Ecology, 88(4), 2007, pp. 817–822

RESOURCE LIMITATION OF BACTERIAL PRODUCTION DISTORTS THE TEMPERATURE DEPENDENCE OF OCEANIC CARBON CYCLING

Ángel López-Urrutia[1] and Xosé Anxelu G. Morán

Centro Oceanográfico de Gijón, Instituto Español de Oceanografía, Camín de L'Arbeyal, s/n, Xixón, Asturies, E-33212 Spain

Abstract. Our view of the effects of temperature on bacterial carbon fluxes in the ocean has been confounded by the interplay of resource availability. Using an extensive compilation of cell-specific bacterial respiration (BR_i) and production (BP_i), we show that both physiological rates respond to changing temperature in a similar manner and follow the predictions of the metabolic theory of ecology. Their apparently different temperature dependence under warm, oligotrophic conditions is due to strong resource limitation of BP_i but not of BR_i. Thus, and despite previous preconception, bacterial growth efficiency ($BGE = BP_i/[BP_i + BR_i]$) is not directly regulated by temperature, but by the availability of substrates for growth. We develop simple equations that can be used for the estimation of bacterial community metabolism from temperature, chlorophyll concentration, and bacterial abundance. Since bacteria are the greatest living planktonic biomass, our results challenge current understanding of how warming and shifts in ecosystem trophic state will modify oceanic carbon cycle feedbacks to climate change.

Key words: bacterial growth efficiency; bacterial production; bacterial respiration; carbon cycling; metabolic theory.

Introduction

Temperature affects most biological processes, including the rates at which organisms grow, respire, and reproduce (Gillooly et al. 2001, 2002, Brown et al. 2004). It is likely that the ongoing warming of the land and oceans will have profound effects on organism physiology and ecosystem properties. Being able to reliably document the direct response of the Earth's biota to changes in temperature is therefore essential to understand the impacts of global warming and the biosphere's feedback to climate change. But, in natural systems, there are many environmental factors other than temperature that covary and, if they also have an effect on organism metabolism, they could mask or modify the true effects of temperature.

Heterotrophic planktonic bacteria dominate the oceanic carbon cycle particularly in oligotrophic areas. They are responsible for a major proportion of oceanic respiration (del Giorgio and Duarte 2002, Robinson and Williams 2005) and their production fuels microbial food webs and therefore they have great influence on the biogeochemical fluxes of carbon and other elements in the oceans (Ducklow 2000). Both physiological processes, individual cell-specific bacterial production (BP_i) and respiration (BR_i), are strongly affected by temperature (White et al. 1991, Robinson and Williams 1993, Pomeroy and Wiebe 2001, Kirchman et al. 2005, Lopez-Urrutia et al. 2006). The bacterial growth efficiency (BGE) is the ratio between BP_i and the total organic carbon assimilated by bacteria ($BGE = BP_i/(BP_i + BR_i)$), i.e., BGE represents the amount of bacterial biomass produced per unit of organic carbon assimilated (del Giorgio and Cole 1998). Understanding the patterns of variation in BGE is fundamental for our knowledge of carbon cycling (del Giorgio et al. 1997, Kirchman 1997, Rivkin and Legendre 2001). There is a lack of consensus, however, on the factors that control BGE. There are currently two widespread types of models to predict variation in BGE. One reports that BGE is an inverse function of temperature (Rivkin and Legendre 2001) while the second model suggests that BGE is mainly controlled by BP_i and related to the availability of mineral nutrients and organic carbon (del Giorgio et al. 1997, del Giorgio and Cole 1998). The decision on which model to use has profound implications on current calculations of oceanic carbon cycling (Hoppe et al. 2002, Morán et al. 2002) and on the predictions of how global warming would modify the biogeochemical cycling of carbon in the upper ocean (Rivkin and Legendre 2001). The dependence of BGE on temperature has the implicit connotation that BP_i and BR_i respond to temperature in a different way. Similarly, the dependence of BGE on resource availability implies that BP_i and BR_i are differentially affected by resource limitation. Here, we use what to our knowledge is the most extensive compilation of oceanic bacterial production and respiration to date to show that neglecting the resource limitation of marine bacterial growth under warm, oligotrophic conditions has confounded our view of the effects of temperature on biogenic carbon cycling.

Manuscript received 29 September 2006; accepted 6 November 2006. Corresponding Editor: S. Findlay.

[1] E-mail: alop@gi.ieo.es

MATERIALS AND METHODS

Data compilation

We searched the primary literature for measurements of epipelagic (surface to 200 m) bacterial community production and concurrent information on bacterioplankton abundance and temperature. Chlorophyll concentration data were also gathered when available. Our study is restricted to marine environments, including coastal embayments that are rapidly renewed by oceanic waters; information from freshwater-influenced ecosystems including estuaries was not analyzed. In a few cases, where the original authors did not respond to our data request or could not be contacted, data were extracted from digitized figures or tables. Community production was divided by total bacterial abundance to obtain an estimate of cell-specific bacterial production (BP_i). Our data set consists of a total of 3195 BP_i measurements. A large amount of our BP_i data came from the U.S. Joint Global Ocean Flux Study (US JGOFS). Only BP_i estimates measured by the incorporation of ^{3}H-leucine (Leu) were considered. When BP_i was reported in units other than pmol Leu it was back converted using the factors in the original study. In order to avoid artifacts due to selection of different leucine to carbon conversion factors all data were then converted using a factor of 1.5 kg C/mol Leu (Kirchman 1993). Similarly, we gathered BR_i measurements from the literature. The data set in Lopez-Urrutia et al. (2006) consisting of 34 BR_i measurements was supplemented with more recent data and by data requests to the authors of the original studies, reaching a final data set of 205 measurements. BR_i was converted to carbon units using a common respiratory quotient of 0.89 (Williams and del Giorgio 2005). The full data set is available in the Supplement.

Calculation of BGE

BP_i measurements are not usually accompanied by concurrent measurement of BR_i. To analyze the dependence of BGE on temperature and resource availability we just need to compare the respective responses of BP_i and BR_i. But in order to obtain a visual representation of these effects on BGE we assigned a simulated BR_i to each BP_i measurement. This BR_i value was calculated, from the temperature associated with each BP_i measurement, using the relationship obtained between BR_i and temperature. BGE was then calculated from these paired BP_i and simulated-BR_i data. To take into account that a BR_i measurement contains variation not accounted for by temperature, we ran 1000 simulations where in each iteration we reestimated the coefficients of the BR_i vs. temperature relationship by sampling a multivariate normal distribution with variance–covariance matrix equal to that of the model parameters. With these new model parameters, we calculated a BR_i for each BP_i from its corresponding temperature and a normal deviate was added to each estimated BR_i. Then, with these paired BP_i–BR_i an estimate of BGE was calculated that takes into account both the observed variability in BP_i and BR_i.

RESULTS

Our data set covers a wide range of oceanic conditions and consists of over 3000 independent BP_i data points and over 200 BR_i measurements. Our analysis shows that BR_i increases exponentially with temperature from $-2°$ to 30°C while BP_i reaches a plateau at ~20°C (Fig. 1A). This differential response of BR_i and BP_i to temperature seems to give support to the hypothesis that BGE is an inverse function of temperature. Nevertheless, the relationship between BGE and temperature differs from the monotonic decrease in BGE with increasing temperature previously suggested (Rivkin and Legendre 2001) (Fig. 1B). If any pattern can be extracted from our BGE–temperature relationship it would be a peak of BGE at temperatures close to 15°C (Fig. 1B). Also, our estimated BGE are on average $<10\%$, much lower than those reported previously (Rivkin and Legendre 2001) suggesting that growth efficiencies assumed in many studies (20–50%) are seldom achieved under natural conditions.

A more in-depth analysis of our data set provides a contrasting view of the differential relationship of BP_i and BR_i with temperature and suggests that the reported temperature dependence of BGE (Rivkin and Legendre 2001) could be just a data collection artifact. When we take into account the trophic state of the ecosystem, commonly approached by using chlorophyll content as a proxy for phytoplankton biomass, we can clearly observe that the plateau reached at temperatures above 20°C is just due to the lack of situations of high resource availability under warm-water conditions (Fig. 2). When we divide our BP_i data set into oligotrophic, mesotrophic, and eutrophic conditions based on the chlorophyll concentration at each study site, the temperature dependence of BP_i is not significantly different from the temperature dependence of BR_i (test of parallelism of regression slopes, $F_{3,1595} = 2.21$, $P = 0.085$). The temperature dependence of biological processes has been traditionally expressed using the Van't Hoff–Arrhenius equation (Arrhenius 1915), also known as Boltzmann's factor (Gillooly et al. 2001, 2002, Brown et al. 2004, Allen et al. 2005). According to this expression, when we plot the natural logarithm of a metabolic rate against the temperature function $1/kT$, where k is Boltzmann's constant and T is the absolute temperature, the slope of this linear relationship represents the activation energy of that particular metabolic process (Gillooly et al. 2001, 2002, Brown et al. 2004, Allen et al. 2005). The activation energies for the temperature dependence of BR_i and BP_i (Figs. 1A and 2) are close to the activation energy of 0.65 eV (1 electron volt $= 1.602 \times 10^{-19}$ J) for heterotrophic organisms predicted by recent theories (Brown et al. 2004, Allen et al. 2005, Lopez-Urrutia et al. 2006). Hence, because BP_i and BR_i depend on

temperature following the same relationship, BGE is by necessity independent of temperature. The use of the BGE vs. temperature equation (Rivkin and Legendre 2001) would lead to an unrealistic assessment of the effects of global warming on oceanic carbon cycling. Furthermore, our analysis shows that global carbon cycle models based on individual metabolism with assumptions of temperature independence of the carbon use efficiency (Allen et al. 2005) could be applied to marine planktonic ecosystems.

On the other hand, accepting that higher chlorophyll concentrations represent higher resource availability for bacteria (Li et al. 2006), our results give support to the hypothesis that BGE varies systematically with the trophic state of the ecosystem (del Giorgio 1997, del Giorgio et al. 1998). Indeed, because BP_i depends on resource availability (Fig. 3A) while BR_i does not (Fig. 3B), there is a strong relationship between BGE and chlorophyll concentration (Fig. 3C). The equation we provide (Table 1) could be used to estimate BGE from the easier to quantify chlorophyll concentration. The effect of temperature and substrate availability on BP_i is not new to microbial ecologists (White et al. 1991, Pomeroy and Wiebe 2001). But in contrast to hypothesis suggesting a strong interaction between resource limitation and temperature (White et al. 1991, Pomeroy and Wiebe 2001), our analysis (Fig. 2) gives support to the idea that the effect of temperature and resource availability on BP_i are independent (Kirchman et al. 2005).

Discussion

It has been repeatedly recognized that our understanding of BGE and plankton community respiration is limited by the lack of knowledge of the factors that affect BR_i (Jahnke and Craven 1995, del Giorgio and Cole 1998, del Giorgio and Duarte 2002). Our analysis helps to fill this major gap in current knowledge. First we show that BR_i strongly depends on temperature (Fig. 1A) and that this temperature dependence is similar to that of BP_i (Fig. 2). Second, we show that, contrary to BP_i, which strongly depends on resource availability (Figs. 2 and 3A), BR_i seems to be unaffected by resource limitation (Fig. 3B). As a consequence, at resource-limiting conditions, while the assimilated carbon does decrease, the maintenance metabolism is held constant so bacteria have less carbon available for growth (i.e., reduced BGE). This is likely to have important consequences on population growth rates, sustainable bacterial populations, and the amount of carbon that is recycled through microbial food webs. It is therefore not surprising that bacterial abundance usually covariates with phytoplankton biomass in oceanic surface waters (Gasol and Duarte 2000, Li et al. 2004). Our results help to better understand the underlaying reasons for the coupled response of bacteria and phytoplankton populations to changing environmental conditions (Li et al. 2006). Although our analysis is restricted to marine

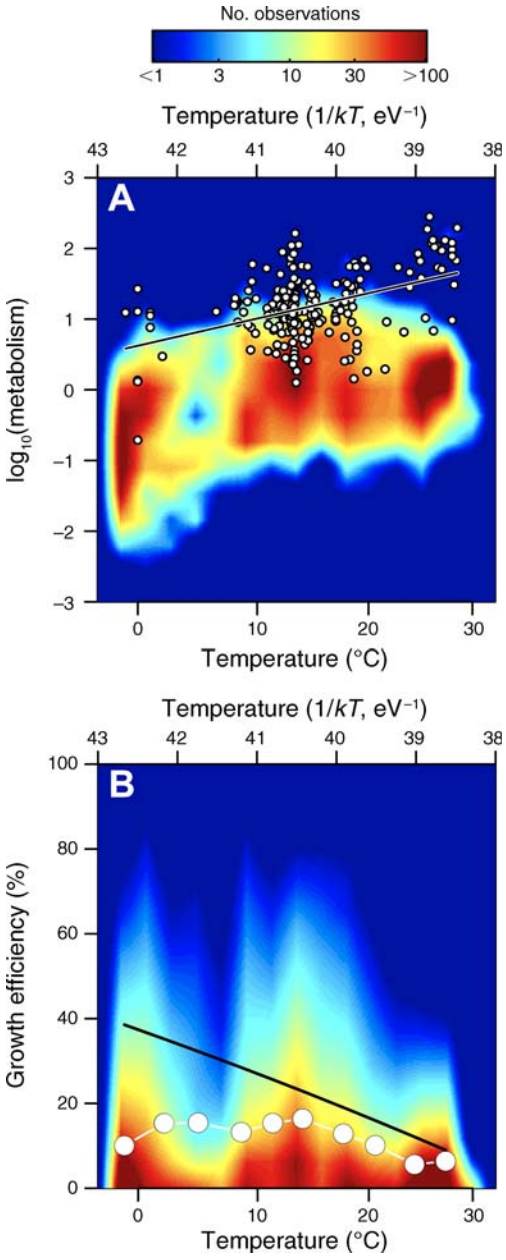

FIG. 1. Effects of temperature on bacterial production (BP_i), respiration (BR_i), and growth efficiency (BGE). (A) Arrhenius plot showing the effect of the temperature function ($1/kT$, upper axis; temperatures in degrees Celsius are presented in the lower axis for convenience) on BR_i (white circles) and BP_i (data density plot). Original units for metabolism (prior to log transformation) are fg C·cell^{-1}·d^{-1}. The black line represents the linear relationship between $\log_e(BR_i)$ and $1/kT$ ($y = 26.494 - 0.589x$, $r^2 = 0.20$, $F_{1,204} = 0.20$, $P < 0.001$; Table 1). (B) The relationship between BGE and temperature. The number of observations in the vertical scale should be multiplied by 1000 for BGE to take into account that the density plot represents the cumulative data set of BGE values obtained from the 1000 iterations in the simulations performed. White circles show the average BGE for 3°C temperature intervals. The black line represents the relationship derived by Rivkin and Legendre (2001).

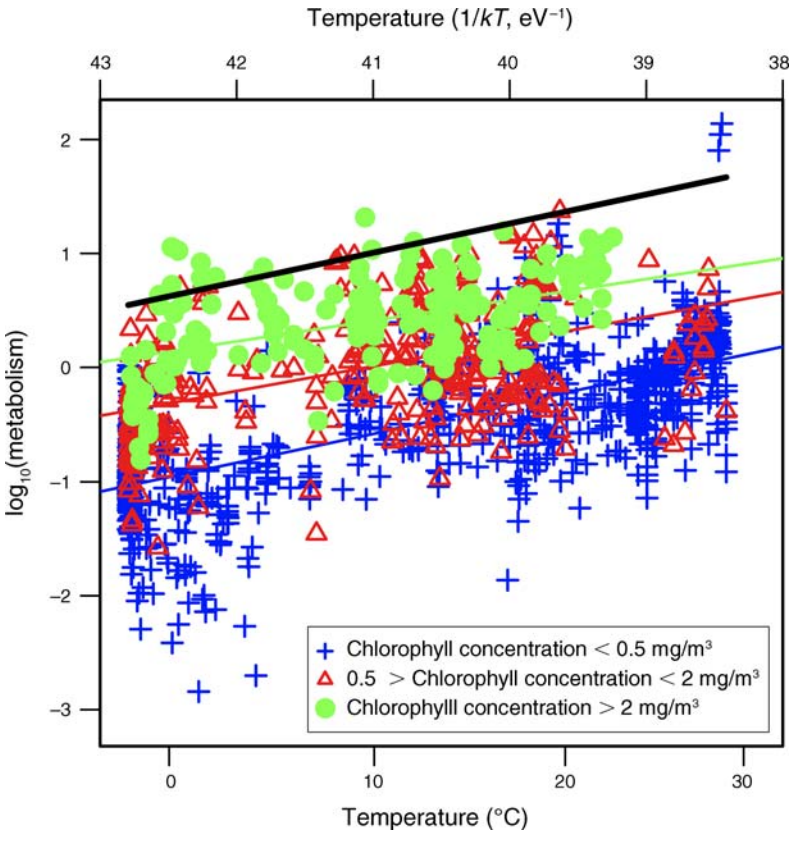

FIG. 2. Effect of temperature on bacterial production (BP_i) at three levels of resource availability. Original units for metabolism (prior to log transformation) are fg C·cell^{-1}·d^{-1}. Blue, red, and green symbols show data collected at chlorophyll concentrations lower than 0.5 mg/m^3, between 0.5 and 2 mg/m^3, and higher than 2 mg/m^3, respectively. The black line represents the relationship between temperature and respiration as shown in Fig. 1A. Colored lines show the respective relationship between $\log_e(BP_i)$ and $1/kT$ (blue line, $y = 22.58 - 0.583x$, $r^2 = 0.46$, $F_{1,850} = 728.9$, $P < 0.001$; red line, $y = 20.54 - 0.5x$, $r^2 = 0.23$, $F_{1,352} = 103.3$, $P < 0.01$; green line, $y = 18.14 - 0.42x$, $r^2 = 0.22$, $F_{1,189} = 53.66$, $P < 0.001$).

ecosystems, similar patterns have also been observed in freshwater-influenced environments (Shiah and Ducklow 1994, Apple et al. 2006). Apple et al. (2006) found that, in salt-marsh estuaries, BR_i was regulated almost exclusively by temperature while BP_i was controlled both by temperature and nutrient availability. Our analysis highlights the possibility that the plateau of BP_i at temperatures above 20°C also observed in estuarine ecosystems could again be due to the intervening effects of resource availability. For these type of systems, however, chlorophyll concentration is probably not such a good proxy for resource limitation, with the quality of the dissolved organic matter also playing a major role (Apple et al. 2006).

The fact that, even under resource-saturating conditions, BR_i doubles BP_i confirms the low BGE values reported for marine heterotrophic prokaryotes (del Giorgio et al. 1997, del Giorgio and Cole 1998) with maxima close to one-third (i.e., only 33% of the assimilated carbon is devoted to growth; Fig. 3). The values of BGE reported depend, however, on the particular leucine-to-carbon conversion factor used. Sensitivity analysis with conversion factors ranging from 0.5 to 3.1 kg C/mol Leu showed that our conclusion of the effects of resource availability on BP_i and BGE is robust to this source of error although the magnitude of BGE changed. For example, the range of the binned mean values presented in Fig. 3C would change from 5–32% BGE using a conversion factor of 1.5 kg C/mol Leu to BGE ranges of 2–17% and 9–45% for conversion factors of 0.5 and 3.1 kg C/mol Leu, respectively. Our results shed no light on whether the decrease in BP_i at low chlorophyll concentrations is due to all cells in the original population having a reduced production or due to the natural assemblage being composed of two or more fractions each with different BP_i (del Giorgio and Cole 1998). What our analysis suggests is that, if there is a partition of the population into cells of different activity, all have similar maintenance energy requirements since BR_i remains the same at different chlorophyll levels (Fig. 3B). This hypothesis is also supported by recent analysis where bacterial composition did not have such a clear-cut effect on BR_i as it had on BP_i (Reinthaler et al. 2005).

The implications of our work for global carbon flux models and climate change prediction scenarios are

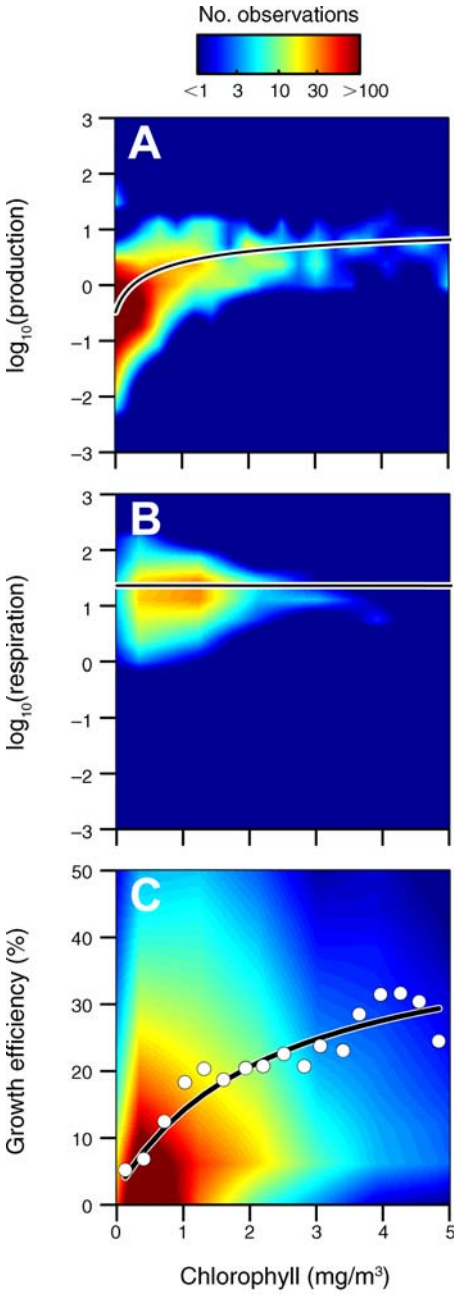

FIG. 3. Effect of resource limitation on (A) temperature-corrected bacterial production (BP_i), (B) temperature-corrected respiration (BR_i), and (C) bacterial growth efficiency (BGE). Original units for production and respiration (prior to log transformation) are fg C·cell^{-1}·d^{-1}. Original BP_i and BR_i data were corrected for the effect of temperature using an activation energy of 0.586 eV (see Figs. 1A and 2; Table 1). Data shown represent the calculated production and respiration at an average temperature of 15°C. The response of BP_i and BGE to changing chlorophyll concentration according to the equations in Table 1 at 15°C are shown as black lines (n = 1396 points). BR_i did not depend on chlorophyll concentration; the linear fit is shown only for reference ($t_{183} = 7.5 \times 10^{-4}$, P = 0.97, r^2 = 0.005). The number of observations in the scale should be multiplied by 1000 for BGE to take into account the number of simulations performed. In (C), circles show the average BGE for 0.3 mg/m^3 intervals.

TABLE 1. Effects of temperature and resource availability on cell-specific bacterial metabolism.

Parameter	Equation
BR_i	$3.21 \times 10^{11} e^{-0.589/kT}$
BP_i	$e^{-0.589/kT} \times \left[\frac{2.33 \times 10^{11}\,\text{chl}}{\text{chl} + 4.08} + 6.77 \times 10^{9}\right]$
BGE	$1 - \frac{1}{0.727 \times \frac{\text{chl}}{\text{chl} + 4.08} + 1.02}$

Notes: Equations show the formulations and estimated parameters for cell-specific bacterial respiration (BR_i), production (BP_i), and growth efficiency (BGE). For a description of the model derivation and fitting procedure, see the Appendix. BP_i and BR_i have units of fg C·cell^{-1}·d^{-1}, T is the absolute temperature, k is Boltzmann's constant (8.62×10^{-5} eV/K), and chl is the chlorophyll concentration in mg/m^3.

evident, given that BR_i may contribute a significant amount to total community respiration, frequently more than 50% (Rivkin and Legendre 2001, del Giorgio and Duarte 2002, Robinson and Williams 2005) and that BP_i represents one of the initial sources of carbon fuelled through the microbial food web. The confounding effects of temperature and resource availability on ecosystem carbon dynamics are tangible when direct measurements of the carbon flux in terrestrial and aquatic ecosystems have been analyzed (Enquist et al. 2003, Sobek et al. 2005). These studies have pointed out that variability in resource availability could mask the observed temperature dependence of CO_2 fluxes. Our work serves to disentangle the effects of temperature and resource availability and could be of use in coupled climate–ecosystem models. We show that both BR_i and BP_i are likely to be similarly modified by climate warming and that despite previous preconception there is no evidence that BGE would directly respond to warming. This does not mean, however, that BGE would not be modified with climate change. Current climate models predict a collapse in plankton stocks during the next century (Schmittner 2005) and an expansion of oligotrophic regions (Sarmiento et al. 2004). According to our results, this shift from higher to lower ecosystem trophic states will result in reduced BP_i but equal BR_i, hence lowering BGE (Fig. 3). This, combined with the expected increase in BP_i and BR_i due to higher temperatures, makes it difficult to foresee changes in bacterial biomass and microbial processes. Assuming constant bacterial biomass, however, with a higher relative increase of BR_i compared to BP_i, global change would translate into a net flux of CO_2 mediated by bacteria from the oceans to the atmosphere as a consequence of the mobilization of organic carbon, particulate plus dissolved, towards the inorganic pool.

ACKNOWLEDGMENTS

We thank J. M. Arrieta, A. Bode, N. Gonzalez, R. Lemée, K. Longnecker, E. F. Møller, N. Navarro, O. Pringault, T. Reinthaler, E. B. Sherr, and A. M. Staroscik for kindly

providing the BR_i and BP_i data. Special thanks go to the U.S. Joint Global Ocean Flux Study program and in particular to F. Azam, D. Smith, H. Ducklow, and D. Kirchman for making the BP_i data available. X. Irigoien, R. P. Harris, R. Scharek, S. V. Smith, and H. Ducklow provided useful comments.

Literature Cited

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. Linking the global carbon cycle to individual metabolism. Functional Ecology 19:202–213.

Apple, J. K., P. A. del Giorgio, and W. M. Kemp. 2006. Temperature regulation of bacterial production, respiration, and growth efficiency in a temperate salt-marsh estuary. Aquatic Microbial Ecology 43:243–254.

Arrhenius, S. 1915. Quantitative laws in biological chemistry. C. Bell and Sons, London, UK.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

del Giorgio, P. A., and J. J. Cole. 1998. Bacterial growth efficiency in natural aquatic systems. Annual Review of Ecology and Systematics 29:503–541.

del Giorgio, P. A., J. J. Cole, and A. Cimbleris. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385:148–151.

del Giorgio, P. A., and C. M. Duarte. 2002. Respiration in the open ocean. Nature 420:379–384.

Ducklow, H. W. 2000. Bacterioplankton production and biomass in the oceans. Pages 85–120 *in* D. Kirchman, editor. Microbial ecology of the oceans. Wiley, New York, New York, USA.

Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. Scaling metabolism from organisms to ecosystems. Nature 423:639–642.

Gasol, J. M., and C. M. Duarte. 2000. Comparative analyses in aquatic microbial ecology: how far do they go? FEMS Microbiology and Ecology 31:99–106.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. Nature 417:70–73.

Hoppe, H. G., K. Gocke, R. Koppe, and C. Begler. 2002. Bacterial growth and primary production along a north-south transect of the Atlantic Ocean. Nature 416:168–171.

Jahnke, R. A., and D. B. Craven. 1995. Quantifying the role of heterotrophic bacteria in the carbon cycle: a need for respiration rate measurements. Limnology and Oceanography 40:436–441.

Kirchman, D. L. 1993. Leucine incorporation as a measure of biomass production by heterotrophic bacteria. Pages 509–512 *in* P. F. Kemp, B. F. Sherr, E. B. Sherr, and J. J. Cole, editors. Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, Florida, USA.

Kirchman, D. L. 1997. Microbial breathing lessons. Nature 385:121–122.

Kirchman, D. L., R. R. Malmstrom, and M. T. Cottrell. 2005. Control of bacterial growth by temperature and organic matter in the Western Arctic. Deep-Sea Research II 52:3386–3395.

Li, W. K. W., W. G. Harrison, and E. J. H. Head. 2006. Coherent sign switching in multiyear trends of microbial plankton. Science 311:1157–1160.

Li, W. K. W., E. J. H. Head, and W. G. Harrison. 2004. Macroecological limits of heterotrophic bacterial abundance in the ocean. Deep-Sea Research II 51:1529–1540.

Lopez-Urrutia, A., E. San Martin, R. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. Proceedings of the National Academy of Sciences (USA) 103:8739–8744.

Morán, X. A. G., M. Estrada, J. M. Gasol, and C. Pedrós-Alió. 2002. Dissolved primary production and the strength of phytoplankton-bacterioplankton coupling in contrasting marine regions. Microbial Ecology 44:217–223.

Pomeroy, L. R., and W. J. Wiebe. 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquatic Microbial Ecology 23:187–204.

Reinthaler, T., C. Winter, and G. J. Herndl. 2005. Relationship between bacterioplankton richness, respiration, and production in the southern North Sea. Applied and Environmental Microbiology 71:2260–2266.

Rivkin, R. B., and L. Legendre. 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291:2398–2400.

Robinson, C., and P. J. l. B. Williams. 1993. Temperature and Antarctic plankton community respiration. Journal of Plankton Research 15:1035–1051.

Robinson, C., and P. J. l. B. Williams. 2005. Respiration and its measurement in surface waters. Pages 147–180 *in* P. del Giorgio and P. J. l. B. Williams, editors. Respiration in aquatic ecosystems. Oxford University Press, Oxford, UK.

Sarmiento, J. L., et al. 2004. Response of ocean ecosystems to climate warming. Global Biogeochemical Cycles 18:GB3003.

Schmittner, A. 2005. Decline of the marine ecosystem caused by a reduction in the Atlantic overturning circulation. Nature 434:628–633.

Shiah, F. K., and H. W. Ducklow. 1994. Temperature and substrate regulation of bacterial abundance, production and specific growth-rate in Chesapeake Bay, USA. Marine Ecology Progress Series 103:297–308.

Sobek, S., L. J. Tranvik, and J. J. Cole. 2005. Temperature independence of carbon dioxide supersaturation in global lakes. Global Biogeochemical Cycles 19:GB2003.

White, P. A., J. Kalff, J. B. Rasmussen, and J. M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microbial Ecology 33:99–118.

Williams, P. J. l. B., and P. del Giorgio. 2005. Respiration in aquatic ecosystems: history and background. Pages 1–17 *in* P. del Giorgio and P. J. l. B. Williams, editors. Respiration in aquatic ecosystems. Oxford University Press, Oxford, UK.

APPENDIX

Modeling heterotrophic bacterial metabolism (*Ecological Archives* E088-050-A1).

SUPPLEMENT

Cell-specific bacterial production and respiration data (*Ecological Archives* E088-050-S1).