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Growth and grazing responses to temperature and prey concentration of *Condylostoma spatiosum*, a large benthic ciliate, feeding on *Oxyrrhis marina*

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ABSTRACT: *Condylostoma* is as a group of very large-sized ciliates frequently dominant in various marine benthic microbial communities. However, little is known about the effects of temperature and food concentration on its growth and grazing. Here, using the heterotrophic dinoflagellate *Oxyrrhis marina* as prey, we determined the specific growth rate, cell volume, specific production, and ingestion rate of *C. spatiosum* at different temperatures and prey concentrations. These growth and grazing parameters typically followed a hyperbolic response to prey concentration. By applying iterative curve-fitting to the data at each temperature, we found that, with increasing temperature, the maximum specific growth rate, maximum specific production, and maximum ingestion rate of *C. spatiosum* generally increased, while the maximum cell volume decreased. The gross growth efficiency of *C. spatiosum* generally decreased at saturated prey concentration from about 45 to 25% as the temperature increased from 12 to 24°C. By fitting these data iteratively to multi-variable nonlinear models, we obtained predictive equations for the growth rate, cell volume, and ingestion rate with respect to temperature and prey concentration.

KEY WORDS: Benthic ciliate · Growth rate · Ingestion rate · Gross growth efficiency · Prey concentration · Temperature

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INTRODUCTION

Temperature and food availability are key factors affecting the growth, consumption, and food utilization efficiencies of ciliates. Temperature affects various biological functions directly by altering the rate of chemical reactions, and indirectly by altering viscosity and diffusion. Food availability affects feeding by determining the rate at which a grazer encounters food items (Begon et al. 1986). The effect of either temperature alone or food concentration alone on the growth and production of protozoa was usually studied until Weisse et al. (2002) studied the 2 factors simultaneously for a small freshwater ciliate. Kimmance et al. (2006) investigated both factors in detail for the dinoflagellate *Oxyrrhis marina* and demonstrated that the interactive effect of temperature and prey concentration could alter the outcome of food-web models. Such studies to date have focused on pelagic protists; no data are available for benthic forms.

Marine benthic habitats are highly heterogeneous and harbor diverse protists, whose abundance and productivity typically exceed those in the water column by one to several orders of magnitude (Fenchel 1969, Epstein 1997, Hamels et al. 2004). It would be particularly interesting to know whether the ecology of these organisms is different from that of pelagic ones. *Condylostoma* spp. are benthic ciliates that are frequently dominant in terms of biomass in various benthic habitats (Simpson et al. 1998, Madoni 2006). The importance of these ciliates in sediments is related to their high biomass and voracious grazing on various food items, including ciliates, flagellates, and even small metazoans (Fenchel 1968, Lei et al. 2010). *C. spatiosum* is a large benthic ciliate that feeds preferentially on *Oxyrrhis marina*, a widely distributed and abundant

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dinoflagellate that has the potential to control red-tide organisms (Jeong et al. 2003, Lowe et al. 2005). In order to gain a better understanding of the effects of temperature and prey concentration on benthic ciliate population dynamics, we investigated the growth and grazing responses of *C. spatiosum* feeding on *O. marina* at a range of temperatures and food concentrations. Based on the data obtained, we developed predictive models that will allow us to estimate the growth and grazing rate of *C. spatiosum* within given ranges of temperature and food concentration.

MATERIALS AND METHODS

Study organisms. The size of the ciliate *Condylostoma spatiosum* was on average 700 × 80 µm (n = 20) and the dinoflagellate *Oxyrrhis marina* was on average 29 × 16 µm (n = 20) *in vivo*. Both species were isolated from the intertidal sediment of the Licun River estuary at Qingdao, China, in July 2007 and were maintained in Petri dishes containing bacterized rice-grain medium at room temperature.

Experimental design. Experiments were run in Petri dishes (diameter 90 mm) in dim light (1.2 to 2.0 µmol m^{-2} s^{-1}) under a 12 h light:12 h dark cycle. The experimental volume in each plate was 20 ml. Ciliates were taken from the exponential growth phase and were adapted to the experimental temperature and prey concentration for at least 24 h before the beginning of the experiments.

Growth and ingestion experiments were run separately at the temperatures of 12, 15, 18, 21, and 24°C. Each treatment was conducted with 20 prey concentrations ranging from about 8×10^2 to 1.3×10^4 cells ml^{-1} (corresponding to 0.21 to 5.69 µg C ml^{-1}). The growth experiments lasted 5 d. Ciliate concentration was determined each day by direct count under a stereomicroscope (magnification 15×, with at least 100 fields counted per plate). The cell size of *Condylostoma spatiosum* was measured *in vivo* from microscopic images and the cell volume was calculated assuming a prolate spheroid shape (with a body width to thickness ratio of about 1.5:1). The size of *Oxyrrhis marina* was also measured *in vivo* microscopically, and its concentration was determined from a Lugol-fixed sample (2% final concentration) using a Sedgewick-Rafter chamber. Prey concentration was adjusted when it deviated more than 20% from the initial concentration. The ingestion experiments lasted 2 d. Cell size and concentration of both prey and predator were determined at the beginning and at the end of each experiment. Petri dishes with the same concentrations of *O. marina* but without predators served as controls. To render the study comparable to previous investigations, we converted the cell volume (v, μm^3) of prey and predator to carbon units using C (pg) = 0.099 μm^{-3} and log C (pg) = −0.639 + 0.984 × log v, respectively (Menden-Deuer & Lessard 2000).

Calculation of experimental results. The log cell number of ciliates was plotted against time, and linear regression was computed for the exponential phase of growth in each case. The specific growth rate (µ) of *Condylostoma spatiosum* was calculated from the slope of the linear regression. The ingestion rate (I) was calculated according to Frost (1972): $I = C_m \times g/R_m$. The grazing rate was calculated as $g = [\ln (C_{ct}/C_{c0}) - \ln (C_t/C_0)]/\Delta t$, where C_{c0} and C_{ct} are respectively the initial and final concentrations of *Oxyrrhis marina* in the controls, and C_0 and C_t are respectively the initial and final concentrations of *O. marina* in the Petri dishes with predators. R_m is the geometric mean of predator concentration during incubation, and was calculated as $R_m = (R_t - R_0)/\ln (R_t - R_0)$, where R_0 and R_t are the initial and final concentrations of *C. spatiosum*, respectively. C_m is the mean concentration of prey during incubation, and was calculated as $C_m = C_0 \times (e^{(k-g)\times\Delta t} - 1)/[\Delta t \times (z - g)]$, where C_0 is the initial concentration of *O. marina*, z denotes the *O. marina* population growth rate in the control without ciliates, and Δt is the duration of the experiment.

The specific production (Sp) of *Condylostoma spatiosum* was calculated as $Sp = \mu \times v$, where v is the cell volume of *C. spatiosum*. Gross growth efficiency (GGE) was calculated from the idealized curves of Sp and I (see 'Response models') according to GGE = $Sp \times$ CC / ($I \times$ OC $\times$ vo), where CC is the carbon density of *C. spatiosum*, OC and vo are the carbon density and cell volume of *Oxyrrhis marina*, respectively.

Response models. As the prey concentrations changed greatly during the course of each experiment, we related the ingestion rates to mean prey concentrations for the analyses of functional responses. Growth rate, cell volume, and specific production were related to initial prey concentrations for the analyses of numerical responses (see Fig. 1).

To characterize the interactive effect of temperature and prey concentration on specific growth rate, ingestion rate, cell volume, and specific production, we fitted established response models (e.g. Montagnes & Lessard 1999, Kimmance et al. 2006) to data from our experiments conducted at the 5 temperatures. Curves were generated by an iterative fitting method, using the Marquardt-Levenberg least-squares algorithm. Growth responses, with non-zero intercepts, were established by fitting Eq. (1) to growth rate data. Functional responses were established by fitting Eq. (2) to ingestion rate data. The response of cell volume to prey concentration was established by fitting Eq. (3) to volume data. The response of specific production to prey

concentration was established by fitting Eq. (4) to specific production data.

$$\mu = [\mu_{max} \times (C_o - p')] / [k_1 + (C_o - p')] \quad (1)$$

$$I = I_{max} \times C_m / (k_2 + C_m) \quad (2)$$

$$v = v_0 + v'_{max} \times C_o / (k_3 + C_o) \quad (3)$$

$$Sp = Sp_{max} \times (C_o - p') / [k_4 + (C_o - p')] \quad (4)$$

where μ_{max} is the maximum specific growth rate; p' is the threshold prey concentration (prey ml^{-1}, the concentration where $\mu = 0$); I_{max} is the maximum ingestion rate; v'_{max} is the maximum cell volume influenced by prey concentration; v_0 is the predicted cell volume at zero prey; Sp_{max} is the maximum specific production; k_1, k_2, k_3, and k_4 are constants.

RESULTS

At all temperatures, the growth rate, cell volume, specific production, and ingestion rate of *Condylostoma spatiosum* followed a rectangular hyperbolic response to food concentration (Fig. 1). Three main changes could be recognized in the pattern of growth response with temperature. μ_{max} increased linearly (slope = 0.05, $p < 0.01$) within the range of 12 to 21°C and then ran into a relatively stable state within the range 21 to 24°C (Fig. 2a). p' fluctuated upwards with temperature (Fig. 2b). The initial slope of the numerical response curve (μ_{max}/k) generally increased within the range 12 to 21°C and then decreased at 24°C (Fig. 2c). The response of μ of *C. spatiosum* to the combined effect of temperature (θ) and p was best described by Eq. (5) ($p < 0.01$, adjusted $R^2 = 0.74$; Fig. 3a):

$$\mu = \{1.047 \times (C_o - 1659) / [4689 + (C_o - 1659)]\} \times 0.026 \times \theta \quad (5)$$

The cell volume of *Condylostoma spatiosum* also increased with food concentration at all temperatures (Fig. 1b). The estimated maximum cell volume slightly decreased with temperature (Fig. 2d). Linear regression ($p = 0.036$) indicated a thermal sensitivity of 0.033 ± 0.009 (mean ± SE) °C^{-1} of the maximum cell volume at the reference temperature of 15°C. The cell volume response of *C. spatiosum* to the combined effect of temperature and food concentration was best described by Eq. (6) ($p < 0.01$, adjusted $R^2 = 0.78$; Fig. 3b):

$$v = \{[8.942 \times C_o / (3004 + C_o)] + 7.105\} \times \theta^{-0.754} \quad (6)$$

The specific production of *Condylostoma spatiosum* increased with increasing food concentration (Fig. 1c). The estimated Sp_{max} gradually increased with temperature, with a sharp increase at 21°C, before falling back to previous levels at 24°C (Fig. 2e).

The ingestion rate of *Condylostoma spatiosum* increased with increasing temperature and food concentration (Fig. 1d). The estimated maximum ingestion rate increased from about 23 to 50 prey cells predator^{-1} h^{-1} (corresponding to 0.023 to 0.086 h^{-1} when normalized against predator volume according to Hansen et al. 1997) within the range 12 to 24°C (Fig. 2f). The ingestion rate response of *C. spatiosum* to the combined effect of temperature and prey concentration was best described by Eq. (7) ($p < 0.01$, adjusted $R^2 = 0.54$; Fig. 3c):

$$I = [23.467 \times C_m / (3606 + C_m)] \times (\theta - 11.448)^{0.203} \quad (7)$$

GGE of *Condylostoma spatiosum* increased rapidly with prey concentration at all temperatures when prey concentration was below a critical level of about 4×10^3 cells ml^{-1}. Above this level, GGE showed different trends with increasing prey concentration at different temperatures: it decreased very slightly at 12°C, was stable at 15, 18, and 24°C, and steadily increased at 21°C. At sub-saturation prey concentrations, GGE increased more rapidly with prey concentration at lower temperatures. At high prey concentrations, GGE dropped from about 45 to 25% within the temperature range 12 to 18°C and showed a further slight decrease at 24°C. GGE was generally lowest at 21°C, showing a strikingly different pattern from that at the other temperatures (Fig. 4).

DISCUSSION

The growth rate, cell volume, specific production, and ingestion rate of *Condylostoma spatiosum* typically followed a rectangular hyperbolic response to prey concentration at all temperatures. It is possible that some protists may elicit a sigmoidal response, but in most studies the data are rarely sufficiently precise to assess this (Kimmance et al. 2006). We chose the hyperbolic model because it is theoretically well-founded and the most frequently used to describe the responses of protists to prey concentrations (Fenchel 1986, Montagnes 1996). These responses have often been incorporated into microbial food-web models and their parameters are useful for assessing the autecology of species (Davidson 1996, Weisse et al. 2002).

Maximum growth rate

The estimated μ_{max} of *Condylostoma spatiosum* was much lower than that of most small ciliates, but fell within the range reported for similar-sized rotifers at comparable temperatures (Hansen et al. 1997). This is reasonable since metabolic rate tends to decrease with body size. Nonetheless, some large ciliates have higher growth rates than smaller ones (Gismervik

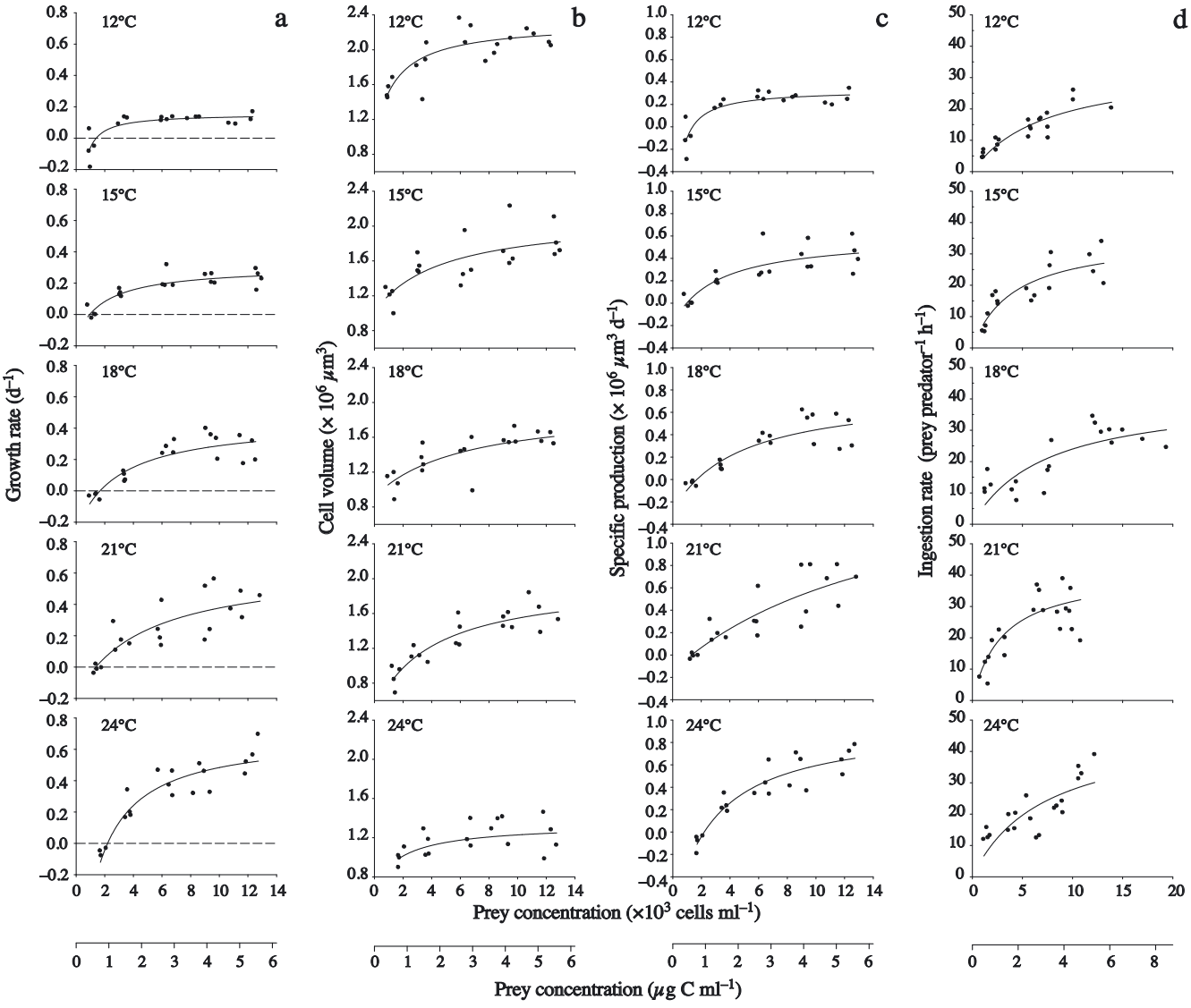

Fig. 1. *Condylostoma spatiosum* feeding on *Oxyrrhis marina*. Responses of (a) specific growth rate, (b) cell volume, (c) specific production, and (d) ingestion rate of *C. spatiosum* to *O. marina* concentration at temperatures ranging from 12 to 24°C. Solid curves are the best fit to data. Dashed lines indicate zero growth

2005). Moreover, even identically incubated conspecific ciliates can exhibit conspicuous differences in μ_{max} if they were isolated from different habitats (Weisse & Montagnes 1998, Müller & Schlegel 1999). Such differences are likely to be attributed to their different regional adaptions. Our data indicate that within the temperature range 12 to 21°C, the μ_{max} typically followed a linear response to temperature, with a slope (i.e. thermal sensitivity) of about 0.05 d^{-1} °C^{-1}. This finding is consistent with the results of Montagnes et al. (2003), who analyzed literature data and suggested a typical linear relationship between μ_{max} and temperature for protists, with an average slope of 0.07 d^{-1} °C^{-1}. Since the growth rate as well as the productivity of *C. spatiosum* is less sensitive to temperature than that of its prey (e.g. 0.08 d^{-1} °C^{-1} for *Oxyrrhis marina*; Kimmance et al. 2006), elevated temperatures would increase the production of the predator at a lower rate than that of its prey and thus reduce competition between predators.

Threshold prey concentration

We obtained a rather high value for p' of 0.237 µg C ml^{-1} at 15°C for the large benthic ciliate *Condylostoma spatiosum*. Although a p' (adjusted to 15°C) as high as 0.325 µg C ml^{-1} has been recorded, most planktonic ciliates exhibit a p' (adjusted to 15°C) ranging from 0.006 to 0.075 µg C ml^{-1} (Jakobsen & Hansen 1997,

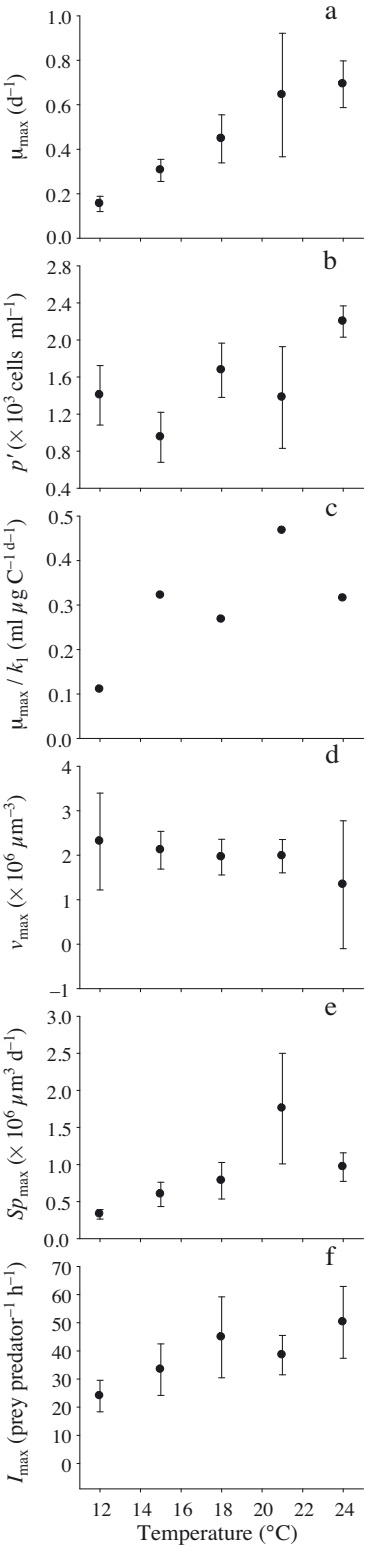

Fig. 2. *Condylostoma spatiosum* feeding on *Oxyrrhis marina*. Response of (a) maximum growth rate (μ_{max}), (b) threshold prey concentration (p'), (c) initial slope of numerical response (μ_{max}/k_1), (d) maximum cell volume (v_{max}), (e) maximum specific production (Sp_{max}), and (f) maximum ingestion rate (I_{max}) to temperature. Error bars denote ± 1 SE

Weisse 2006, and references therein). Usually, high values of p' are attributed to suboptimal prey property (prey size, toxicity, nutrient ratio, etc.) or methodological limitations (Müller 1991, Weisse & Müller 1998). This may partly explain the high p' for *C. spatiosum*

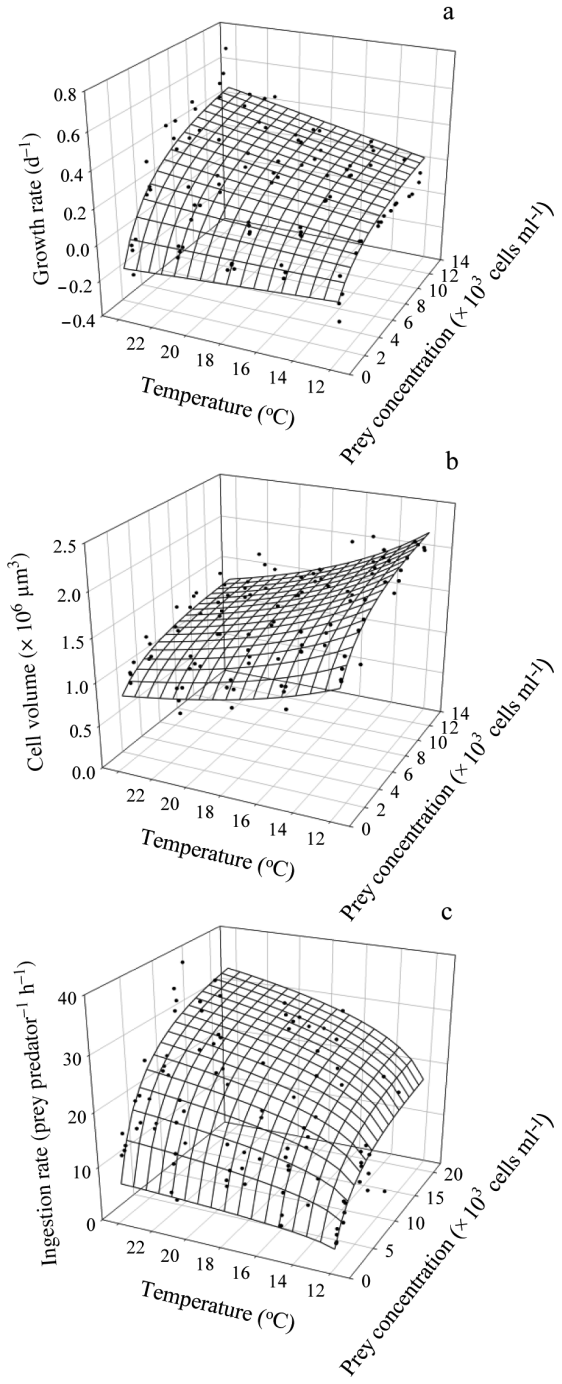

Fig. 3. *Condylostoma spatiosum* feeding on *Oxyrrhis marina*. Response of (a) specific growth rate, (b) cell volume, and (c) ingestion rate of *C. spatiosum* to the combined effects of temperature and *O. marina* concentration. Data points obtained from all experiments. Fits to data in (a), (b), and (c) follow Eqs. (5), (6), and (7), respectively

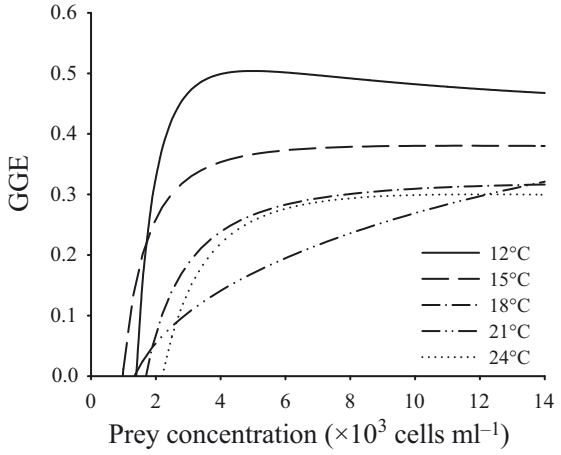

Fig. 4. *Condylostoma spatiosum* feeding on *Oxyrrhis marina*. Response of gross growth efficiency (GGE) of *C. spatiosum* to *O. marina* concentration at temperatures ranging from 12 to 24°C. Curves were calculated from curves of growth responses and ingestion responses

recorded in the present study, since only one type of food was offered to this large, omnivorous ciliate. The true threshold prey concentration would be lower for *C. spatiosum* in the field, where an array of various food items is available. On the other hand, considering the different food availability between benthic and planktonic habitats, we have an alternative explanation for the high p' for the benthic ciliate. Generally, a lower p' confers a selective advantage to species more capable of exploring food at low prey levels. This is essential for ciliates adapted to pelagic water, where prey concentrations are generally low, and thus planktonic ciliates generally present low values of p'. By contrast, the concentrations of food items are one to several orders higher in benthic environments than planktonic ones (Epstein 1997, Hamels et al. 2004), making the capability of exploring food at low prey levels superfluous for benthic ciliates. This may explain the high threshold prey concentration for *C. spatiosum* and why this ciliate prefers benthic environments, where food items are abundant. However, whether benthic ciliates generally exhibit a p' higher than planktonic ciliates needs further investigation.

We are also aware of the fluctuations in p' and the initial slope ($\alpha = \mu_{max}/k_1$) with increasing temperature for *C. spatiosum*. For example, p' at 12°C was higher than that at 15°C ($p = 0.14$), while α was the opposite. Weisse et al. (2002) also observed a high p' and low α at low temperatures for the small freshwater ciliate *Urotricha farcta* and attributed it to temperature stress. However, in the present study, temperature stress could not explain why p' was lower ($p = 0.08$) and α was higher at 21°C. Likewise, Kimmance et al. (2006) observed a lower p' for the flagellate *Oxyrrhis marina* at 15°C, whereas p' increased linearly from 8 to 25°C. Possibly the relationship between p' and temperature is species-specific. On the other hand, experimental error or methodological limitations may also result in deviations (Montagnes & Berges 2004). Nevertheless, higher p' values at high temperatures would mean that a predator dies from starvation rather than being consumed by other predators, and this is critical for modeling food webs (Montagnes 1996).

Maximum cell volume

Similar to previous studies (Weisse et al. 2002, Kimmance et al. 2006), we observed a linear reduction in v_{max} with increasing temperature for *Condylostoma spatiosum*. The slope of the linear regression ($-0.03°C^{-1}$) is also close to the average thermal sensitivity of $-0.04\ °C^{-1}$ suggested by Atkinson et al. (2003). It is still not clear why cell size decreases with temperature. One possible reason is that the reduction in size, and hence increase in the surface area relative to the metabolizing cell mass, is a necessary compensation for the reduced supply to consumption ratio of the limiting resource (e.g. oxygen, carbon dioxide) at high temperatures (Atkinson et al. 2003). But this does not explain similar trends found in other organisms (e.g. fish, amphibians, insects) (Atkinson 1994). An alternative explanation involves separating the effects of temperature on the processes that control cell size and development, i.e. differentiation or change in life stage. Size reduction at high temperature could result from a greater thermal sensitivity of the developmental rate than that of the cell growth rate (Kingsolver & Huey 2008). Nevertheless, the decrease in cell size with temperature results in a reduction of specific production for *C. spatiosum* at high temperature (24°C) while growth rate is still increasing. The effect of temperature on production would be overestimated if the temperature effect on cell size was ignored (Brush et al. 2002, Atkinson et al. 2003).

Maximum grazing rate

Although the volume-normalized I_{max} of *Condylostoma spatiosum* (0.023 to 0.086 h^{-1}) is very low compared to many other ciliates (0.1 to 0.48 h^{-1}), it overlaps with the range of I_{max} (0.054 to 0.17 h^{-1}) reported for similar-sized rotifers (Hansen et al. 1997). The positive linear relationship between I_{max} and temperature is consistent with that reported by Kimmance et al. (2006). However, the typical sigmoid response of I_{max} to temperature has also been documented, possibly due to the broad range of temperatures (6 to 41°C) evalu-

ated (Montagnes et al. 2001). Nevertheless, an elevated I_{max} indicates an enhanced feeding activity resulting in higher prey productivity by reducing competition within prey groups, particularly among those very abundant organisms (e.g. diatoms and flagellates) in benthic environments. High values of I_{max} at high temperatures would also result in high carbon flux in benthic microbial food webs.

Gross growth efficiency

GGE is useful for assessing the reliability of growth and grazing data (Gismervik 2005), but estimation of GGE is often greatly influenced by environmental factors and methodological protocols. The GGE data obtained from the growth and grazing response curves of *Condylostoma spatiosum* fall within the interquartile range of 10 to 45% suggested for ciliates (Straile 1997). At high prey levels, the GGE of *C. spatiosum* showed different trends with increasing prey concentration at different temperatures. This is consistent with the results of Straile (1997), who analyzed literature data and concluded that the effect of prey concentration on GGE could be either negative or positive depending on the data sets included in the analysis. The mechanisms involved in the response of GGE to prey concentration are complex. A useful framework for understanding this involves dividing GGE (growth/ingestion) into assimilation efficiency (AE = (growth + respiration)/ingestion) and net growth efficiency (NGE = growth/(growth + respiration)). Both AE and NGE are influenced by ambient prey concentration. On the one hand, high prey concentration could result in superfluous feeding or insufficient digestion and thus a reduction in AE. On the other hand, NGE might increase at high prey concentrations as energy lost through prey capture decreases with increased prey availability. The synergistic effect of AE and NGE may result in a complex relationship between GGE and prey concentration, as shown both in the present study and previously (Vidal 1980, Straile 1997, and references therein). Fenton et al. (2010), however, demonstrated that, depending on the relationship between the half-saturation constant of the grazing response (k_2) and growth response ($k_1 - p'$), AE could either increase if $k_2 < (k_1 - p')$ or decrease if $k_2 > (k_1 - p')$ with increasing prey concentration. However, NGE derived from the expression for GGE and AE follows a hyperbolic increase relative to prey concentration regardless of the relationship between k_2 and $k_1 - p'$. That is to say GGE would definitely increase with prey concentration when $k_2 < (k_1 - p')$. Our data suggest that with increasing prey concentration, the GGE pattern at 21°C was clearly different from that at the other temperatures. Interestingly, the different patterns coincide with the different relationships between the half-saturation constants of both the grazing and the growth responses of *C. spatiosum*: this relationship was $k_2 < (k_1 - p')$ at 21°C, while at the other temperatures it was $k_2 > (k_1 - p')$ (data not shown). Therefore the GGE at 21°C continuously increased with increasing prey concentration. However, we could not explain why the relationship at 21°C was different from those at other temperatures. The different patterns between GGE and prey concentration at different temperatures possibly reflect an interactive effect of prey concentration and temperature.

The GGE at saturated prey concentration generally decreased from about 45 to 25% with increasing temperature, suggesting a suppression effect of temperature on the GGE of *Condylostoma spatiosum*. This is consistent with the findings of Straile (1997), who showed that the GGE of ciliates is negatively correlated with temperature. The decline in GGE at high temperatures could be partially explained by the constant carbon density of *Oxyrrhis marina* used for the calculation of GGE, whereas in fact the carbon density of *O. marina* might decrease with temperature (Montagnes & Franklin 2001). A more general explanation likely involves the von Bertalanffy-Perrin model, which states that catabolic processes are more sensitive to temperature than anabolic processes (Perrin 1995). In other words, respiration increased more rapidly than cell growth at high temperature, causing a reduction in NGE. Thus, GGE would decrease with temperature unless AE increased appreciably (Malloy & Targett 1991). In contrast to the negative correlation for ciliates, there is a positive relationship between GGE and temperature for nano- and microflagellates and no significant relationship for rotifers (Straile 1997). Angilletta & Dunham (2003) also observed positive relationships for many other ectotherms and argued reasons for the failure of the von Bertalanffy-Perrin model; for example, the assumed allometries of anabolism and catabolism in the model might be unrealistic for some species. The mechanism of the response of GGE to temperature remains enigmatic.

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