

Temperature dependence of planktonic metabolism in the ocean

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Received 28 June 2010; revised 20 September 2011; accepted 29 November 2011; published 4 February 2012.

[1] Standard metabolic theory predicts that both respiration and photosynthesis should increase with increasing temperature, albeit at different rates. However, test of this prediction for ocean planktonic communities is limited, despite the broad consequences of this prediction in the present context of global ocean warming. We compiled a large data set on volumetric planktonic metabolism in the open ocean and tested the relationship between specific metabolic rates and water temperature. The relationships derived are consistent with predictions derived from metabolic theory of ecology, yielding activation energy for planktonic metabolism consistent with predictions from the metabolic theory. These relationships can be used to predict the effect of warming on ocean metabolism and, thus, the role of planktonic communities in the flow of carbon in the global ocean.

Citation: Regaudie-de-Gioux, A., and C. M. Duarte (2012), Temperature dependence of planktonic metabolism in the ocean, *Global Biogeochem. Cycles*, 26, GB1015, doi:10.1029/2010GB003907.

1. Introduction

[2] Ocean biota play through their metabolic processes a major role in controlling the CO₂ partial pressure and hence, the air-sea exchange, which depends, therefore, on the metabolic balance of planktonic communities [Calleja *et al.*, 2005]. The metabolic balance of planktonic communities refers to the balance between gross primary production (GPP) and community respiration (CR), defining whether plankton communities act as net CO₂ sources (CR > GPP) or sinks (CR < GPP) in the ecosystem. Although the metabolism of oceanic planktonic communities appears to be in approximate balance across large scales (GPP ≈ CR) [Duarte and Agustí, 1998; Williams, 1998; Duarte *et al.*, 2001; del Giorgio and Duarte, 2002], regional disequilibria may be brought about by allochthonous inputs of organic matter, which generates a potential for CR to exceed GPP [Smith and Hollibaugh, 1993; del Giorgio and Duarte, 2002; Duarte and Prairie, 2005] or upwelling of deep, nutrient-rich waters, which enhances GPP [Marra *et al.*, 1990; Falkowski *et al.*, 1998]. Metabolic processes are also greatly affected by temperature, as described by the Arrhenius equation, which represents the foundation of the metabolic theory of ecology [Brown *et al.*, 2004]. The metabolic theory of ecology introduced by Gillooly *et al.* [2001] and Brown *et al.* [2004] uses first principles to predict the role of temperature in regulating the metabolism of an ecosystem and how metabolic rate controls ecological processes at all levels of organization. Metabolic theory predicts that both respiration and photosynthesis should increase with increasing

temperature, albeit at different rates [Brown *et al.*, 2004; Harris *et al.*, 2006; López-Urrutia *et al.*, 2006].

[3] The predicted role of temperature in modulating metabolic rates is of fundamental importance as a framework to predict the response of the metabolic balance of planktonic communities in the ocean to global warming and, therefore, possible feedbacks between warming and the global carbon cycle. The Intergovernmental Panel on Climate Change (IPCC) predicts that increased greenhouse gases in the atmosphere are expected to raise air temperatures by about 3–4°C with an increase of sea surface temperature between 1 and 3°C [Houghton, 2001; IPCC, 2007]. In particular, metabolic theory predicts that heterotrophic respiration should increase faster in response to warming than production rate does [Harris *et al.*, 2006], thereby weakening CO₂ uptake by ocean biota [López-Urrutia *et al.*, 2006]. Metabolic theory predicts the activation energy for photosynthesis, describing its functional response to temperature, to be 0.32 eV, whereas that for respiration is expected to be 0.65 eV [López-Urrutia *et al.*, 2006]. However, test of this prediction for ocean planktonic communities is limited, despite the broad consequences of this prediction in the present context of global ocean warming, because the temperature dependence of planktonic metabolism in the ocean has not yet been examined at the global scale.

[4] We examine here the temperature-dependence of planktonic metabolism in the oceans. We do so on the basis of a data set including 1156 volumetric estimates of oceanic planktonic metabolism and temperature in the euphotic layer of the ocean, where planktonic communities receive sufficient sunlight for photosynthesis. We test here the predicted rate of increase in photosynthesis and respiration with increasing temperature and use the relationships derived here to formulate predictions on the role of ocean biota in CO₂ budgets in a warmer ocean.

2. Methods

[5] A database containing volumetric (i.e., per unit volume) estimates of GPP (Gross Primary Production) and CR

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Table 1. Sources of Data on Plankton Metabolic Rates, Water Temperature and Chlorophyll A Concentration for Different Oceans and the Number of Observations Derived From Each of Them (N Data)

Ocean	Reference	N Data	Ocean	Reference	N Data
Arctic	<i>Cota et al.</i> [1996]	37	Mediterranean Sea	<i>Navarro et al.</i> [2004]	15
	<i>Cottrell et al.</i> [2006]	59		<i>Regaudie-de-Gioux et al.</i> [2009]	44
	<i>Regaudie-de-Gioux and Duarte</i> [2010a]	66		D. Lefèvre, unpublished data (2005) ^a	41
	<i>Robinson et al.</i> [2002] ^b	34		Antarctic	<i>Agusti et al.</i> [2004]
R. Vaquer-Sunyer, unpublished data, (2006)	79	<i>Bender et al.</i> [2000]	58		
Atlantic	<i>González et al.</i> [2002]	22	S. Blight, unpublished data (1994); <i>Blight</i> [1996]		17
	<i>González et al.</i> [2003]	12	<i>Dickson and Orchado</i> [2001]		12
	<i>Morán et al.</i> [2004]	33	<i>Lefèvre et al.</i> [2008]	42	
	<i>Regaudie-de-Gioux and Duarte</i> [2010b]	71	N. Navarro et al., unpublished data (2005)	33	
	<i>Robinson et al.</i> [2006] ^b	11	<i>Odate et al.</i> [2002]	12	
	<i>Serret et al.</i> [1999]	45	A. Regaudie-de-Gioux, unpublished data (2009)	74	
	<i>Serret et al.</i> [2001b]	20	<i>Robinson et al.</i> [1999] ^b	11	
Pacific	<i>Serret et al.</i> [2001b]; <i>Robinson et al.</i> [2002] ^b	111	Indian	<i>Robinson et al.</i> [2001a] ^c	20
	<i>Teira et al.</i> [2001]	31		<i>Dickson et al.</i> [2001]	19
	D. Karl et al., unpublished data (2007–2009) ^d	14		<i>Robinson and Williams</i> [1999] ^b	35
	<i>Williams et al.</i> [2004]	55			
	C. M. Duarte, unpublished data (2009)	15			
Total N Data		1156			

^aData held at C. Robinson database at www.pml.ac.uk/amt/data/respiration.xls.

^bData also held at the British Oceanographic Data Centre (www.bodc.ac.uk).

^cData held at PANGEA data collection.

^dData held at CMORE data collection.

(Community Respiration) across the euphotic zone of the ocean, where planktonic communities receive sufficient sunlight for photosynthesis, was composed by compounding the data set compiled by *Robinson and Williams* [2005], with recently published data and our own unpublished data (A. Regaudie-de-Gioux and C. M. Duarte, 2006–2010). The data was extracted from 32 individual reports collected between 1996 and 2010, from stations in the Open Ocean and the Mediterranean Sea (Table 1). The resulting database contained 1156 estimates of volumetric metabolic rates and the corresponding water temperature (Table 1 and Figure 1). For each report, the chlorophyll a concentration and bacterial abundance were recorded when reported.

[6] Warm ocean waters are typically prevalent in oligotrophic, regions of the oceans whereas cold waters are generally more productive, supporting higher plankton biomass, as is evident from examining the correspondence between global maps of chlorophyll a and temperature in the ocean [*Hoegh-Guldberg and Bruno*, 2010]. Hence, the examination of the role of temperature in regulating metabolic rates needs to account for co-variance between temperature and plankton biomass in the ocean. We, therefore, standardized rates to chlorophyll a concentration, as the most widely available metric of plankton biomass. The relationship between metabolic rates and temperature was examined here

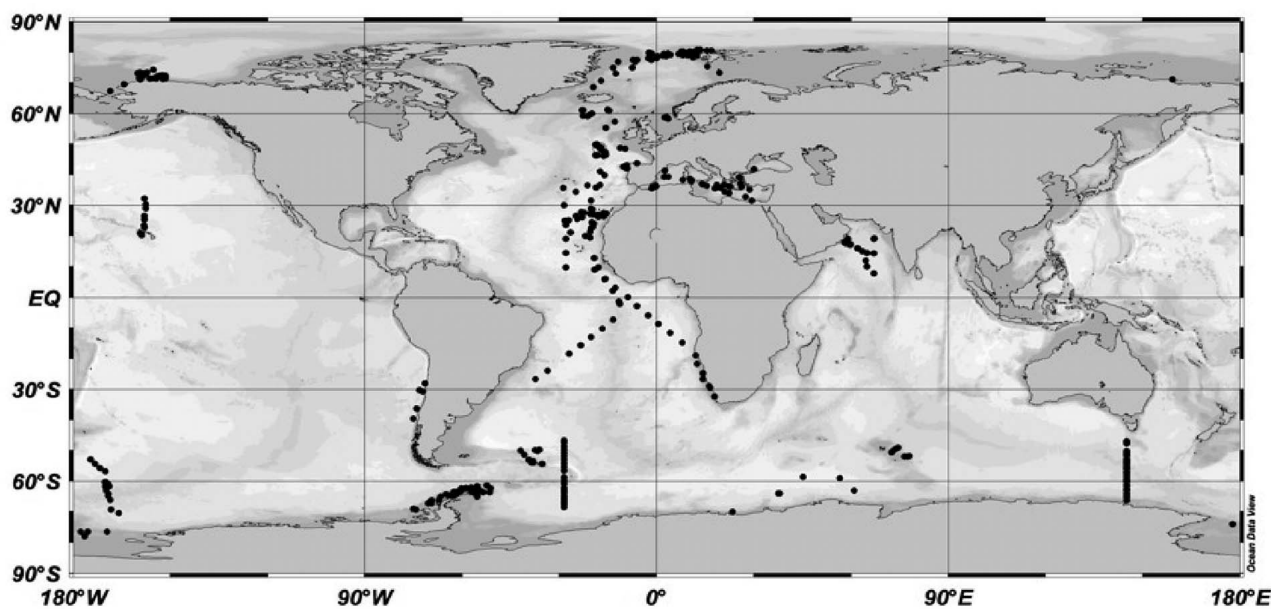


Figure 1. Map showing the locations in the data set (Table 1) containing records of plankton metabolic rates, water temperature and chlorophyll a concentration (Table 1).

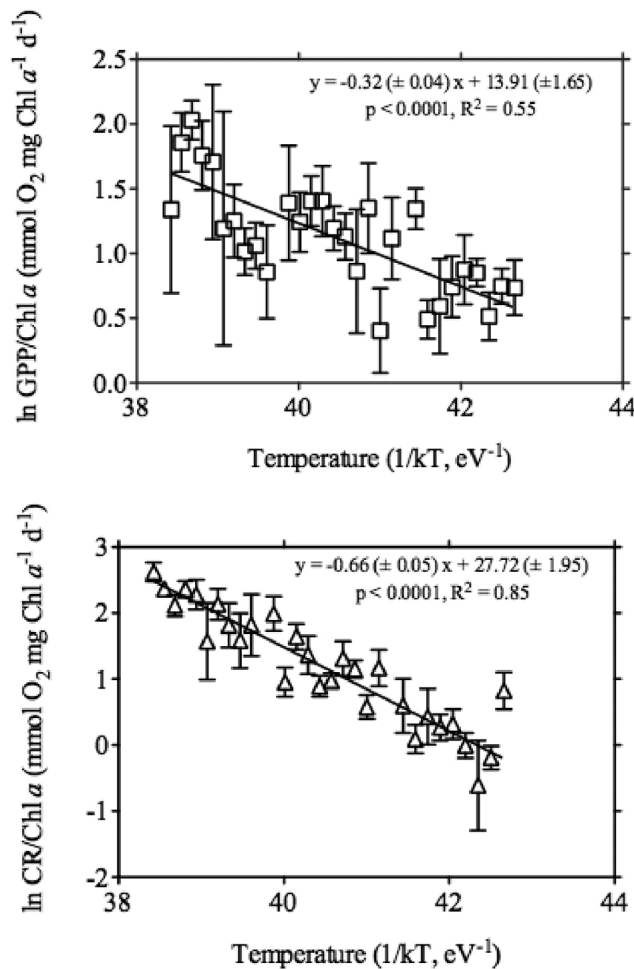


Figure 2. The relationship between the natural logarithm of the average \pm SE volumetric specific chlorophyll *a* metabolic rates within 1°C bins (GPP, a, and CR, b) and the inverted water temperature ($1/kT$ with k , the Boltzmann's constant ($8.617734 \cdot 10^{-5} \text{ eV K}^{-1}$) and with T , the water temperature ($^{\circ}\text{K}$)). The solid line shows the regression equation fitted using model II regression.

on the basis of chlorophyll *a* specific metabolic rates. The specific metabolic rates were subsequently binned by one $^{\circ}\text{C}$ interval before analyses. The relationship between the natural logarithm of the specific metabolic rates and water temperature was examined by fitting a model II regression equation describing the relationship between the natural logarithm of specific chlorophyll *a* metabolic rates and the reciprocal of temperature in $^{\circ}\text{Kelvin}$ [Gillooly *et al.*, 2001; Brown *et al.*, 2004]. The regression slope, a , equals:

$$a = -Ea/k \quad (1)$$

Where Ea represents the average activation energy and k is the Boltzmann's constant ($8.617734 \cdot 10^{-5} \text{ eV K}^{-1}$). Thus, the activation energy can be calculated from the regression slope as:

$$Ea = -a k \quad (2)$$

The Q_{10} describing the temperature-dependence of the metabolic rate was determined following Dixon and Webb [1964] as

$$Q_{10} = \exp(10 Ea/k.T^2) \quad (3)$$

where T is the mean temperature ($^{\circ}\text{K}$) in the database.

3. Results

[7] The chlorophyll *a* specific GPP and CR rates increased significantly with increasing water temperature (Figure 2), although the relationship between the specific CR and temperature was much stronger than that for GPP ($R^2 = 0.85$ and 0.55 , respectively, both $P < 0.0001$). No significant relationship was observed between the specific chlorophyll *a* NCP (Net Community Production) and the temperature ($R^2 = 0.12$, $P = 0.0769$) (data not shown here). No significant relationship was observed between the specific bacterial abundance CR rates and temperature ($R^2 = 0.00$, $P = 0.86$). Hence, accounting for differences in bacterial abundance across communities did not contribute to explain differences in community respiration rate with temperature increase.

[8] The corresponding activation energy describing the temperature-dependence of specific GPP and CR rates of planktonic communities in the ocean averaged (\pm SE) $0.32 \pm 0.04 \text{ eV}$ for GPP_{Chla} and $0.66 \pm 0.05 \text{ eV}$ for CR_{Chla} , corresponding to average Q_{10} values of 1.56 for GPP and 2.52 for CR rates.

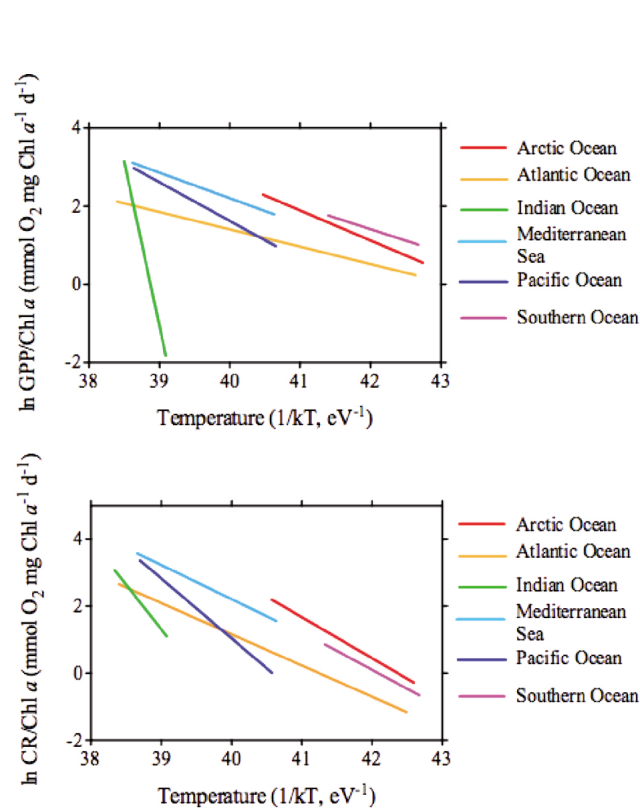
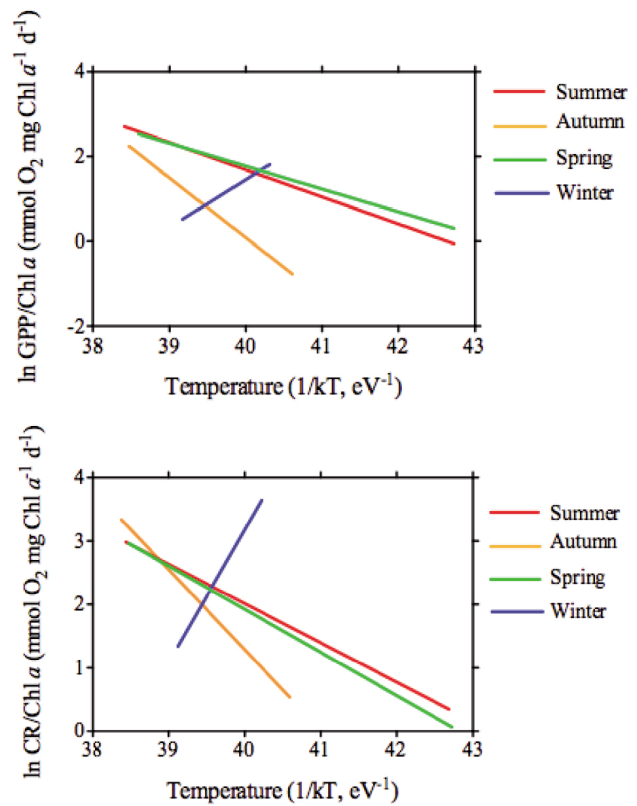
[9] The specific GPP and CR, relative to chlorophyll *a*, increased with increasing water temperature for communities at all oceans and the Mediterranean Sea (Table 2 and Figure 3) albeit at different rates. In this study, planktonic communities from the Indian Ocean showed the highest activation energy describing the temperature-dependence of specific GPP and CR, with on average (\pm SE), $10.83 \pm 3.32 \text{ eV}$ for GPP_{Chla} and $3.19 \pm 0.60 \text{ eV}$ for CR_{Chla} (Table 2). On contrary, planktonic communities from the Atlantic Ocean showed the lowest activation energy describing the temperature-dependence of specific GPP and CR, with, on average, $0.52 \pm 0.11 \text{ eV}$ for GPP_{Chla} and $0.92 \pm 0.11 \text{ eV}$ for CR_{Chla} (Table 2).

[10] The temperature-dependence of specific GPP and CR varied also between the different seasons (Table 2 and Figure 4). During the summer, the spring and the autumn, the specific chlorophyll *a* GPP and CR increased with increasing water temperature (Table 2 and Figure 4). The highest activation energy was observed during the autumn, with, on average, $1.30 \pm 0.34 \text{ eV}$ for GPP_{Chla} and $0.94 \pm 0.15 \text{ eV}$ for CR_{Chla} (Table 2), and the lowest activation energy was observed during the spring, with on average, $0.59 \pm 0.12 \text{ eV}$ for GPP_{Chla} and $0.67 \pm 0.09 \text{ eV}$ for CR_{Chla} (Table 2). Winter specific CR was independent of temperature ($P = 0.541$) and the specific GPP showed a weak tendency to decrease with increasing temperature ($P = 0.031$), but the temperature range for this relationship was rather narrow and the significance of the relationship was driven by a single data point (Table 2 and Figure 4). The specific GPP and CR of the planktonic communities studied here increased with increasing water temperature in communities at both hemispheres (Table 2 and Figure 5). The activation energies for GPP_{Chla} and CR_{Chla} were comparable for the Southern and Northern Hemispheres (Table 2).

Table 2. Parameters of the Relationship Between the Natural Logarithm of Chlorophyll A–Specific Metabolic Rates ($\text{mmol O}_2 \text{ mg Chl a}^{-1} \text{ d}^{-1}$) Versus Inverted Temperature (eV^{-1}) for the Different Oceans, Seasons and Hemispheres^a

Ocean, Season, or Hemisphere	Temperature Range	N	Slope (\pm SE)	Intercept (\pm SE)	R ²	P	Ea	Q ₁₀
<i>Regression: Ln GPP/Chla vs. 1/kT</i>								
Arctic Ocean	−1°C–13°C	13	−1.00 \pm 0.23	42.65 \pm 9.64	0.41	0.0185	1.00 \pm 0.23	4.45
Atlantic Ocean	0°C–29°C	22	−0.52 \pm 0.11	21.8 \pm 4.6	0.04	0.3936	0.52 \pm 0.11	2.04
Indian Ocean	23°C–29°C	5	−10.83 \pm 3.32	420.0 \pm 128.5	0.72	0.07	10.83 \pm 3.32	> 10
Mediterranean Sea	13°C–27°C	15	−0.96 \pm 0.23	40.34 \pm 9.27	0.23	0.0688	0.96 \pm 0.23	3.66
Pacific Ocean	13°C–27°C	11	−1.18 \pm 0.31	48.38 \pm 12.16	0.39	0.0401	1.18 \pm 0.31	4.93
Southern Ocean	−1°C–11°C	8	−0.65 \pm 0.15	28.20 \pm 6.43	0.67	0.0136	0.65 \pm 0.15	2.65
Winter	15°C–23°C	5	1.21 \pm 0.29	−47.01 \pm 11.34	0.83	0.0308	−1.21 \pm 0.29	0.19
Spring	−1°C–28°C	20	−0.59 \pm 0.12	25.61 \pm 4.79	0.29	0.0150	0.59 \pm 0.12	2.28
Summer	−1°C–29°C	27	−0.65 \pm 0.08	27.54 \pm 3.24	0.62	< 0.0001	0.65 \pm 0.08	2.50
Autumn	13°C–29°C	16	−1.30 \pm 0.34	52.03 \pm 13.64	0.00	0.8118	1.30 \pm 0.34	5.73
Northern Hemisphere	−1°C–29°C	29	−0.48 \pm 0.07	20.52 \pm 2.92	0.39	0.0003	0.48 \pm 0.07	1.96
Southern Hemisphere	−1°C–19°C	15	−0.45 \pm 0.09	19.56 \pm 3.83	0.44	0.0071	0.45 \pm 0.09	1.93
<i>Regression: Ln CR/Chla vs. 1/kT</i>								
Arctic Ocean	−1°C–13°C	13	−1.14 \pm 0.29	48.22 \pm 11.89	0.30	0.0513	1.14 \pm 0.29	5.47
Atlantic Ocean	0°C–29°C	23	−0.92 \pm 0.11	37.96 \pm 4.28	0.73	< 0.0001	0.92 \pm 0.11	3.53
Indian Ocean	23°C–29°C	5	−3.19 \pm 0.60	125.65 \pm 23.29	0.89	0.0153	3.19 \pm 0.60	> 10
Mediterranean Sea	13°C–27°C	15	−1.10 \pm 0.29	46.20 \pm 11.36	0.12	0.2106	1.10 \pm 0.29	4.42
Pacific Ocean	13°C–27°C	13	−1.64 \pm 0.34	66.62 \pm 13.59	0.52	0.0055	1.64 \pm 0.34	9.18
Southern Ocean	−1°C–11°C	8	−1.03 \pm 0.39	43.31 \pm 16.23	0.15	0.3433	1.03 \pm 0.39	4.70
Winter	15°C–23°C	4	2.13 \pm 1.34	−83.50 \pm 53.08	0.21	0.5411	−2.13 \pm 1.34	0.06
Spring	−1°C–28°C	21	−0.67 \pm 0.09	28.68 \pm 3.74	0.63	< 0.0001	0.67 \pm 0.09	2.55
Summer	−1°C–29°C	29	−0.76 \pm 0.08	31.85 \pm 3.35	0.68	< 0.0001	0.76 \pm 0.08	2.92
Autumn	13°C–29°C	17	−0.94 \pm 0.15	38.50 \pm 6.05	0.60	0.0003	0.94 \pm 0.15	3.53
Northern Hemisphere	−1°C–29°C	29	−0.64 \pm 0.07	27.30 \pm 2.96	0.65	< 0.0001	0.64 \pm 0.07	2.45
Southern Hemisphere	−1°C–19°C	19	−0.64 \pm 0.09	26.96 \pm 3.75	0.65	< 0.0001	0.64 \pm 0.09	2.50

^aThe temperature range (°C), number of binned points (N), slope (\pm Standard Error), intercept (\pm Standard Error), R², probability (P), activation energy (Ea, eV), and Q₁₀ are reported.

**Figure 3.** Regression lines (model II regression) of the relationships between the natural logarithm of the specific metabolic rates (GPP and CR) and the inverted water temperature for the different oceans.**Figure 4.** Regression lines (model II regression) of the relationships between the natural logarithm of the specific metabolic rates (GPP and CR) and the inverted water temperature at different seasons.

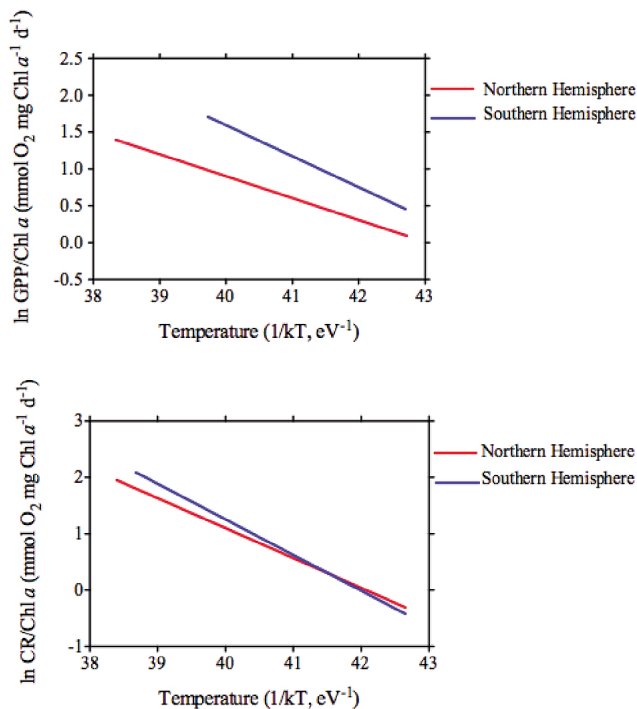


Figure 5. Regression lines (model II regression) of the relationships between the natural logarithm of the specific metabolic rates (GPP and CR) and the inverted water temperature for the two different hemispheres.

[11] No significant relationship was observed between the P/R ratio and temperature for communities growing in waters warmer than 21°C ($R^2 = 0.06$, $P = 0.5414$) whereas a strong negative relationship was observed between the P/R ratio and temperature in waters colder than 21°C ($R^2 = 0.55$, $P < 0.05$, Figure 6). Furthermore, 62% of the communities in our data set growing in waters warmer than 21°C were heterotrophic compared to only 36% in waters colder than 21°C.

4. Discussion

[12] The results derived here showed a strong temperature-dependence of the *chl a*-specific metabolic rates of oceanic planktonic communities across the ocean, consistent with the dependence of mass-normalized metabolic rates on temperature expected from metabolic theory [West *et al.*, 1997; Gillooly *et al.*, 2001; Brown *et al.*, 2004; Harris *et al.*, 2006; López-Urrutia *et al.*, 2006]. Moreover, as predicted from metabolic theory [Harris *et al.*, 2006; López-Urrutia *et al.*, 2006], the temperature dependence of community respiration was stronger, as reflected in a higher activation energy, $E_a = 0.66 \pm 0.04$ eV, for community respiration than for gross primary production, $E_a = 0.32 \pm 0.05$ eV. This results, in turn, in a decline in the P/R ratio for planktonic communities with increasing temperature, also in agreement with predictions from metabolic theory [Harris *et al.*, 2006; López-Urrutia *et al.*, 2006].

[13] This study reveals a general temperature-dependence of *chl a*-specific metabolic rates of oceanic planktonic communities. Indeed, the *chl a*-specific metabolic rates (GPP and

CR) tended to increase with increasing temperature for the different oceans, for the different hemispheres and at different seasons, except for winter (Figures 3, 4, and 5 and Table 2). There was no relationship between the *chl a*-specific CR and temperature and that for *chl a*-specific CR was weak and driven by a single data point (Table 2; also see the auxiliary material), possibly because less than 20% of the data set was obtained in winter.¹

[14] Rivkin and Legendre [2001] reported an inverse relationship between temperature and bacterial growth efficiency (BGE), with a decrease of BGE by 2.5% per 1°C increase, suggesting that bacteria should allocate a larger fraction of the carbon flow to respiration as temperature increases. Here, no significant relationship was observed between the bacterial abundance-specific respiration rates and water temperature, whereas strong patterns emerged when examining chlorophyll-specific respiration rates.

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GB003907.

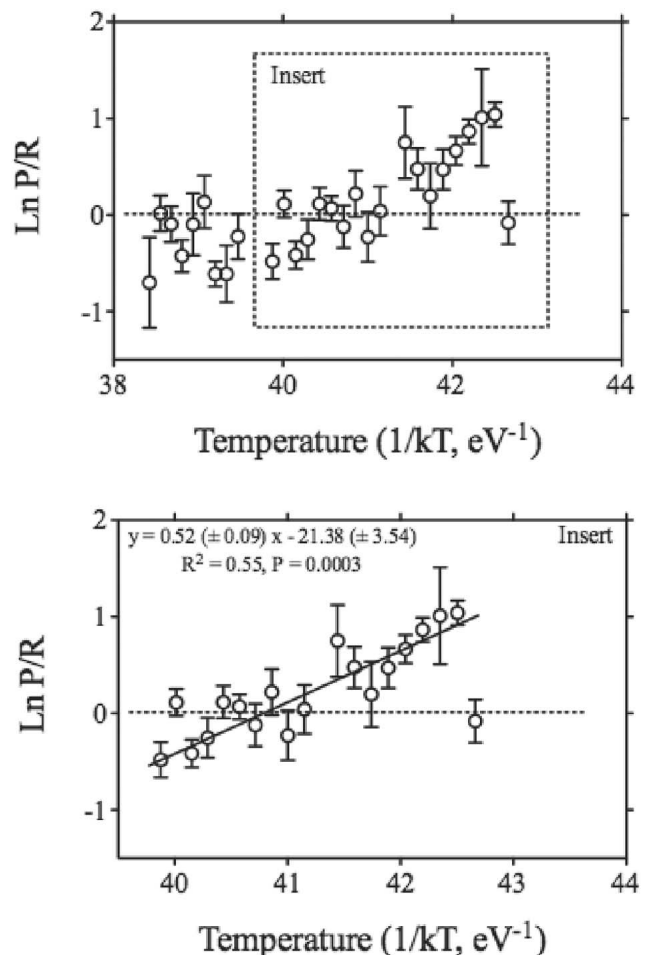


Figure 6. The relationship between the average \pm SE volumetric natural logarithm of P/R ratio within 1°C bins and the inverted water temperature ($1/kT$ with k , the Boltzmann's constant ($8.617734 \cdot 10^{-5}$ eV K⁻¹) and with T , the water temperature (°K)). The solid line shows the regression equation fitted using model II regression and the dashed line represents the line $P/R = 1$.

Failure of standardization to bacterial abundance to help explain responses of community respiration to temperature suggests that bacterial abundance maybe a weak descriptor of bacterial respiration, possibly because a substantial fraction of the cells in bacterial communities are metabolically inactive [Gasol *et al.*, 1995]. Community respiration is the sum of the contributions of autotrophs (R_a) and heterotrophs (R_h). Whereas chlorophyll a concentrations may be expected to be best related to R_a , they do also relate to R_h through a variety of processes affecting R_h mediated by autotrophic biomass, including food availability to support zooplankton metabolism, and the flux of dissolved organic matter from autotrophs through extracellular release, sloppy feeding and viral lysis. Chlorophyll a, therefore, serves as a proxy for the potential energy dissipation in the ecosystem, thus explaining the strong relationships between the CR/Chl a ratio and temperature reported here. Furthermore, the majority of the respiration data analyzed in this work were collected during summer and spring (85% of the data), when the contribution of autotrophic respiration to plankton community respiration is likely to be higher, further accounting for the effectiveness of the CR/Chl a ratio in revealing the temperature dependence of plankton respiration rates. In contrast, however, standardizing respiration rates to chlorophyll a helped derive the different responses to temperature increasing noticed between this study and temperature-dependence of respiration rates, consistent with the strong relationship between community respiration rates and chlorophyll a concentration reported in earlier comparative analyses [Robinson and Williams, 2005].

[15] The activation energy observed here for community respiration was similar to that observed by Yvon-Durocher *et al.* [2010] for freshwater CR ($E_a = 0.62$ eV). However, the E_a for gross production observed here was lower than that observed by Yvon-Durocher *et al.* [2010] ($E_a = 0.45$ eV). Yvon-Durocher *et al.* [2010] examined the temperature dependence on the metabolic balance of freshwater planktonic communities using mesocosms controlling environmental conditions, such as temperature and nutrient concentration. The difference observed between the E_a for GPP can be explained by limitations of mesocosms, such as differences in light attenuation and differences of wall area to the unit volume of the containers [Petersen *et al.*, 1997].

[16] Steeper activation energies for specific GPP ($E_a = 0.52$ eV) and CR ($E_a = 0.92$ eV) were observed for planktonic communities from the Atlantic Ocean (Table 2) than those derived by López-Urrutia *et al.* [2006] for Atlantic communities ($E_{aGPP} = 0.32$ eV and $E_{aCR} = 0.65$ eV). López-Urrutia *et al.* [2006] derived the E_a for planktonic production on the basis of particulate primary production derived with the ^{14}C method [Steeman Nielsen, 1952], which underestimates gross primary production due to remineralization and release as dissolved organic carbon (DOC) of some of the organic carbon produced during the incubation period [Bender *et al.*, 1987]. Peterson [1980] reported that the ^{14}C method underestimated the GPP rates by a factor of 2 to 100. Moreover, these effects maybe temperature-dependent as planktonic communities in warm oceanic waters often release a higher percent of the fixed carbon as DOC [Zlotnik and Dubinsky, 1989] and remineralization rates are likely to be higher in warmer waters, which support higher specific

respiration rates, thereby introducing bias in the estimates of primary production derived from the ^{14}C method.

[17] The global activation energy observed in this study for community respiration ($E_{aCR} = 0.66 \pm 0.04$ eV) is comparable to the activation energy of planktonic respiration observed by Aristegui and Montero [1995] ($E_{aCR} = 0.70 \pm 0.09$ eV) derived from ETS (Electron Transport System) activity. However, the activation energy for community respiration is much higher than reported earlier from ETS activity for Antarctic plankton communities (Mean $E_a = 1.03$ eV, this study; Mean $E_a = 0.52$ eV, Aristegui and Montero [1995]; Mean $E_a = 0.52$ eV, Martínez and Estrada [1992]), as well as for the Pacific Ocean (Mean $E_a = 1.64$ eV, this study; Mean $E_a = 0.69$ eV, Packard *et al.* [1975]), and the Arctic Ocean (Mean $E_a = 1.14$ eV, this study; mean $E_a = 0.50$ eV, Martínez [1992]). Those published activation energies derived from, for each study, one experimental oceanographic cruise and one region of the studied ocean. In contrast, in this study, the activation energies reported for the different oceans derived from broad comparative analyses across natural communities often encompassing multiple cruises.

[18] The Q_{10} for CR in this study (Table 2) was lower than the Q_{10} for CR reported in the past, including Arctic planktonic communities (Mean $Q_{10} = 5.47$, this study; Mean $Q_{10} = 8.54 \pm 2.88$, Vaquer-Sunyer *et al.* [2010]), Antarctic planktonic communities (Mean $Q_{10} = 4.70$, this study; Mean $Q_{10} = 4.93 \pm 1.10$, Robinson and Williams [1993]) or temperate planktonic communities (Mean $Q_{10} = 3.53$, this study; Mean $Q_{10} = 5.53 \pm 0.60$, Lefèvre *et al.* [1994]). However, the Q_{10} for primary production derived in this study (Table 2) was higher than published Q_{10} estimates for primary production evaluated for Antarctic planktonic communities (Mean $Q_{10} = 2.65$, this study; Mean $Q_{10} = 1.62 \pm 0.41$, Neori and Holm-Hansen [1982]), Arctic planktonic communities (Mean $Q_{10} = 4.45$, this study; Mean $Q_{10} = 1.19 \pm 0.10$, Michel *et al.* [1989]) and temperate planktonic communities (Mean $Q_{10} = 2.04$, this study; Mean $Q_{10} = 1.81 \pm 0.28$, Lefèvre *et al.* [1994]). Published estimates of Q_{10} values for community metabolism have all been derived experimentally, through short-term experiments across temperature gradients. These experiments do not allow the planktonic community structure to change in response to temperature, whereas the Q_{10} values reported here derive from a large number of natural communities growing across a range of ambient temperatures. Q_{10} values derived from comparative analyses across natural communities, such as those reported here, can reflect effects derived from responses in community structure and relevant processes other than the direct physiological effect of temperature on metabolism that co-vary with temperature. Indeed, the primary production contributed by picoplankton increases strongly with increasing temperature in oceanic communities, from < 10% in polar waters to > 50% in warm tropical waters [Agawin *et al.*, 2000]. A dominance of picoplankton has been associated with low P/R ratio [Serret *et al.*, 2001a], and the percent extracellular release by primary producers tends to be greater in warmer waters [Zlotnik and Dubinsky, 1989], which also should enhance respiration rates. Accordingly, a greater fraction of primary production is channeled through the microbial food web in warm, picoplankton-dominated waters. Metabolic theory predicts that specific

metabolic rates should increase with decreasing size [Peters, 1983; West *et al.*, 1997; Gillooly *et al.*, 2001; Brown *et al.*, 2004]. The tendency for autotroph cell size to decrease with increasing temperature, with an associated increase in specific metabolic rates, compounds with the direct effect of temperature on metabolism to yield the higher activation energy and Q_{10} values derived here compared to those expected on the basis of the effect of temperature on specific metabolism alone.

[19] Our results show that, in waters colder than 21°C, the P/R ratio tends to decline with increasing temperature, as a result of the steeper temperature-dependence of community respiration compared to gross primary production. Indeed, our results show that the planktonic communities in water warmer than 21°C tend to be heterotrophic. This is consistent with the observation that communities in tropical and subtropical oceans are often been reported to be heterotrophic [Duarte and Agustí, 1998; Duarte *et al.*, 2001; Williams *et al.*, 2004] with these regions often acting as CO₂ sources to the atmosphere [Duarte and Prairie, 2005].

[20] Differences have been observed along the latitudes in CO₂ exchange, with positive mean net air-sea CO₂ flux at low-latitude and with negative mean net air-sea CO₂ flux at high-latitude [Takahashi *et al.*, 2002]. The strong CO₂ uptake in polar oceans is mainly due to the efficiency of the solubility pump. Indeed, sequestration of atmospheric CO₂ in the ocean is controlled by the formation of cold, dense water masses at high latitudes [Falkowski *et al.*, 2000]. Global warming may affect the efficiency of the solubility pump at high latitude, affecting the thermohaline circulation and ocean ventilation. Whereas the reduction on net community metabolism with warming discussed here is also expected to operate in the polar oceans [e.g., Vaquer-Sunyer *et al.*, 2010], reduced ice cover may also increase light availability and, thus, net community production [Arrigo *et al.*, 2008]. However, the sequestration of atmospheric CO₂ at high-latitudes due to the solubility pump is also expected to weaken with ocean warming [Takahashi *et al.*, 2002; Le Quéré *et al.*, 2007]. Furthermore, the net flux of CO₂ between the atmosphere and the ocean is controlled by the balance between primary production, community respiration and the dissolved and biogenic carbon export [Rivkin and Legendre, 2001]. The major limitations of the planktonic metabolism are the light, the nutrient availability and the temperature [Field *et al.*, 1998]. In addition so to the differences in incident radiation, rates of nutrient and CO₂ solubility, our suggestion that autotrophic communities should prevail in high-latitude ocean is consistent with observations [Hoppe *et al.*, 2002] and the role of these regions as strong CO₂ sinks [Takahashi *et al.*, 2002]. Moreover, planktonic communities in temperate oceans should oscillate from strongly autotrophic in winter to heterotrophic when the water temperature exceeds 21°C in the summer, also consistent with observations from seasonal shifts in planktonic metabolism [e.g., Duarte *et al.*, 2004; Navarro *et al.*, 2004; Williams *et al.*, 2004]. Hence, the temperature-dependence of planktonic metabolism reported here helps explain both spatial and seasonal patterns in planktonic metabolism in the ocean.

[21] Most important, the derivation of the activation energy for metabolism of planktonic communities across the ocean provided here helps to predict the response of planktonic

metabolism to the forecasted ocean warming. Ocean warming is expected to lead to increased metabolic rates. Indeed, Duarte *et al.* [2004] report a 2.5-fold increase in warming for a 10 years data set of weekly measurements of planktonic metabolism data in the Bay of Blanes, NW Mediterranean. Harris *et al.* [2006] predicted, on the basis of general metabolic theory, that a four degree increase in summer water temperatures, a likely scenario for the end of this century [Meehl *et al.*, 2007], will result in a 20% increase in net primary production and a 43% increase in heterotrophic metabolism, resulting in a 16% decrease of the P/R ratios and an increasing likelihood of system heterotrophy. Our results validate this prediction, as the activation energy for planktonic metabolism derived empirically here predict that GPP and CR would increase by 19% and 44% with a 4°C temperature increase, remarkably close to predictions based on first principles of metabolic theory [Harris *et al.*, 2006]. However, our results predict a steeper decline, by 25%, in P/R ratios with a 4°C warming than that predicted by Harris *et al.* [2006].

[22] The predictions formulated here hold for metabolic rates per unit chlorophyll, and the absolute change in metabolic rates will depend, therefore, on parallel changes in chlorophyll across the ocean, although the predicted decline of P/R ratios by 25% with a 4°C warming is independent of biomass changes. Because the P/R ratio of planktonic communities in the ocean is very close to 1 [Duarte and Agustí, 1998; Williams, 1998; Robinson and Williams, 2005], a 25% decline in P/R ratios, on average, across the ocean, will greatly increase the prevalence of heterotrophic planktonic communities and revert many ocean regions from supporting planktonic communities acting as a sink for CO₂ to support communities acting as a source of CO₂ to the atmosphere. This prediction is consistent with evidence of a recent weakening of the ocean carbon sink [Cox *et al.*, 2000]. Further weakening, possibly reverting the role of oceanic plankton in the global budget, may be expected as result of the decline P/R ratio predicted from ocean warming forecasted for the 21st Century.

[23] Ocean warming has a broad range of impacts, including greater water column stratification, affecting nutrient fluxes and primary production, and in some situations, increased upwelling from increased wind strength [Hoegh-Guldberg and Bruno, 2010; O'Connor *et al.*, 2009]. Various climate models predict that ocean warming will lead to changes in vertical stratification resulting in reduced nutrient supply due to increased vertical stability and reduced vertical mixing, with a corresponding reduction in new production [Cox *et al.*, 2000; IPCC, 2001; Boyd and Doney, 2002; Sarmiento *et al.*, 2004]. Indeed, ocean stratification is expected to increase with global warming, decreasing nutrient supply to the mixed layer through vertical mixing and leading to a decline in net and new primary production [Behrenfeld *et al.*, 2006], as new production is closely linked with net community production through the relationship between the f -ratio, defining the fraction of GPP that represents new production, and the community P/R ratio [Quiñones and Platt, 1991]. In turn, phytoplankton community structure is closely controlled by water column stratification, with increased stratification resulting in a dominance of picoautotrophs [Bouman *et al.*, 2011]. Indeed, the dominance of picoautotrophs, which channel most of their production to support heterotrophic respiration, has been associated with both high temperature and low nutrient supply

[Agawin *et al.*, 2000], with the implication that the dominance of picoautotrophs should increase with ocean warming [Morán *et al.*, 2010]. Indeed, recent reports have shown that the oceanic deserts have expanded in size [Polovina *et al.*, 2008] and that chlorophyll *a* concentration has declined globally at rates of about 1% per year, related to increasing sea surface temperature and vertical stratification [Boyce *et al.*, 2010]. These observations are consistent with the expected decline in net community production with increasing temperature derived here, and support our argument that the rates reported here are somewhat steeper than expected from metabolic theory because they compound effects of warming on plankton physiology as well as the indirect effects of warming on vertical stratification, nutrient supply and plankton community structure. Increased CO₂ concentration in ocean waters may help reduce the extent of decline in primary production with ocean warming since experimental evidence indicates that increased CO₂ may improve phytoplankton photosynthetic performance [Riebesell *et al.*, 2007; Hendriks *et al.*, 2010]. Consumer production can be impacted directly, from metabolic effects, or indirectly, through the impacts of temperature effects on primary production and respiration [O'Connor *et al.*, 2009]. All these consequences of ocean warming contribute directly and indirectly to the steep response of planktonic respiration rates to warming, which predicts a weakening of the role of ocean plankton as CO₂ sinks with warming.

[24] The key role of respiration in the metabolic balance of the ocean ecosystem is parallel to that in forests [Valentini *et al.*, 2000]. Indeed, soil respiration has also been predicted to increase in response to increased warming [Bond-Lamberty and Thomson, 2010]. However, whereas the response of soil respiration to warming is expected to be a transient response, buffered by soil moisture [Melillo *et al.*, 2002], our results predict a steep and sustained increase of the planktonic respiration with warming. A shift toward a prevalence of heterotrophy in oceanic planktonic communities in a warmer ocean maybe constrained by the availability and supply of organic carbon to support excess respiration over production. However, the ocean receives significant inputs of organic carbon, in dry and wet deposition [Jurado *et al.*, 2008], as well as volatile organic carbon [Dachs *et al.*, 2005; Ruiz-Halpern *et al.*, 2010] to support heterotrophy, which may also proceed by using further the large stock of dissolved organic carbon in the ocean.

[25] Whereas many properties of the ocean are presently monitored at the global scale, including chlorophyll *a* concentration, temperature and CO₂, our current observational effort on planktonic metabolism is scattered and discontinuous, resulting in an inability to detect changes in planktonic metabolic rates, shall these occur. New developments in profiling instruments, such as ARGO floats or gliders fitted with oxygen optodes [Martz *et al.*, 2008; Johnson *et al.*, 2009] will prove instrumental in helping infer changes in the oxygen budget of the ocean with warming. Provided the predictions derived here and the major role of ocean plankton in the carbon budget, improving our observational basis on plankton metabolism is a matter of urgency.

[26] **Acknowledgments.** This is a contribution to the “*Malaspina 2010*” CONSOLIDER project funded by the Spanish Ministry of Science and Innovation (ref. CSD2008-00077) and the Metaoceans Marie Curie Early Stage Research Network (019678-2), funded by the Framework

Program 6 of the EU. We thank C. Robinson, R. Vaquer-Sunyer, P. J. le B. Williams, D. Karl and S. Agustí for providing data. A. Regaudie-de-Gioux was supported by the Metaoceans project. We thank two anonymous reviewers for their useful comments and advice.

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