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Does warming enhance the effect of microzooplankton grazing on marine phytoplankton in the ocean?

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Abstract

We evaluated a hypothesis derived from the metabolic theory of ecology (MTE) that the ratio of microzooplankton herbivory (m) to phytoplankton growth (μ) will arise in a warming ocean because of the different temperature dependencies of autotrophic and heterotrophic organisms. Using community-level growth and grazing data from dilution experiments, generalized additive models (GAMs) were constructed to describe the effects of temperature and chlorophyll on $m:\mu$. At low chlorophyll levels, $m:\mu$ decreases with increasing temperature, whereas at high chlorophyll levels, $m:\mu$ increases initially with temperature before reaching a peak and then declines. These complex responses of $m:\mu$ result from mixed effects of temperature and chlorophyll on microzooplankton biomass (B_z), biomass-specific microzooplankton grazing rate ($m:B_z$), and phytoplankton growth rate (μ). B_z decreases with rising temperature and increases with rising chlorophyll. $m:B_z$ increases with temperature and decreases with chlorophyll. Nutrient-enriched growth rate of phytoplankton (μ_n) and μ increase with increasing temperature and chlorophyll. Holding chlorophyll constant, the calculated activation energies of $m:B_z$ and μ_n are 0.67 ± 0.05 and 0.36 ± 0.05 eV, respectively, both consistent with previous MTE estimates for heterotrophs and autotrophs. Our study indicates that warming may enhance phytoplankton losses to microzooplankton herbivory in eutrophic but not in oligotrophic waters. The GAM analysis also provides important insights into underlying system relationships and reasons why community-level responses in natural systems may depart from theory based on laboratory data and individual species.

Recent reports have suggested that open-ocean chlorophyll concentrations have declined and areas of oligotrophy have expanded over the last few decades (Behrenfeld et al. 2006; Irwin and Oliver 2009; Boyce et al. 2010). Although these conclusions remain controversial (Mackas 2011; McQuatters-Gollop et al. 2011; Rykaczewski and Dunne 2011), they have sparked broad interest in understanding the processes that might explain or be affected by changes of such global significance. Mechanistically, reduced phytoplankton biomass is an expected consequence of reduced nutrient fluxes arising from increased water-column stratification due to surface-ocean warming (Behrenfeld et al. 2006; Irwin and Oliver 2009; Boyce et al. 2010). This bottom-up explanation is not, however, the only temperature-related effect that could contribute to changes in phytoplankton standing stock. Here we consider the potential that a temperature-related increase in grazing pressure of microzooplankton could help draw phytoplankton biomass lower as the oceans warm.

This issue arises because the rate processes of heterotrophs are thought to have higher temperature dependencies than those of autotrophs as they are defined by different rate-limiting biochemical reactions—adenosine triphosphate (ATP) synthesis vs. ribulose bisphosphate carboxylase oxygenase (Rubisco) carboxylation (Allen et al. 2005; Lopez-Urrutia et al. 2006; Lopez-Urrutia 2008). According to the metabolic theory of ecology (MTE; Brown et al. 2004), the metabolic rate (R), which fuels all activities of an organism, can be expressed as a function of body temperature (T, °K) and mass (M):

$$R = R_0 e^{-E/kT} M^{\alpha} \quad (1)$$

where R_0 is a normalization constant, E (in electron volts [eV], 1 eV = 96.49 kJ mol^{-1}) is the activation energy that does not vary with T and M, k is the Boltzmann's constant (8.62×10^5 eV K^{-1}), and α is the allometric exponent. Activation energy is the energy barrier (i.e., the enthalpy difference between the transition state complex and the reactants) for enzymatic reactions (Ratkowsky et al. 2005). The rate of whole-body metabolism is usually limited by the production of ATP from glycolysis and the tricarboxylic acid cycle, accompanied by the reduction of oxygen to water. Activation energy should be constant (~ 0.6–0.7 eV) for all aerobic organisms, given non-limiting respiratory substrates (Gillooly et al. 2001; Lopez-Urrutia et al. 2006). For autotrophs, however, the temperature-driven antagonistic effects of oxygen and carbon dioxide binding with Rubisco during photosynthesis lead to a lower activation energy of ~ 0.32 eV (Allen et al. 2005; Lopez-Urrutia et al. 2006).

Although the above activation energies are based on individual rates, they are assumed constant among taxa and therefore can be scaled up to community levels, which is an important application of MTE (Savage et al. 2004; Allen et al. 2005). Indeed, based on the activation energy

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difference between autotrophs and heterotrophs, Lopez-Urrutia et al. (2006) found that the ratio of community respiration to production decreases with increasing temperature. Rose and Caron (2007) also observed that the slope of the log maximal growth rate of heterotrophic protists against temperature is significantly higher than for phytoplankton. From this, they deduced that phytoplankton blooms at high latitudes could result from the release of top-down control due to temperature limitation of microzooplankton growth and grazing rates. By similar logic, increased temperature of the surface ocean could lead to stronger grazer regulation of phytoplankton standing stock.

As Rose and Caron (2007) acknowledged, however, the elevated growth rate potential of microzooplankton at high temperature might not translate directly into higher grazing rates because temperature is not the only factor affecting grazer activity levels. Microzooplankton community grazing is, in fact, a complex function of many grazer and prey characteristics, including grazer community biomass, predator–prey size relationships, food quality and quantity, etc. (Peters 1994; Poulin and Franks 2010). Because composition and biomass of both predators and prey may covary with temperature, the temperature dependence of community grazing effect can clearly differ from the grazing activity responses of individual consumers. Similarly, temperature–growth relationships for phytoplankton can differ for individual species and mixed communities because of temperature covariance of growth-relevant factors like light, nutrients, and cell size (Lopez-Urrutia et al. 2006; Chen and Liu 2010; Finkel et al. 2010). Thus, for predicting the consequences of ocean warming on natural complex assemblages, analyses of experiments conducted with natural communities under in situ environmental conditions might yield different, and perhaps more reliable, inferences of underlying temperature relationships than the coefficients derived from laboratory experiments with individual cultures.

In the present study, we first use data from dilution experiments to examine whether increasing temperature stimulates the community grazing effect of marine microzooplankton on primary production, the ratio of microzooplankton grazing rate (m, d^{-1}) to phytoplankton in situ growth rate (μ, d^{-1}) (Landry and Hassett 1982; Calbet and Landry 2004). We next investigate whether the variation of $m:\mu$ with temperature can be explained by difference of activation energy between phytoplankton (E_p) and microzooplankton (E_z), the temperature coefficients of individual rates predicted by MTE (Allen et al. 2005; Lopez-Urrutia et al. 2006). To achieve these goals, the effects of other factors, such as phytoplankton and microzooplankton biomass, are incorporated into generalized additive models (GAMs) that predict in situ rates of phytoplankton growth and microzooplankton grazing at the community level.

Methods

General approach for estimating E_z *from dilution experiments*—To simplify the problem of using field-derived experimental data, here we consider an ideal case where the clearance rate of microzooplankton grazers is dependent only on their body size and food concentration. For such circumstances, microzooplankton community grazing rate (m) measured by the dilution technique is the sum of clearance rates of individual grazers in a unit water parcel:

$$m = \sum_{i=1}^{N} C_i = \sum_{i=1}^{N} C_{m,i} f(P_i), \tag{2}$$

where N is the total abundance of the grazers, C_i is the clearance rate of the i^{th} grazer, $C_{m,i}$ is the maximal clearance rate of the i^{th} grazer, and $f(P_i)$ describes the functional response for clearance rate vs. prey concentration (P_i). There are a number of expressions for $f(P_i)$, which is usually a decreasing function of P_i (Gentleman et al. 2003). To facilitate the analysis, we assume that $f(P_i)$ is the same for all grazers and is negatively related to total prey concentration P (i.e., $f(P_i) = f(P)$ for all i).

Applying MTE theory (Eq. 1), where the maximal clearance rate of a grazer can be expressed as a function of temperature and body size, Eq. 2 becomes

$$\begin{aligned} m &= \sum_{i=1}^{N} C_{m,i} f(P) \\ &= \sum_{i=1}^{N} C_0 M_i^{\beta} e^{-E_z/kT} f(P) \\ &= C_0 e^{-E_z/kT} f(P) \sum_{i=1}^{N} M_i^{\beta} \end{aligned} \tag{3}$$

where C_0 is a normalization constant, M_i is the body size of the i^{th} grazer, β is the allometric exponent, and E_z is the activation energy for microzooplankton grazing.

Lastly, when the unit of M_i is individual carbon content, then $\beta \approx 1$ (Hansen et al. 1997; Lopez-Urrutia et al. 2006) and Eq. 3 becomes

$$m \approx C_0 e^{-E_z/kT} f(P) B_z \tag{4}$$

where B_z is the total biomass of the microzooplankton community in the water parcel. In our idealized case, therefore, temperature, total microzooplankton and phytoplankton biomass should be the primary factors affecting the microzooplankton community grazing rate. By obtaining data of m, P, and B_z, model fitting can be used to estimate E_z. The exact form of $f(P)$ is not critical in later analysis.

To estimate E_p from μ, we must take into account other factors that affect μ, such as light and nutrients. The majority of dilution experiments are conducted in the surface mixed layer (Buitenhuis et al. 2010), where the light level should be saturating. In some dilution experiments, incubation bottles are enriched with inorganic nutrients and an estimate of phytoplankton nutrient-enriched growth rate (μ_n) can be obtained, thereby allowing a nutrient limitation effect to be isolated. Phytoplankton mean cell size, another factor affecting μ_n, is well correlated with total chlorophyll concentration (Chen and Liu 2010; Barnes et al. 2011). By controlling chlorophyll and relating μ_n to temperature, an estimate of E_P can be obtained.

Table 1. List of GAMs and associated statistics used in this study. R^2 is the adjusted proportion of total variability explained by the model. GCV, generalized cross-validation score; n, the total number of measurements; m, microzooplankton community grazing rate (d^{-1}); μ, phytoplankton in situ growth rate (d^{-1}); te, tensor product spline; t, temperature in °C; [Chl], chlorophyll concentration (mg m^{-3}); B_z, microzooplankton biomass (mg C m^{-3}); s, thin plate regression spline; k, Boltzmann constant; T, temperature in °K; μ_n, phytoplankton nutrient-enriched growth rate (d^{-1}).

Model	R^2	GCV	n
1. arctangent $m:\mu \sim$ te(t,*ln*[Chl])	0.04	0.13	1232
2. *ln* $B_z \sim$ s(t)+s(*ln*[Chl])	0.26	0.85	595
3. *ln* $m:B_z \sim$ s(1/kT)+s(*ln*[Chl])	0.49	1.53	1377
4. *ln* $\mu_n \sim$ s(1/kT)+s(*ln*[Chl])	0.29	0.44	611
5. *ln* $\mu \sim$ s(1/kT)+s(*ln*[Chl])	0.25	0.87	1232

As further described below, we use GAMs to relate the rates of interest to environmental measurements of temperature and chlorophyll (Hastie and Tibshirani 1989; Wood 2006). GAMs have the advantage of not requiring an a priori specification of functional relationships, which is particularly suitable for describing complex ecological interactions. The resulting statistical models and parameterizations are therefore useful for constructing mechanistic models and assessing the responses of marine ecosystems to global change and can be incorporated into more complicated biogeochemical models.

Data analyses—We compiled a data set of μ and m and affiliating measurements of temperature, chlorophyll *a* concentrations, and B_z from the literature, as an expansion of the data set previously compiled by Calbet and Landry (2004) (*see* Web Appendix, www.aslo.org/lo/toc/vol_57/issue_2/0519a.html). All rates were measured using the dilution technique (Landry and Hassett 1982), in which phytoplankton net growth rates were first determined for each dilution treatment and instantaneous mass-specific growth and grazing rates were derived from linear regressions of phytoplankton net growth rates against dilution factor. We restricted our data points to the surface mixed layer with light level of no less than 10% of surface irradiance, where light is assumed non-limiting for phytoplankton growth (Landry et al. 2011). In some experiments, inorganic nutrients were added to the incubation bottles, giving estimates of the nutrient-enriched phytoplankton growth rate (μ_n). Microzooplankton biomass (B_z, μg C L^{-1}) was the total estimate for nanoflagellates, ciliates, and heterotrophic dinoflagellates. The numbers of experiments with data for μ_n and B_z was approximately one third of the total number of experiments.

We constructed GAMs to describe $m:\mu$, B_z, $m:B_z$, μ_n, and μ as functions of temperature and chlorophyll using the function "gam" in the R package mgcv developed by Wood (2006) (Table 1). We used arctangent transformations for $m:\mu$ (Calbet and Landry 2004) and natural log (*ln*) transformations for chlorophyll, B_z, $m:B_z$, μ_n, and μ to achieve approximate normal distributions. Zero or negative estimates of m, μ_n, and μ were assigned a value of 0.01 d^{-1} before *ln* transformation (Calbet and Landry 2004). Other choices, such as 0.001 d^{-1}, do not significantly change the results. To control the degree of smoothing and minimize overfitting to the data, a penalty term was added in the regression, and we set the gamma = 1.4 in gam, which forces each effective degree of freedom of the model to count as 1.4 degrees of freedom in the generalized cross-validation score. Thin plate regression splines were used for one-dimensional effects, and tensor product splines were used for two-dimensional effects of temperature and *ln* chlorophyll (*ln*[Chl]), as the two variables have different units (Wood 2006).

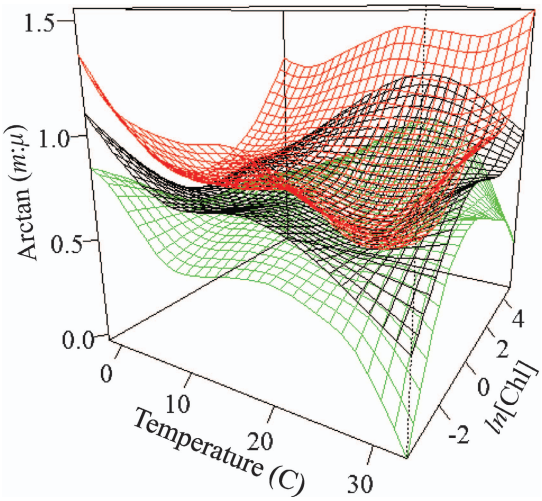

Fig. 1. Tensor product surface of arctangent transformed proportions of primary production consumed by microzooplankton ($m:\mu$) against temperature (°C) and *ln*[Chl]. Red and green surfaces are 95% confidential intervals.

In accordance with MTE (Brown et al. 2004; Lopez-Urrutia 2008), we used the Van't Hoff–Arrhenius equation instead of the exponential Q_{10}-like function to describe the partial effects of 1/kT on $m:B_z$, μ_n, and μ in the GAMs. By coercing the partial effect of temperature to be linear, E_P and E_z can be obtained as the positivized slope of the linear function. Graph plotting and statistical analysis were conducted using R (version 2.12.2; R Development Core Team 2011).

Results

Variations of m:μ *with temperature and chlorophyll*—When the predictors are linear additions of functions of temperature and *ln*[Chl], arctangent $m:\mu$ is significantly related to *ln*[Chl] ($p < 0.001$), but not to temperature ($p > 0.05$). The model is improved (R^2 from 0.029 to 0.042) by allowing interactions between temperature and *ln*[Chl] (Table 1), and arctangent $m:\mu$ is a complex function of temperature and *ln*[Chl] (Fig. 1). Although the R^2 is low, the trend is highly significant ($p < 0.001$). At low chlorophyll levels, arctangent $m:\mu$ decreases with increasing temperature, whereas at high chlorophyll, arctangent $m:\mu$ increases initially with increasing temperature before reaching a peak and then declining.

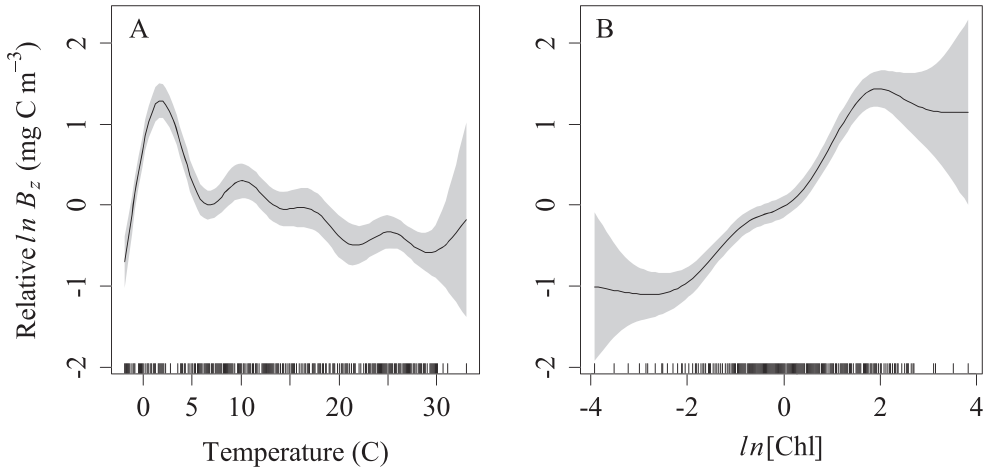

Fig. 2. Partial effects of (A) temperature (°C) and (B) *ln*[Chl] on relative *ln* B_z (difference of *ln* B_z from the mean). Shaded areas denote 95% confidential intervals.

Functional responses of B_z *and biomass-specific microzooplankton grazing rates to temperature and chlorophyll*—Both temperature and *ln*[Chl] are highly significant predictors for modeling *ln* B_z using GAM (Table 1). Allowing interactions between temperature and *ln*[Chl] does not improve the model. For water temperature above 2°C, *ln* B_z decreases with increasing temperature (Fig. 2A). *ln* B_z increases with *ln*[Chl] up to concentration of e^2 = 7.4 mg m^{-3} (Fig. 2B). We used this GAM model to generate B_z estimates for the dilution experiments for which original B_z data were unavailable.

Using the data of B_z obtained from the GAM model predicted from temperature and *ln*[Chl], we estimated the dependency of biomass-specific microzooplankton grazing rates ($m : B_z$) on $1/kT$ and *ln*[Chl] (Fig. 3). As expected, *ln* $m : B_z$ decreases with increasing $1/kT$ except at very low temperature (< 2°C). By coercing the function to be linear, the positivized regression slope of the linear fit is 0.67 ± 0.05 (95% confidence interval [CI]) eV. *ln* $m : B_z$ decreases with increasing *ln*[Chl], reflecting the functional response of grazing activity to variations in phytoplankton concentration.

Functional responses of μ_n *and* μ *to temperature and chlorophyll*—The partial effect of $1/kT$ on *ln* μ_n is essentially linear (Fig. 4A), and the positivized regression slope is 0.36 ± 0.05 (95% CI) eV. *Ln* μ_n increases with increasing *ln*[Chl], but levels off at the high end (Fig. 4B). The effects of temperature and *ln*[Chl] on *ln* μ (Fig. 4C,D) are qualitatively similar to those on *ln* μ_n, but the relationships are not as close to linear.

Discussion

Does increasing temperature stimulate microzooplankton grazing on phytoplankton?—The complex responses of the proportion of daily primary production grazed by microzooplankton ($m : \mu$) to temperature and chlorophyll (Fig. 1) suggest that the temperature effect on microzooplankton

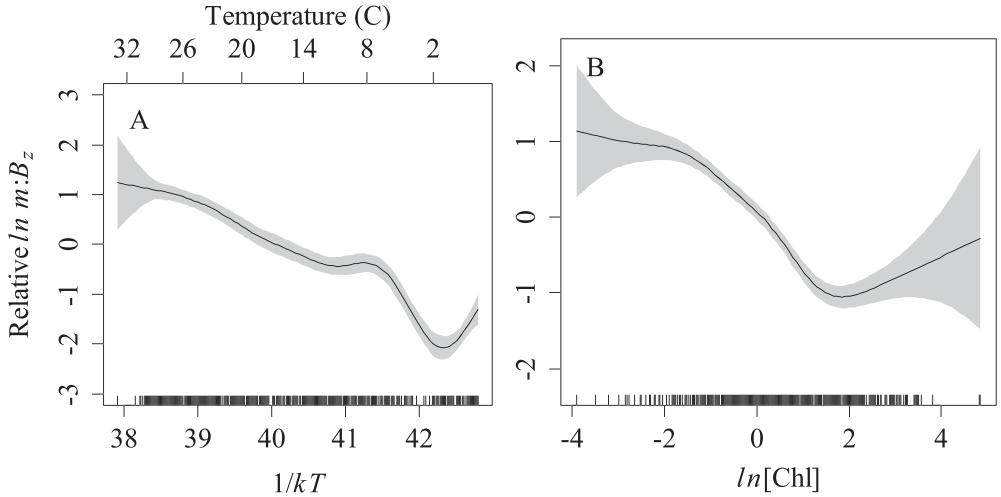

Fig. 3. Partial effects of (A) temperature and (B) *ln*[Chl] on relative *ln* microzooplankton biomass-specific grazing rate ($m : B_z$, L μg C^{-1} d^{-1}).

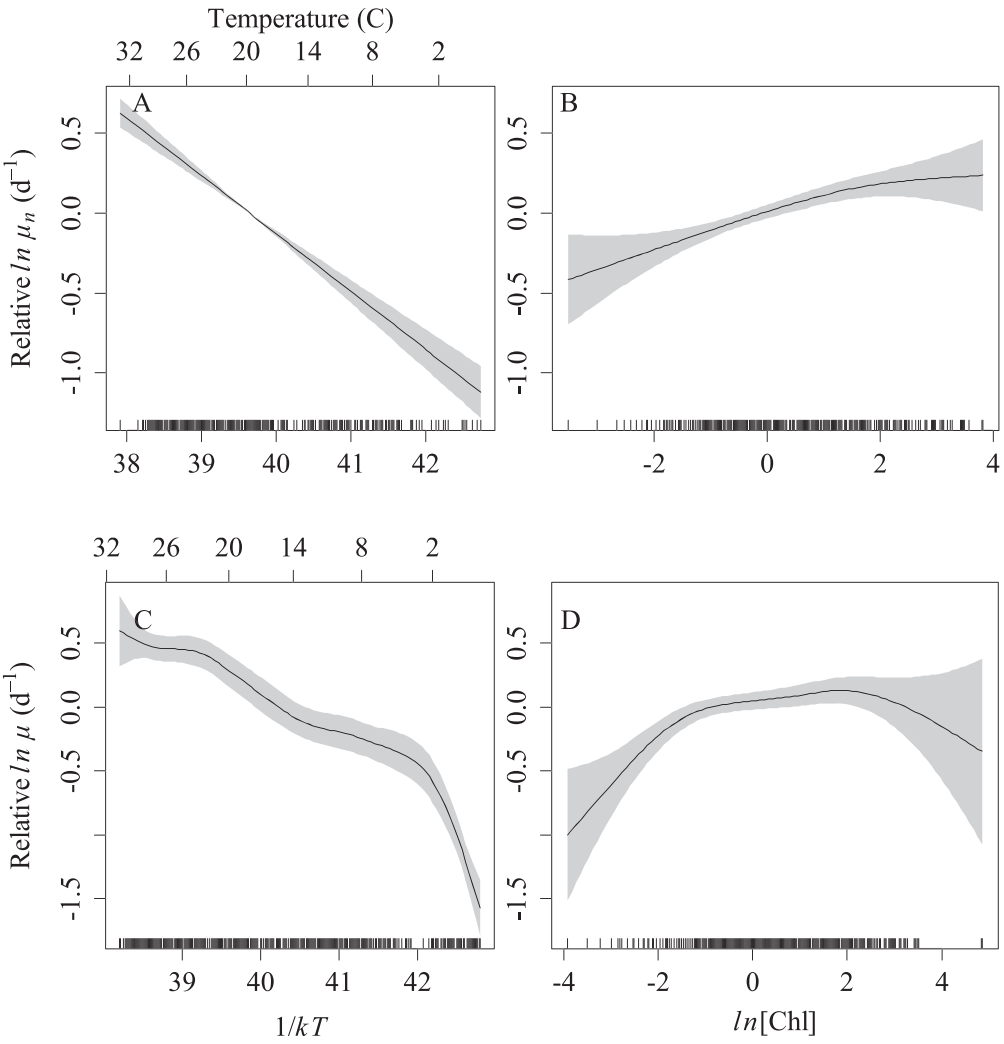

Fig. 4. Partial effects of temperature and *ln*[Chl] on phytoplankton (A, B) nutrient-enriched growth rate (μ_n, d^{-1}) and (C, D) non-enriched growth rate (μ, d^{-1}).

herbivory depends on the trophic status of the system. For eutrophic waters, we find that $m:\mu$ increases with increasing temperature, supporting Rose and Caron's (2007) contention that temperature can decouple trophic interactions between phytoplankton and herbivorous grazers because of the different metabolic temperature dependencies of auto- and heterotrophs (Allen et al. 2005; Lopez-Urrutia et al. 2006). Indeed, by ruling out the effect of chlorophyll, we find that the activation energy for biomass-specific microzooplankton grazing (0.67 eV) is significantly higher than that for phytoplankton specific growth rate (0.36 eV) under nutrient-enriched conditions. Both of these values are consistent with previous estimates derived from controlled experiments with laboratory cultures (Allen et al. 2005; Lopez-Urrutia et al. 2006), which suggests that Eq. 4, although simple, may be a reasonably good model for describing microzooplankton community grazing rate in the sea (also *see* Model 3 in Table 1).

Contrary to the argument in Rose and Caron (2007), we find that $m:\mu$ decreases with increasing temperature in oligotrophic waters when holding chlorophyll constant. The underlying cause is likely the decreasing trend of B_z with increasing temperature (Fig. 2A), which overweighs the effect of higher E_z over E_p. The decreasing trend of B_z with increasing temperature could, in turn, be a consequence of increasing top-down controls on microzooplankton (Strom et al. 2007), increasing respiratory demand and/or elevated feeding thresholds in warmer waters (Rivkin and Legendre 2001; Buitenhuis et al. 2010).

Taken at face value, our results indicate that there should not be a temperature-related ratcheting effect on microzooplankton grazing that would contribute to reduced chlorophyll standing stocks in warm and oligotrophic areas of the ocean (Behrenfeld et al. 2006; Irwin and Oliver 2009; Boyce et al. 2010). In eutrophic systems, the signal of enhanced microzooplankton herbivory with increasing seawater temperature is better defined. This increased top-down effect on phytoplankton could, however, be counteracted by enhanced eutrophication, if that in fact were be a consequence of warming in some coastal waters (Gregg et al. 2005; Boyce et al. 2010; Rykaczewski and Dunne 2010). We might reasonably conclude, there-

fore, that temperature-enhanced microzooplankton herbivory may play a role in reducing phytoplankton biomass in some warming areas of the oceans (those that are currently cooler and more eutrophic), but it is likely secondary to the bottom-up factors that affect nutrient fluxes (Irwin and Finkel 2008).

In spite of the above argument, it is still meaningful to understand how the proportion of net phytoplankton production consumed by microzooplankton (the ratio $m:\mu$) responds to ocean variability, because it greatly affects the efficiency of the biological pump (Landry et al. 1995*a*) and the resources available to higher-level consumers (Landry and Calbet 2004). Fig. 1 provides a framework for predicting changes in the $m:\mu$ ratio based on readily measured changes in temperature and chlorophyll. Although it may not be practical to test such predictions directly for the slow rates expected of climate changes (Doney 2006), within given regions the shorter time scales and greater magnitudes of temperature and chlorophyll variability associated with seasonal and interannual changes could lend themselves to such testing.

Dilution effects on temperature–grazing rate relationships—As this study relies heavily on estimates of microzooplankton community herbivory by the dilution technique, it is prudent to ask how methodological biases may affect our conclusions. For example, treatment differences in food resources supporting microzooplankton growth during 24-h incubations could lead to overestimates of microzooplankton grazing rates if they are not offset by other dilution effects, such as microzooplankton losses to predators (Landry 1993; Dolan and McKeon 2005; Landry and Calbet 2005). Systematic temperature effects on microzooplankton growth during dilution incubations could also affect E_z estimates.

Results of experimental examinations of the microzooplankton growth effect in incubation bottles are mixed. Landry et al. (1995*b*) found that using the disappearance rates of fluorescent labeled prey as an alternative to the dilution factor did not yield results significantly different from those of the usual approach based on initial biomass. First et al. (2007) also reported that grazing estimates were not significantly affected by corrections for microzooplankton growth. Nonetheless, Modigh and Franze (2009) observed that bottle growth of microzooplankton could be substantial under eutrophic conditions, leading to overestimates of grazing rates. However, using the equation in fig. 6a of Modigh and Franze (2009) to correct for microzooplankton bottle growth, we found an insignificant effect on the slope of $ln\ m:B_z \sim 1/kT$. The mean grazing rates at 30°C and 0°C are 0.8 d^{-1} and 0.07 d^{-1}, respectively, and the overestimates are roughly 0.1 and 0.01 d^{-1}, respectively. In addition, the E_z estimate (= 0.67 eV) from present GAM analysis matches very closely with the canonical 0.65 eV expected from MTE. Although this agreement does not specifically validate our results, neither does it suggest a gross departure from theory that might be a symptom of systematic bias.

Dependence of phytoplankton growth rate on chlorophyll concentration—Unlike microzooplankton grazing rate, phytoplankton growth was not explicitly modeled in this study. In spite of this, the temperature effect was still well modeled using GAM (Fig. 4A). For chlorophyll, the increasing trend of nutrient-sufficient growth rate ($ln\ \mu_n$) with chlorophyll (Fig. 4B) likely reflects the effect of compositional changes in the phytoplankton assemblage with system trophic state. Low-chlorophyll waters are usually dominated by pico-sized phytoplankton, whereas large diatoms often dominate high-chlorophyll waters. Some studies have shown that biomass-specific growth rates increase from picophytoplankton (e.g., *Prochlorococcus*) to medium-sized phytoplankton cells (Bec et al. 2008; Chen and Liu 2010, 2011). Thus, as mean cell size of phytoplankton is well related to total chlorophyll (Chen and Liu 2010; Barnes et al. 2011), an increasing trend of $ln\ \mu_n$ with chlorophyll should be expected. Such growth–biomass relationships at the community level could underlie the strong coupling of phytoplankton growth and microzooplankton grazing rate in the sea (Murrell et al. 2002; McManus et al. 2007; Chen et al. 2009), and should be taken into account in biogeochemical models (Gan et al. 2010).

Compositional changes and environmental factors complicate the scaling of temperature–rate relationships from individual species to the aggregate community rates of most interest to climate prediction and ocean biogeochemistry research. Such complications are the consequence of many interacting variables, which are often, and perhaps typically, nonlinear. Thus, theory derived from species-level or laboratory data may not easily translate into comparable responses for complex communities in natural systems. As part of our efforts to evaluate an MTE prediction about the changing relationship of microzooplankton herbivory to primary production in a warming ocean, here we have shown the value of modern statistical approaches (e.g., GAM) to help disentangle covarying environmental effects in field data on community-level rate processes. As we have shown, such an approach can provide important insights into underlying relationships and reasons why community responses may depart from theory, and they thus have the potential to lead to better understanding of natural system dynamics and future responses to global change.

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