$$f(N) = \frac{T}{h + (\frac{1}{aN^q N})}$$

Here, $f(N)$ is the number of prey eaten in time T, N is the number of prey at the start of the experiment and h is the handling rate. Within this model, the variable q within the attack rate term aN^q (Real, 1977) determines the functional response type: when q is 0, the equation is a Type II functional response and the attack rate a is the same across prey densities. When $q > 0$, the equation is a Type III response and the attack rate increases with prey density. Following the consumption of a prey item, the number of prey items decreases, meaning prey density is non-constant. To overcome this issue, we used a numerical integration of declining density to quantify the true proportion (and therefore number) of prey consumed. Use of this method has been made publicly available by Ben Bolker (Bolker, 2012). The model was fit to the data using the mle2 function (maximum likelihood estimator) in R. This found the best parameter values (h, a, and q) according to the maximum likelihood method. We quantified the form of the functional response (either Type II or Type III) by looking at whether parameter q significantly differed from 0, and also by calculating AIC values for models with and without the N^q term in the model. After we ascertained the functional response type, parameter estimates for a and h were compared across treatment level combinations to understand how changes to prey morphology and movement rate altered the shape of the functional response.

Results

In terms of *Paramecium* spp. size, we found a significant temperature:species interaction ($F_{(1,29)} = 68.53$, $P < 0.001$) indicating the relationship between size temperature differed for the two species. *Paramecium multimicronucleatum* were 36.12% ± 3.6% (mean and standard error) smaller at 19°C compared to their body length at 14°C ($P < 0.001$, post-hoc Tukey's test, Fig. 1a), while *P. aurelia* showed no difference in body length at the two temperatures ($P = 0.95$, post-hoc Tukey's test, Fig. 1a). Across all temperatures, *P. aurelia* were 55.0% ± 15.31% (mean and standard error) smaller than *P. multimicronucleatum* ($P < 0.001$, post-hoc Tukey's test). The length of *S. virginianum* was 27.72% ± 7.68% (mean and standard error) greater at 19°C compared to at 14°C ($F_{(1,15)} = 13.97$, $P = 0.002$, Fig. 1a). Temperature also increased the movement rate of both prey species, although we found no temperature:species interaction ($F_{(1,\ 32)} = 1.03$, $P = 0.32$) indicating the effect of temperature was not different between the two species. At 19°C, *P. multimicronucleatum* moved 17.76% ± 13.07% (mean and standard error) faster than at 14°C ($P = 0.036$, Post-hoc Tukey test, Fig. 1b). The movement rate of *P. aurelia* was 36.67% ± 12.09% (mean and standard error) greater at 19°C compared to 14°C ($P = 0.036$, Post-hoc Tukey test, Fig. 1b). At 19°C, *P. multimicronucleatum* moved 24.16% ± 7.21% (mean and standard error) faster than *P. aurelia* ($P < 0.001$, post-hoc Tukey's test, Fig. 1b). At 14°C, we found no difference in movement rates between the two *Paramecium* species ($P = 0.26$, post-hoc Tukey's test, Fig. 1b). The movement rate of *S. virginianum* had no significant change with temperature ($F_{(1,14)} = 2.72$, $P = 0.12$, ANOVA Fig. 1b).

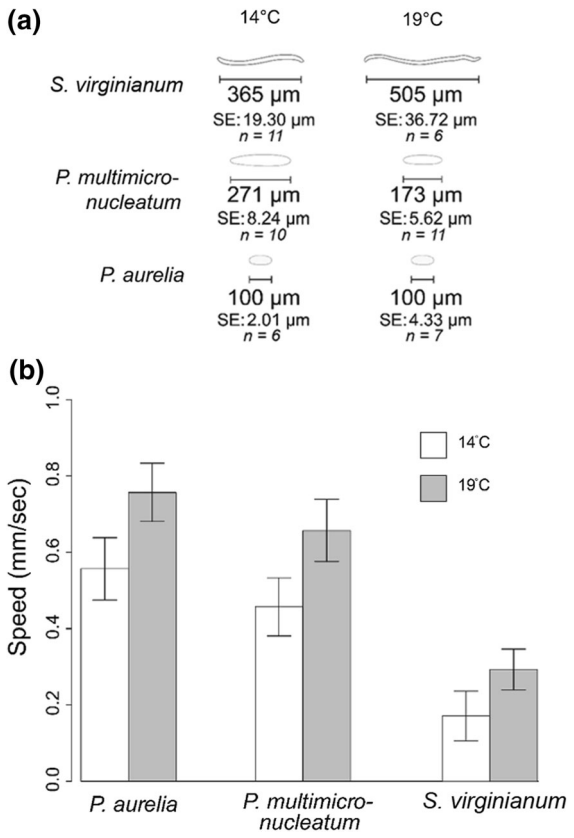

Fig. 1 **a** body length differences among the two prey (*Paramecium ssp.*) and the predator (*S. virginianum*) species at 14°C and 19°C. **b** changes in the movement rate among the two prey and the predator species at 14°C and 19°C. Error bars indicate standard errors

We observed no significant differences between *Paramecium* spp. densities at the end of our control trials and the densities we assumed we introduced into the replicates containing predators (ANCOVA, for all species at all temperature, covariate $P > 0.05$). This means that densities at each species:temperature:density combination were not significantly different from what we had intended them to be. We can therefore have confidence that counting errors during the inoculation phase, and *Paramecium* spp. reproduction within the experimental trials themselves, did not confound our results.

In terms of the Type of the functional response, we found that the standard error estimates for parameter q included zero for both species at both temperatures (Table 1), indicating that predator consumption rates were best described with a Type II functional response. In addition, AIC values for models containing the N^q terms (i.e. Type III) were 432.90 and 274.02 for both species at 14°C and 19°C respectively, but were 428.39 and 266.87 when q was 0, indicating a Type II response was a more parsimonious fit to the data. Attack rates for *S. virginianum* consuming *P. multimicronucleatum* were 86.74% ± 12.32% (mean and standard error) lower than when the predators were consuming *P. aurelia* (mean difference between the species at each temperature, Fig. 2; Table 1). However, attack rates for *P. multimicronucleatum* at 14°C were 56.72% ± 16.42% (mean and standard error) lower than at 19°C. Attack rates for *S.*

Table 1 Type II functional response parameters by temperature and species

Temperature—prey species	Type II or II (q)	SE	Attack rate (a)	SE	Handling time (h)	SE
14°C—*P. aurelia*	0.021	0.037	0.242	0.055	0.123	0.032
14°C—*P. multimicronucleatum*	0.035	0.05	0.029	0.006	0.0001	0.113
19°C—*P. aurelia*	0.05	0.036	0.461	0.063	0.034	0.009
19°C—*P. multimicronucleatum*	-0.027	0.039	0.067	0.016	0.104	0.087

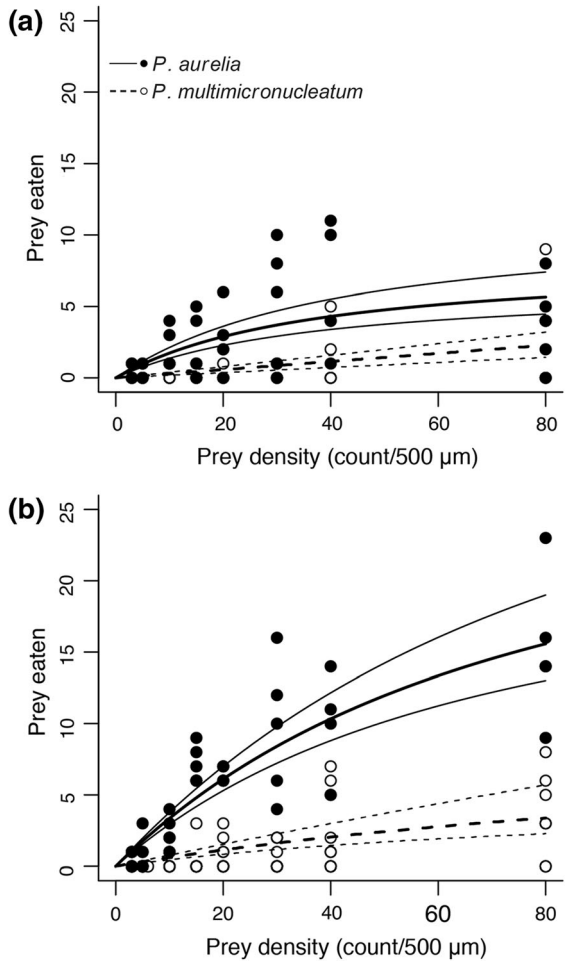

Fig. 2 Changes in temperature and interspecific differences in prey traits lead to alterations to the relationship between prey density and prey ingestion rates. Type II functional response curves are used to describe how the ratio of prey eaten changes with prey density at **a** 14°C and **b** 19°C. Central lines represent model outputs, thinner lines represent model standard errors. We performed five replicates of each species:temperature:density combination, in instances where five points cannot be observed, overlapping has occurred

virginianum consumption of *P. aurelia* increased by 47.51% ± 10.30% when temperatures were increased from 14 to 19°C (Fig. 2; Table 1). In considering handling time, *S. virginianum* predators on average took 83.61% ± 15.57% (mean and standard error) less time to handle *P. aurelia* than they did *P. multimicronucleatum* (Fig. 2; Table 1). Changes in temperature were associated with changes in handling time for *P. aurelia,* with predators taking 72.36% ± 16.67% (mean and standard error) more time to handle *P. aurelia* at 14°C (Fig. 2; Table 1). We found no differences in handling time for *P. multimicronucleatum* between temperatures (Fig. 2; Table 1).

Discussion

Changes in the morphological and behavioral traits of prey have the potential to impact different components of the functional response. Here we found that interspecific differences in prey length and environmentally-driven changes in movement rate were associated with changes in the components of a predator's functional response (Haddaway et al., 2012).

We found clear differences in *S. virginianum*'s attack rate between the two species of *Paramecium.* Due to the similarities in the morphological structure of *Paramecium* spp., this difference in attack rate is likely attributable to differences in body size (Hammill et al., 2010b; Kalinoski & DeLong, 2016). Although attack rates have been observed to be greater for larger prey items since larger individuals are easier to detect (Chang & Hanazato, 2005; McCoy et al., 2011), attack rates have been seen to decline when prey are excessively large compared to their predators (Aljetlawi et al., 2004). In the current study, attack rates when predators were offered *P.*

multimicronucleatum were generally at least one order of magnitude lower than when predators were consuming *P. aurelia*, and the proportion of *P. multimicronucleatum* consumed was generally very low, suggesting that that they are not a preferred prey item (Elkinton et al., 2004). Previous studies using a range of prey species have demonstrated that prey size, rather than taxonomy, is a major driver of consumption rates in *S. virginianum* (Núñez-Ortiz et al., 2016), with prey greater than the gape limit of *S. virginianum* not being consumed. Across both *Paramecium* we observed increased attack rates as temperatures increased. Since the movement rate of *Paramecium* spp. increases with temperature (Glaser, 1924), increased temperature led to more encounters between predator and prey (Kalinoski & DeLong, 2016). For *P. aurelia,* we found that the magnitude of increase in attack rate (47.51% ± 12.79%) associated with increased temperature was within one standard error of the increase in movement rate associated with higher temperatures (36.67% ± 12.09%). This agreement between increases in movement rate and attack rate for *P. aurelia* highlights the relationship between movement rate and rates of encounter. However, in the case of *P. multimicronucleatum,* the increase in attack rate associated with increased temperature was much greater than the increase in movement rate and may be related to the reduction in size in *P. multimicronucleatum*, and the increase in *S. virginianum* size observed at higher temperatures. As *S. virginianum* are gape limited predators (Hammill et al., 2010b), the decreased size of *P. multimicronucleatum* observed at 19°C may reduce the chance that they are rejected by *S. virginianum* following an encounter, leading to increased attack rates. In addition, the larger body size of *S. virginianum* at 19°C may increase the size of its gape, increasing its ability to ingest *P. multimicronucleatum.* This role of temperature in changing the body size of both predators and prey substantially alters body size ratios. The change in the relative body sizes of predators and prey has been shown to influence functional responses (Kalinoski & DeLong, 2016; Núñez-Ortiz et al., 2016; Uiterwaal & DeLong, 2020) and in the current study, a larger body size in predators relative to prey appears to make prey more susceptible to predation. The data across both *Paramecium* spp. therefore indicate that temperature may influence predation rates not only by altering encounters (Kalinoski & DeLong, 2016), but also through changing morphological traits that reduce the relative body size of prey increasing their suitability for predators (Aljetlawi et al., 2004). These morphological changes represent a mechanism that highlights a potential indirect role of temperature in influencing predation rates.

Previous studies have shown that increased temperatures bring about increased metabolic rates (Clarke & Fraser, 2004), potentially explaining the decrease in handling time between the two temperatures when *P. aurelia* was the prey. A major assumption of Type II functional responses is that the predator continues to search for food immediately following consuming a prey item, which may not occur if predators become satiated. At 14°C predators may be able to consume sufficient *Paramecium* spp. to fulfill their metabolic demands and become satiated, i.e. their consumption rates exceed their maximum metabolic processing rates. At this point, predators may cease hunting as they are unable to process the food they catch, which leads to higher overall handling times. However, should they have higher metabolic rates at higher temperatures, their rates of metabolic processing may be greater, meaning they can consume more prey prior to becoming satiated, and reducing handling times. While this reasoning provides a potential explanation for our observed results, and has been suggested as an explanation for inverse relationships between temperature and handling times previously (McCoull et al., 1998; Jalali et al., 2010), we did not measure metabolic processes in either predator or prey, and this reasoning is therefore purely speculative.

In contrast to *P. aurelia*, a large increase in handling time was observed with *P. multimicronucleatum* as temperatures increased. This is likely explained by the near-linear relationship of *P. multimicronucleatum* density and prey consumed, causing an abnormally low handling time, which in turn may be related to the differences in size observed for *P. multimicronucleatum* at different temperatures. At 14°C, attack rates for *P. multimicronucleatum* were very low, indicating they may be rejected as potential prey (Aljetlawi et al., 2004). However, at 19°C *P. multimicronucleatum* decreased in size, which may have made them a more attractive prey item for gape limited predators, leading to increased attack rates (Kalinoski & DeLong, 2016). We suspect therefore that the handling time for *P. multimicronucleatum* at

14°C is not near-zero, but that given the very low attack rates the handling time is very difficult to calculate. Due to this conclusion, the handling time change of *P. aurelia* is more representative of how attack rates are influenced by temperature in this predator–prey interaction.

In term of generality and applicability to other predator–prey interactions, our results highlight how temperature and changes in morphology affect components of a functional response in a relatively simple system. Predators in our system require physical contact in order to detect their prey (Nuttycombe & Waters, 1935; Núñez-Ortiz et al., 2016), making it difficult to assess prey quality and avoid attacking inferior prey (Wise & Toft, 1999). Our experiment also utilized a single predator per trial for the function response experiment, making it impossible to quantify how intra-specific interference among predators contributes to consumption rates (Skalski & Gilliam, 2001; Kratina et al., 2009). In nature, predator–prey pairs rarely exist in isolation, and are embedded in a diverse community with multiple trophic and competitive links (McCann, 2000). The presence of other species in the community, can lead to prey switching by predators (Vallina et al., 2014) while unpalatable "non-prey" species have been shown to reduce consumption rates and alter the shape of functional responses (Kratina et al., 2007; Hammill et al., 2015b). Both of these mechanisms can reduce prey extinctions and increase overall community stability. Within our simplified system, we are unable to assess the impact of these community-level processes, and quantify their effects on stability. What we are able to show however, is how changes in temperature may alter predator consumption rates, and suggest that overexploitation of prey by predators may be more likely at higher temperatures.

The results we present here contribute to the understanding of the relationships between environmental factors, prey traits, and trophic interactions in simple food webs. The differences we observe in prey morphology and movement rate, both interspecific and in response to environmental change, indicate how changes to prey traits affect trophic interactions. These interspecific discrepancies in traits and their associated alterations in predation may help explain differences in species distributions observed in nature in response to differences in predation (Wellborn et al., 1996; Chesson & Kuang, 2008; Siepielski et al., 2011; Garcia & Mittelbach, 2016). This supports further exploration into complex ecological communities and supports the development of rigorous hypotheses about the effects of abiotic factors on these communities. Additionally, this research lays a groundwork to investigate how temperature influences the effectiveness of induced defenses initiated by the presence of predators (Chivers & Mirza, 2001; Hammill et al., 2008; Torres-Dowdall et al., 2012). More generally, our results show that increased temperature is associated with increased consumption rates for both species. Given that lower strength trophic interactions are associated with increased levels of population stability (McCann, 2000), our results suggest that increased consumption rates associated with higher temperature have the potential to reduce population and community stability.

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Author contributions MR collected the data within the laboratory, Statistical analyses and fitting of mechanistic models were performed by MR under the supervision of EH. MR led the writing of the MS, which was edited by EH.

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Data availability Data will be made available on an online database following acceptance.

Declarations

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval NA not required for *Paramecium* spp. or *S. virginianum*. Additional declarations for articles in life science journals that report the results of studies involving humans and/or animals.

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