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Key Points:
- We assess the temperature dependence of oceanic plankton community metabolic rates
- The ratio gross primary production/community respiration decreases with warming
- Ultraviolet radiation influences the temperature dependence of surface productivity

Supporting Information:
- Supporting Information S1

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Temperature dependence of plankton community metabolism in the subtropical and tropical oceans

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Abstract Here we assess the temperature dependence of the metabolic rates (gross primary production (GPP), community respiration (CR), and the ratio GPP/CR) of oceanic plankton communities. We compile data from 133 stations of the Malaspina 2010 Expedition, distributed among the subtropical and tropical Atlantic, Pacific, and Indian oceans. We used the in vitro technique to measured metabolic rates during 24 h incubations at three different sampled depths: surface, 20%, and 1% of the photosynthetically active radiation measured at surface. We also measured the % of ultraviolet B radiation (UVB) penetrating at surface waters. GPP and CR rates increased with warming, albeit different responses were observed for each sampled depth. The overall GPP/CR ratio declined with warming. Higher activation energies (E_a) were derived for both processes (GPP_{Chla} = 0.97; CR_{Chla} = 1.26; CR_{HPA} = 0.95 eV) compared to those previously reported. The Indian Ocean showed the highest E_a (GPP_{Chla} = 1.70; CR_{Chla} = 1.48; CR_{HPA} = 0.57 eV), while the Atlantic Ocean showed the lowest (GPP_{Chla} = 0.86; CR_{Chla} = 0.77; CR_{HPA} = −0.13 eV). We believe that the difference between previous assessments and the ones presented here can be explained by the overrepresentation of Atlantic communities in the previous data sets. We found that UVB radiation also affects the temperature dependence of surface GPP, which decreased rather than increased under high levels of UVB. Ocean warming, which causes stratification and oligotrophication of the subtropical and tropical oceans, may lead to reduced surface GPP as a result of increased penetration of UVB radiation.

1. Introduction

The tropical and subtropical marine regions include the five large oligotrophic gyres, which represent about 40% of the Earth's surface. These oligotrophic gyres rank among the most unproductive marine environments in the planet [*Field et al.*, 1998] and have been increasing in extent from 0.8 to 4.3%/yr [*McClain et al.*, 2004; *Polovina et al.*, 2008; *Irwin and Oliver*, 2009] in the last decade. Moreover, the oligotrophic gyres are forecasted to continue to expand in a warmer ocean by 4% in the Northern Hemisphere and by 9.4% in the Southern Hemisphere [*Sarmiento et al.*, 2004], and with further oligotrophication, net primary production in the ocean is expected to decline [*Signorini et al.*, 2015]. The expansion and oligotrophication of the gyres are believed to result from reduced vertical diffusive nutrient fluxes across a steeper thermocline as the ocean warms [*Sarmiento et al.*, 2004; *Signorini et al.*, 2015]. However, warming also affects metabolic processes directly (e.g., metabolic theory of ecology, or MTE) [*Gillooly et al.*, 2001; *Brown et al.*, 2004] and is expected to affect respiration rates more strongly than primary production rates [*Harris et al.*, 2006; *López-Urrutia et al.*, 2006; *Garcia-Corral et al.*, 2014], thereby affecting the metabolic balance of plankton communities [*Regaudie-de-Gioux and Duarte*, 2012].

Net community production (NCP = GPP − CR) is the difference between gross primary production (GPP) and community respiration (CR). NCP distinguishes the role of plankton communities as autotrophic or sinks of CO_2 from the atmosphere where productivity is the dominant process (NCP > 0, GPP > CR), from heterotrophic communities, which act as sources of CO_2 to the atmosphere [*Del Giorgio and Duarte*, 2002] where respiration is the predominant metabolic process oxidizing organic matter (NCP < 0, GPP < CR). Sustained

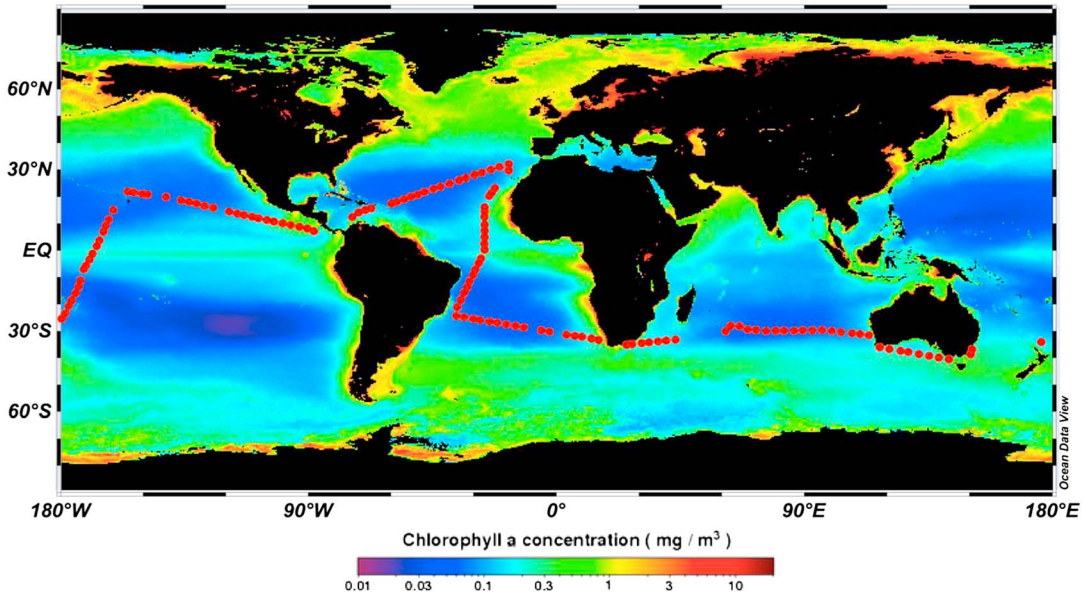

Figure 1. Positions of the 133 stations sampled along the track of the Malaspina 2010 Circumnavigation Expedition, starting in Spain in December 2010; crossing the Atlantic, Indian, and Pacific Oceans; and returning to Spain in July 2011. The chlorophyll *a* map (NASA SeaWiFs) shows the regions with chlorophyll *a* concentrations lower than 0.1 mg m^{-3} in the oligotrophic gyres of the tropical and subtropical oceans.

heterotrophic community metabolism requires, however, allochtonous inputs of organic carbon [*Del Giorgio and Duarte*, 2002; *Duarte et al.*, 2013], which may be derived, in magnitudes sufficient to affect plankton metabolism in the open ocean, from coastal [e.g., *Barrón and Duarte*, 2015] and atmospheric inputs [e.g., *Dachs et al.*, 2005; *Jurado et al.*, 2008; *Gonzalez-Gaya et al.*, 2016]. As a consequence of the steeper response of CR to warming compared with GPP [*Harris et al.*, 2006; *López-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012; *Garcia-Corral et al.*, 2014], heterotrophic communities are expected to increase in a warmer ocean [*Duarte et al.*, 2013]. However, most assessments of the temperature dependence of plankton metabolism are still dominated by data from relatively productive regions of the oceans, such as equatorial and coastal permanent upwelling regions [*Regaudie-de-Gioux and Duarte*, 2012]. Reports of the temperature dependence of plankton metabolism in subtropical regions are mostly derived from the Atlantic Ocean [*López-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012; *Garcia-Corral et al.*, 2014], and reports of plankton metabolism from other oligotrophic areas of the ocean, particularly from the Indian Ocean, are lacking [*Regaudie-de-Gioux and Duarte*, 2012; *Duarte et al.*, 2013].

In this study, we compile planktonic metabolic rates measured in the epipelagic ocean during the Malaspina 2010 Circumnavigation Expedition, a global survey that sampled the subtropical and tropical Atlantic, Pacific, and Indian oceans (Figure 1) [*Duarte*, 2015]. Here we assess the temperature dependence of the metabolic rates (GPP, CR, and the ratio GPP/CR) of plankton communities in the subtropical and tropical oceans for the first time using a consistent sampling approach along 7 months.

2. Material and Methods

The Malaspina 2010 Circumnavigation Expedition [*Duarte*, 2015] was carried out on board the Spanish R/V *Hespérides* encompassing a latitudinal range spanning from 35.2°N to 40.5°S. The expedition departed from Spain on 13 December 2010; crossed the North and South Atlantic Oceans, the Indian Ocean, and the Pacific Ocean; and returned to Spain on 14 July 2011 after crossing again the North Atlantic (Figure 2).

Metabolic rates of the plankton communities were measured at three depths at a total of 133 stations comprising 390 distinct measurements of planktonic metabolism, distributed among the Atlantic (57 stations, 171 measurements), Indian (34 stations, 95 measurements), and Pacific (42 stations, 124 measurements) oceans (Figure 2).

Seawater was sampled at three different depths within the photic epipelagic layer: at surface (~3 m); at the deep chlorophyll maximum depth (DCM; mean ± SE: 100 ± 3 m), receiving on average of 1% of the incident

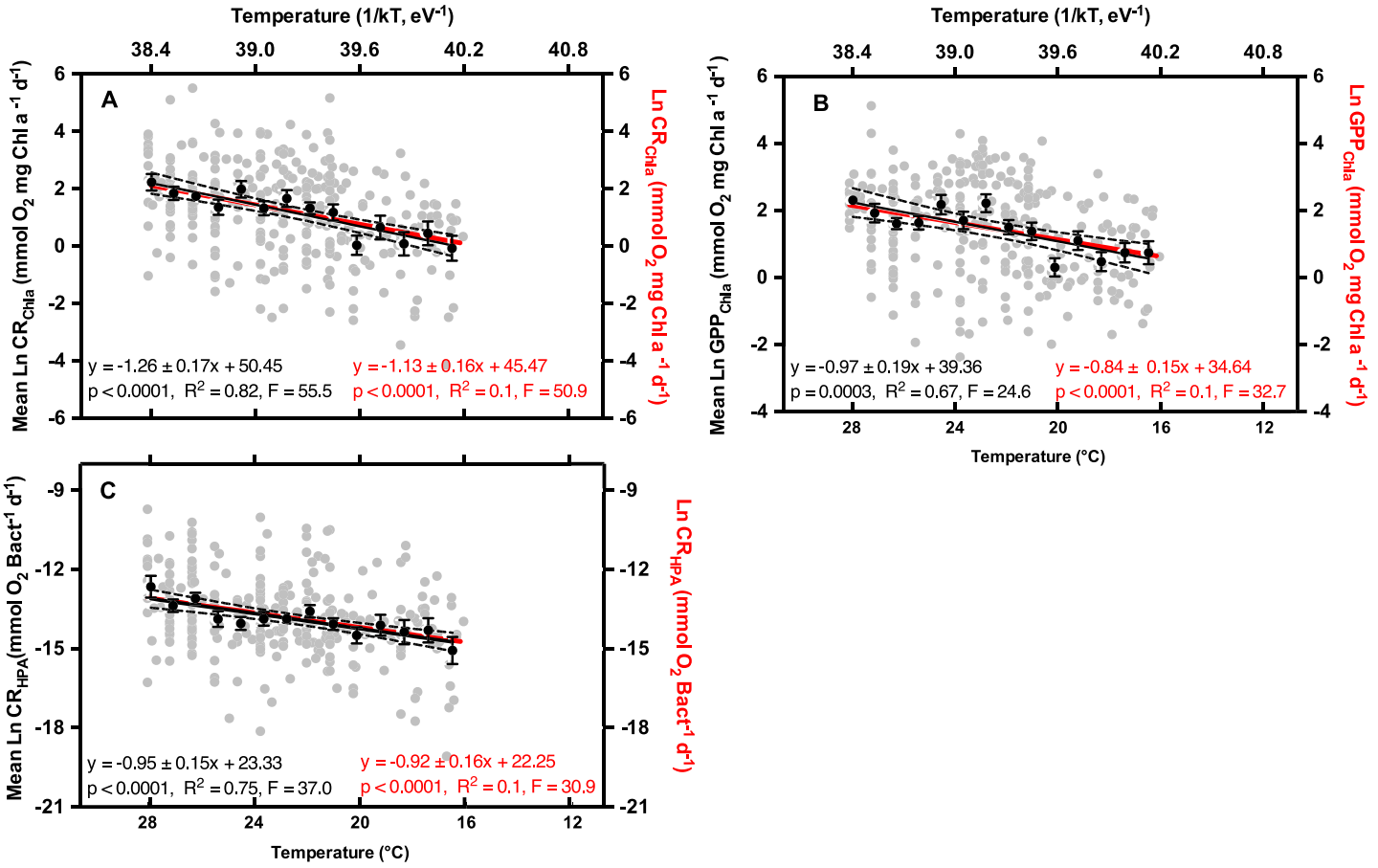

Figure 2. Arrhenius plots showing the relationship between the natural logarithm of metabolic rates and the inverse of water temperature ($1/kT$, where k is the Boltzmann's constant, 8.62×10^{-5} eV k^{-1}, and T is the water temperature (°K) for raw data (grey circles) and averaged within 1°C bins (black triangles) for (a) CRC_{hla}, (b) GPP_{Chla}, and (c) CR_{HPA}. The solid black lines and black font equation show the fitted Type I linear regression for the averaged data (binned by 1°C) with the dotted lines representing the 95% intervals of confidence. The solid red line and red font equation indicate the fitted Type I linear regression of the raw data.

photosynthetically active radiation (PAR); and an intermediate depth between the surface and DCM (mean ± SE: 38 ± 1 m), receiving 20% of the incident PAR. Surface waters were sampled with a 30 L Niskin bottle, while intermediate and DCM depths were sampled using a Rosette sampler system fitted with a calibrated Sea-Bird SBE 9 CTD and 12-L Niskin bottles. Seawater was siphoned with a silicon tube directly from the Niskin bottles into precalibrated 100 mL borosilicate glass narrow-mouth Winkler dissolved oxygen bottles (BRAND®, Sigma-Aldrich) or 100 mL quartz bottles (Trallero and Schlee), overflowing at least the double of the bottle volume > 200 mL.

First, for each depth, seven replicates were immediately fixed, stopping biological activity, and used to estimate the initial dissolved oxygen concentrations. For surface communities, five replicates were incubated in quartz bottles for the light treatment and seven replicates in dark bottles for the dark treatment. Quartz bottles were used instead of glass transparent Winkler bottles so as to allow the full solar radiation spectrum to penetrate, as borosilicate glass bottles remove much of the UV radiation, which affects metabolic rate estimates [*Regaudie-de-Gioux et al.*, 2014b; *Garcia-Corral et al.*, 2016]. For the two deeper samples (20% PAR and DCM), sets of seven replicates were filled in dark and glass transparent borosilicate bottles each, as UV radiation received is negligible or absent in deeper waters so the use of borosilicate glass for the light treatment does not bias the estimates.

The light and temperature conditions experienced by the incubated communities were designed to mimic conditions experienced by each community at each depth, with the exception of mixing processes that cannot be reproduced. Surface communities were incubated on-deck for 24 h in a 2000 L tank with continuous surface seawater circulating to maintain the approximate in situ temperature and covered with neutral

density screens to reduce incident radiation by 20% [*Agusti et al.*, 2014], thereby simulating the irradiance at surface. To incubate the intermediate and DCM replicated samples, the dark and glass transparent bottles were placed inside opaque PVC and transparent polycarbonate incubation tubes, respectively. The natural in situ irradiance levels experienced by the communities at these depths were simulated using a combination of neutral density (LEE 210) and blue (HT061 Mist blue) filters fitted to the transparent incubation tubes. Incubation tubes were filled with surface seawater and connected to a closed circuit with a pump and temperature-controlled heater-chiller incubator that maintained the temperature at ±0.5°C the in situ temperature, as determined from the CTD cast. After 24 h, light and dark bottles from each depth were fixed to determine final dissolved oxygen concentrations.

Dissolved oxygen concentrations in initial and incubated bottles were determined by automated high-precision Winkler titration. Measurements were performed with a Titrando 808 (Metrohm) and a Titrino 716 DMS (Metrohm) using calibrated potentiometric electrodes and automated end-point detection [*Oudot et al.*, 1988]. CR and NCP were calculated from changes in dissolved oxygen concentrations, before and after incubation of samples in dark and transparent conditions, respectively, and GPP was calculated as NCP + CR [*Carrit and Carpenter*, 1966]. Bulk volumetric rates were calculated as mmol O_2 m^{-3} d^{-1}, but metabolic rates were standardized using chlorophyll *a* concentration (Chl *a*) as a proxy for autotrophic biomass (expressed as mmol O_2 mg Chl-a^{-1} d^{-1}) and heterotrophic prokaryote abundance (HPA) as a proxy for heterotrophic biomass (expressed as mmol O_2 10^6 $cells^{-1}$ d^{-1}). HPA was used to standardized CR as heterotrophic prokaryotic respiration represents ~50% of total community respiration [*Rivkin and Legendre*, 2001; *Del Giorgio and Duarte*, 2002; *Robinson and Williams*, 2005].

Total chlorophyll *a* concentration was determined fluorometrically following *Yentsch and Menzel* [1963], using acetone extraction of chlorophyll *a* from the cells retained on GF/F filters after filtering 200–500 mL of sample water. The abundance of heterotrophic prokaryotes was determined by flow cytometry [*Gasol and Del Giorgio*, 2000].

Vertical profiles were performed at each station using a PRR-800 Underwater Profiling Radiometer (Biospherical Instruments). In this study, we used the measurements of underwater solar radiation at 305 nm (in the UVB band). Percentages of UVB radiation received at the sampling depth (3 m) were calculated relative to the irradiance values measured at the surface, using the downwelling attenuation coefficients (K_d), obtained from the linear regression between the natural log transformed radiation measurements versus depth. These measurements were used to test whether UVB radiation (280–320 nm) affects the relationship between metabolic rates of surface communities and temperature.

The temperature sensitivity of metabolic rates was assessed by calculating the corresponding activation energy (E_a, eV). The E_a is determined from the slope of the Arrhenius plot of the natural logarithm of the standardized metabolic rate (GPP and CR by chlorophyll *a*—$LnGPP_{Chla}$ and $LnCR_{Chla}$—and CR by heterotrophic prokaryote abundance—$LnCR_{HPA}$) versus the inverse of the seawater temperature binned by 1°C ($1/kT$), where k is the Boltzmann constant (8.617×10^{-5} eV K^{-1}) and T is the temperature in Kelvin (K). The Arrhenius equation was fitted using a Type I regression, as a Monte Carlo simulation revealed that use of Type II linear regression as done in the past [*Regaudie-de-Gioux and Duarte*, 2012; *Garcia-Corral et al.*, 2014] overestimates E_a (slope) while increasing the standard error of the data. This evaluation resulted from the comparison of the robustness of E_a estimates fitted using Type I and Type II regressions. To perform this comparison, we used the linear regression Type I equation of the Arrhenius plot, in this case, for $LnCR_{Chla}$ versus $1/kT$ (see above for parameter details), and generated a random normal distribution of the CR rate for the temperature range of our data set. We ran the random distribution 10 times and multiplied each outcome by a different value of standard deviation (from 10–90%) to increase the coefficient of variation, therefore increasing the error of the data. We plotted the coefficient of variation (y) versus the inverse of temperature (x) and fitted Type I and Type II linear regressions to compare the slope (E_a) of both equations. We found that the slopes were significantly different ($F = 57.77$, $p < 0.0001$, DFd = 176) and that Type I regression gave nonbiased estimates of E_a (see Appendices S1A and S1B in the supporting information for a full account of the simulation results). This result is consistent with the general guidance to apply Type 1 regression whenever the error in Y, the natural log of community metabolism, is >3 times larger than the error in X [*Legendre and Legendre*, 2012], the inverse of temperature in this case, which is measured with far greater precision than community metabolism. All statistical analyses were performed using JMP and Graphpad Prism software.

3. Results

Seawater temperature ranged from 16°C to 29°C across the 390 sampled depths in this study. Differences in the measured temperatures among the ocean basins examined were found: stations sampled in the Indian Ocean were the coldest with mean surface (~3 m) waters of 22°C, 21°C at the 20% PAR depth (mean 39 m), and 18°C at the DCM (mean 105 m). The warmest temperatures were found in the Pacific Ocean with a mean surface (~3 m) temperature of 26°C, 25°C at the 20% PAR depth (mean 37 m), and 23°C at the DCM (mean 87 m). The Atlantic Ocean stations showed intermediate temperatures with mean surface waters at 25°C (~3 m), 20% PAR (mean 38 m) at 24°C, and DCM at 21°C (mean 108 m).

Plankton communities sampled were mostly in oligotrophic waters in the three ocean basins. Surface communities showed low chlorophyll *a* concentrations (average ± SE) of 0.12 ± 0.01 and 0.15 ± 0.02 mg m^{-3} in the Atlantic and Indian Oceans and significant higher concentrations (*t* test < 0.05) in the Pacific Ocean with 0.22 ± 0.02 mg m^{-3} of chlorophyll *a*. At the 20% PAR depth, mean (±SE) chlorophyll *a* concentrations showed similar values to those measured at surface following the same pattern, with 0.15 ± 0.02 and 0.14 ± 0.01 mg m^{-3} for the Atlantic and Indian Oceans, respectively, and significant higher (*t* test < 0.05) concentrations of 0.28 ± 0.03 mg m^{-3} in the Pacific Ocean. At the deep chlorophyll maximum depth (DCM), mean chlorophyll *a* (±SE) concentrations were not significantly different (*t* test $p > 0.05$) between oceans, with 0.48 ± 0.02, 0.46 ± 0.06, and 0.48 ± 0.04 mg m^{-3} for the Atlantic, Indian, and Pacific Oceans, respectively (data not shown).

Specific gross primary production (GPP_{Chla}) and specific community respiration (CR_{Chla} and CR_{HPA}) rates increased strongly with temperature. Overall metabolic rates binned by 1°C showed a corresponding Arrhenius relationship weaker for GPP_{Chla} ($F = 24.6$, $R^2 = 0.67$, $p = 0.0003$; Table 1 and Figure 3) than for CR, both when CR was standardized by chlorophyll *a* (CR_{Chla}, $F = 55.5$, $R^2 = 0.82$, $p < 0.0001$) and by heterotrophic prokaryote abundance (CR_{HPA}, $F = 37$, $R^2 = 0.75$, $p < 0.0001$; Table 1 and Figure 3). The corresponding activation energies (E_a) derived from the slope of the Arrhenius plots ($E_a = -$slope) were 0.97 ± 0.19 eV for GPP_{Chla}, 1.26 ± 0.17 eV for CR_{Chla}, and 0.95 ± 0.15 eV for CR_{HPA}. In addition, the GPP/CR ratio declined with increasing temperature ($F = 11$, $R^2 = 0.48$, $p = 0.006$), with an overall E_a of −0.32 ± 0.09 eV (Table 1 and Figure 4).

The relationship of GPP_{Chla} and CR_{Chla} with temperature showed a significant and strong increase with increasing temperature for the three ocean basins (Table 1), although no ocean basin showed temperature dependence for CR_{HPA} or for GPP/CR ratio (Table 1). The temperature dependence of GPP and CR was not significantly different between oceans, as reflected by the similar activation energies in the Atlantic, Pacific, and Indian Oceans (Table 1). However, E_a for GPP_{Chla}, CR_{Chla}, and CR_{HPA} showed consistently higher values ($p < 0.05$) for communities in the Indian Ocean (1.70 ± 0.37, 1.48 ± 0.35, and 0.57 ± 0.35 eV, respectively) compared to those derived from the Pacific Ocean (1.07 ± 0.29, 0.82 ± 0.36, and 0.51 ± 0.46 eV, respectively) and the Atlantic Ocean, which showed the lowest E_a values (0.86 ± 0.20, 0.77 ± 0.25, and −0.13 ± 0.21 eV, respectively, Table 1).

Indeed, the mean metabolic rates showed different temperature dependence with depth. Both, CR_{Chla} and CR_{HPA} rates showed stronger relationships (higher R^2 and higher significance) with temperature at surface waters and intermediate depths receiving 20% of incident PAR than at the DCM (Figures 5a–5f and Table 1). In contrast, GPP_{Chla} showed no significant relationship with temperature at the surface and DCM ($p > 0.05$), but a significant, although weak ($R^2 = 0.30$, $p = 0.04$), relationship was seen at the intermediate depth where 20% PAR was received (Figures 5g–5i and Table 1). The GPP/CR ratio showed a significant negative relationship with temperature at all the three sampled depths (Figures 5j–5l and Table 1).

However, a closer examination of the relationship between GPP_{Chla} and temperature in surface waters revealed a distinct response to warming. GPP_{Chla} increased as temperature rose to 23°C ($R^2 = 0.71$, $p = 0.008$, $n = 8$) and decreased as temperature increased further ($R^2 = 0.64$, $p = 0.03$, $n = 7$; Figure 5 and Table 1). This observation suggests that the temperature sensitivity of GPP_{Chla} rates in surface waters may be modulated by other factors. A general linear model revealed a significant interaction ($p < 0.05$) between UVB radiation and surface water temperature ($1/kT$) as described by the fitted equation:

Table 1. Arrhenius Relationships Between the Natural Logarithm of the Metabolic Rates, Averaged Over 1°C Bins, and the Inverse Temperature ($1/kT$) for the Overall Means and Aggregated by the Different Sampled Depths and Ocean Basins[a]

	Rate	Intercept ± SE	Slope ($-E_a$) ± SE	Conf Intervals (E_a)	*df*	*F*	R^2	*p*	*n*
Overall mean	GPP_{Chla}	39.36 ± 7.65	−0.97 ± 0.19	−1.39, −0.54	12	24.61	0.67	0.0003	14
	CR_{Chla}	50.45 ± 6.62	−1.26 ± 0.17	−1.62, −0.89	12	55.54	0.82	<0.0001	14
	CR_{HPA}	23.33 ± 6.12	−0.95 ± 0.15	−1.29, −0.61	12	37.02	0.75	<0.0001	14
	GPP/CR	−12.15 ± 3.74	0.32 ± 0.09	0.12, 0.52	12	11.02	0.48	0.006	14
Surface	GPP_{Chla}	2.45 ± 7.28	−0.00 ± 0.02	−0.40, 0.40	12	0	0.00	0.97	14
	GPP_{Chla} (16–23°C)	40.50 ± 9.87	−0.95 ± 0.25	−1.57, −0.35	6	14.84	0.71	0.008	8
	GPP_{Chla} (23–29°C)	−45.40 ± 15.94	1.23 ± 0.41	0.18, 2.29	5	9.01	0.64	0.03	7
	CR_{Chla}	36.64 ± 8.77	−0.89 ± 0.22	−1.38, −0.41	12	16.05	0.57	0.002	14
	CR_{HPA}	24.94 ± 8.68	−0.99 ± 0.22	−1.47, −0.51	12	20.11	0.63	0.0007	14
	GPP/CR	−34.00 ± 5.61	0.89 ± 0.14	0.58, 1.20	12	38.78	0.76	<0.0001	14
20% PAR	GPP_{Chla}	−14.93 ± 5.87	−0.34 ± 0.15	−0.66, −0.01	12	5.1	0.30	0.04	14
	CR_{Chla}	42.18 ± 7.45	−1.03 ± 0.19	−1.45, −0.62	12	29.75	0.71	<0.0001	14
	CR_{HPA}	30.59 ± 11.97	−1.13 ± 0.30	−1.79, −0.47	12	13.76	0.53	0.003	14
	GPP/CR	−27.21 ± 9.59	0.69 ± 0.24	0.16, 1.23	12	8.15	0.40	0.01	14
DCM (1% PAR)	GPP_{Chla}	−11.89 ± 10.32	0.30 ± 0.26	−0.28, 0.88	11	1.31	0.10	0.27	13
	CR_{Chla}	24.56 ± 14.32	−0.62 ± 0.36	−1.42, 0.18	11	2.89	0.21	0.12	13
	CR_{HPA}	29.95 ± 17.81	−1.12 ± 0.45	−2.11, −0.12	11	6.08	0.35	0.03	13
	GPP/CR	−40.16 ± 6.19	1.01 ± 0.16	0.67, 1.36	11	41.41	0.79	<0.0001	13
Atlantic Ocean	GPP_{Chla}	35.29 ± 8.11	−0.86 ± 0.21	−1.31, −0.41	12	17.52	0.59	0.001	14
	CR_{Chla}	31.53 ± 9.95	−0.77 ± 0.25	−1.33, −0.22	12	9.33	0.44	0.01	14
	CR_{HPA}	−18.91 ± 8.40	0.13 ± 0.21	−0.34, 0.59	12	0.36	0.003	0.56	14
	GPP/CR	3.65 ± 7.79	−0.08 ± 0.20	−5.20, 0.34	12	0.19	0.01	0.67	14
Indian Ocean	GPP_{Chla}	68.43 ± 14.64	−1.70 ± 0.37	−2.54, −0.86	9	20.93	0.70	0.001	11
	CR_{Chla}	59.42 ± 13.82	−1.48 ± 0.35	−2.28, −0.69	9	17.97	0.67	0.002	11
	CR_{HPA}	7.85 ± 13.87	−0.57 ± 0.35	−1.36, 0.23	9	2.61	0.22	0.14	11
	GPP/CR	8.31 ± 14.79	−0.19 ± 0.37	−1.04, 0.65	9	0.27	0.02	0.61	11
Pacific Ocean	GPP_{Chla}	43.42 ± 11.53	−1.07 ± 0.29	−1.72, −0.43	11	13.33	0.55	0.004	13
	CR_{Chla}	33.46 ± 14.23	−0.82 ± 0.36	−1.62, −0.02	11	5.1	0.32	0.04	13
	CR_{HPA}	6.71 ± 18.12	−0.51 ± 0.46	−1.54, 0.52	10	1.22	0.11	0.29	13
	GPP/CR	8.07 ± 18.18	−0.21 ± 0.31	−0.89, 0.48	11	0.44	0.04	0.52	13

[a]Intercept ± SE, slope ± SE (E_a = −slope), 95% confident intervals for the slope, *F*, R^2, *p*-values, and number of data points analyzed after binning by 1°C the whole data set (*n*).

$$\text{Ln GPP}_{Chla} = -27.24 + (0.02\%\text{UVB}) + (0.74\ 1/kT) + 0.05\ (\%\text{UVB}–57.98)^{*}(1/kT–38.97)$$
$$(R^2 = 0.13, F = 4.6, p = 0.005, n = 99) \quad (1)$$

suggesting that high UVB radiation results in lower GPP_{Chla} rates in warmer waters (Figure 6). The median percentage of UVB radiation measured during the circumnavigation did not significantly differ between ocean basins (60%, 58.5%, and 59% in the Atlantic, Indian, and Pacific Oceans, respectively). This result suggests that when the percentage of UVB radiation received is greater than 50% of the irradiance measured in the air, higher %UVB radiation may account for the observed trend toward decreasing GPP_{Chla} rates with increasing temperature in plankton communities at surface layers.

4. Discussion

The results presented here confirm a strong temperature dependence of the metabolic rates of plankton communities in the subtropical and tropical oceans, with both main biological processes, GPP and CR, increasing with temperature increase. This pattern was predicted by the MTE [*Gillooly et al.*, 2001; *Brown et al.*, 2004], although the response to temperature has been reported to be different for each rate, with CR rates increasing faster with warming than GPP reflected by higher activation energies of the former [*Harris et al.*, 2006; *López-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012; *Garcia-Corral et al.*, 2014]. In our study the overall results are partially in concordance with the studies mentioned above, as our E_a for CR_{Chla} (1.26 ± 0.17 eV) was higher than that for GPP_{Chla} (0.97 ± 0.19 eV). Conversely to previous efforts [e.g., *Regaudie-de-Gioux and Duarte*, 2012], we were able to derive an E_a estimated for CR standardized by

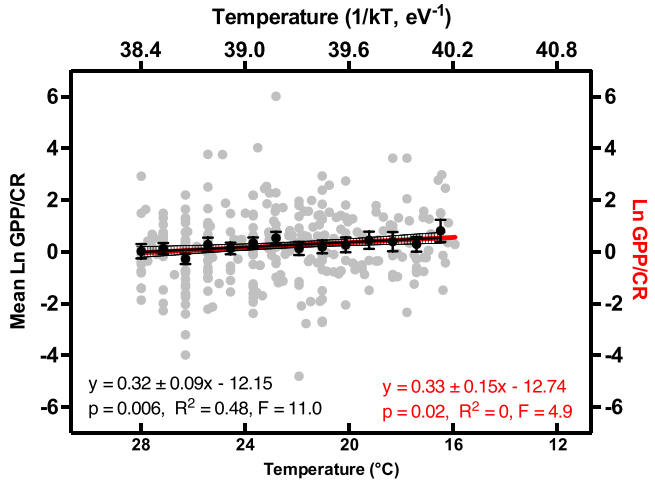

Figure 3. Relationship between the natural logarithm of the GPP/CR ratio and the inverse of water temperature ($1/kT$, where k is the Boltzmann's constant, 8.62×10^{-5} eV k^{-1}, and T is the water temperature, °K). The grey circles represent the raw data, and the solid red line and red font equation show the fitted linear regression Type I. The full black triangles show the data averaged within 1°C bins, the solid black line and the black font equation show the fitted linear regression Type I, and the dotted lines indicate the 95% intervals of confidence.

HPA. However, when the E_a of GPP_{Chla} was compared to E_a of CR_{HPA} (0.95 ± 0.15 eV), the values of the slopes (E_a) were very similar, showing no significant difference in the temperature dependence of CR and GPP.

Moreover, the E_a derived here for both metabolic rates of plankton communities in the subtropical and tropical oceans were consistently higher than those predicted by the MTE (~0.6 and ~0.3 eV for respiration and primary production, respectively [*Brown et al.*, 2004]), although these values were derived from terrestrial processes, which may differ from the metabolic processes of open ocean planktonic communities. Specialized studies where the temperature dependence of plankton metabolic rates was assessed reported lower E_a compared to our values for both metabolic processes, CR and GPP. For instance, *López-Urrutia et al.* [2006] modeled E_a of 0.56 and 0.33 eV for heterotrophic and autotrophic respirations, respectively, and 0.29 eV for autotrophic net production of plankton communities in the Atlantic Ocean. *Yvon-Durocher et al.* [2012] derived an E_a of 0.57 eV for marine microbial respiration, and *Regaudie-de-Gioux and Duarte* [2012] reported E_a for CR_{Chla} of 0.66 eV and 0.32 eV for GPP_{Chla} based on a global meta-analysis of planktonic metabolic rates. In contrast, *Garcia-Corral et al.* [2014] reported an E_a for CR_{Chla} of 1.64 eV, steeper than that reported here, derived from experimental temperature manipulations in the Subtropical North Atlantic Ocean, which was consistent with the observed CR_{Chla} E_a values reported in the same area during winter and spring of 1.37 eV and 1.74 eV, respectively [*Garcia-Corral et al.*, 2014].

The lower activation energies reported in studies based on meta-analysis compared to those based on comparative analyses of data obtained in the same cruises or experimental manipulations might be attributed to the different methodologies used by the primary data providers, accumulating error due to differences in methods and assumptions. For instance, the in vitro ^{14}C [*Nielsen*, 1952] and ^{13}C methodologies [*Slawyk et al.*, 1977] have been shown to underestimate GPP because they exclude the organic carbon released and remineralized during the incubations. Similarly, in situ measurements such as the FRRF method (fast repetition rate fluorometry [*Kolber and Falkowski*, 1993]) could be biased because of the presence of colored dissolved organic matter, and it presents difficulties to extrapolate in time scales [*Longhurst et al.*, 1995; *Regaudie-de-Gioux et al.*, 2014a]. Thus, the resulting amalgam of methods could bias the results of the temperature-dependence of marine plankton communities. In contrast, this study, like that of *Garcia-Corral et al.* [2014], consistently used the same materials and methods for all the 133 stations sampled across the Subtropical North and South Atlantic, the North Pacific, and the Indian gyres, reducing the accumulated error in the data set due to varying methodologies. Standardized metabolic rates showed high variability for any one temperature and explained only a small part of the variability. This is likely associated to variability in community structure, such as taxonomic distribution of primary producers and heterotrophs and changes in traits such as size distribution and food web structure, which are poorly captured by crude proxies such as chlorophyll *a* concentration and heterotrophic prokaryote abundance used here to standardized metabolic rates. In addition, we confirmed that the use of Type II linear regression to fit the Arrhenius equation inflates E_a values as the error in metabolic estimates increases.

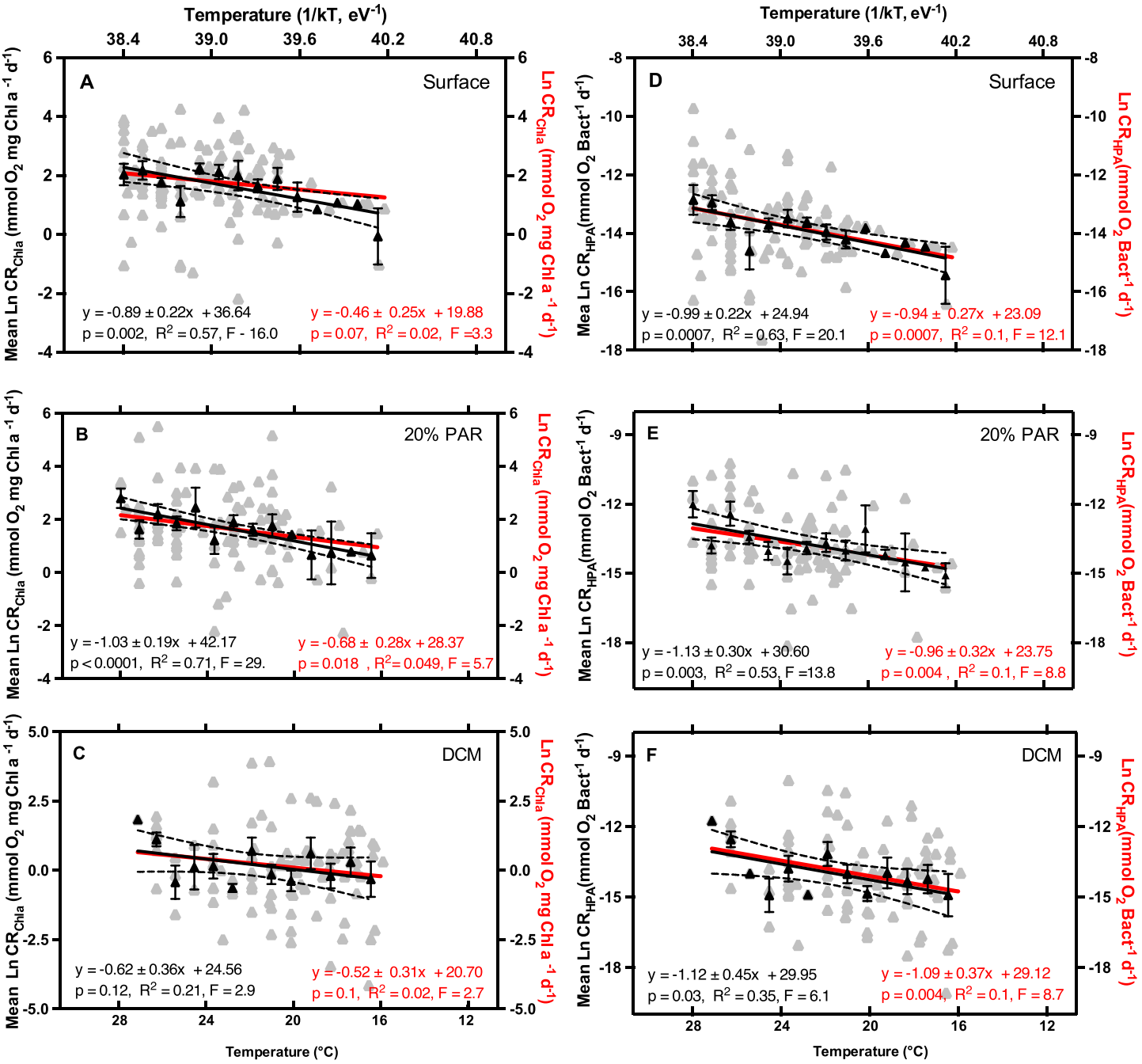

Figure 4. The Arrhenius relationship for (a–c) CR_{Chla}, (d–f) CR_{HPA}, (g–i) GPP_{Chla}, and (j–l) GPP/CR ratio and the inverse of temperature for the three sampled depths (surface, 20% PAR and 1% PAR). The grey triangles show raw data of the metabolic rates and solid black triangles the averaged data binned by 1°C. The solid lines represent the fitted linear regression Type I for raw data (red line and red font equation) and averaged data (black line and black font equation), and the dotted lines indicate the 95% intervals of confidence.

Despite of the differences in E_a for the specific metabolic rates, the overall GPP/CR ratio showed an $E_a = -0.32$ eV, indicative of a decline in the GPP/CR ratio with increasing temperature. This value is very similar to that obtained by *López-Urrutia et al.* [2006] of −0.36 eV, but smaller, although not significantly, than the E_a of 0.52 ± 0.09 reported for the global ocean by *Regaudie-de-Gioux and Duarte* [2012]. Therefore, the conclusion of a decline in the production to respiration ratio with increasing temperature drawn from the

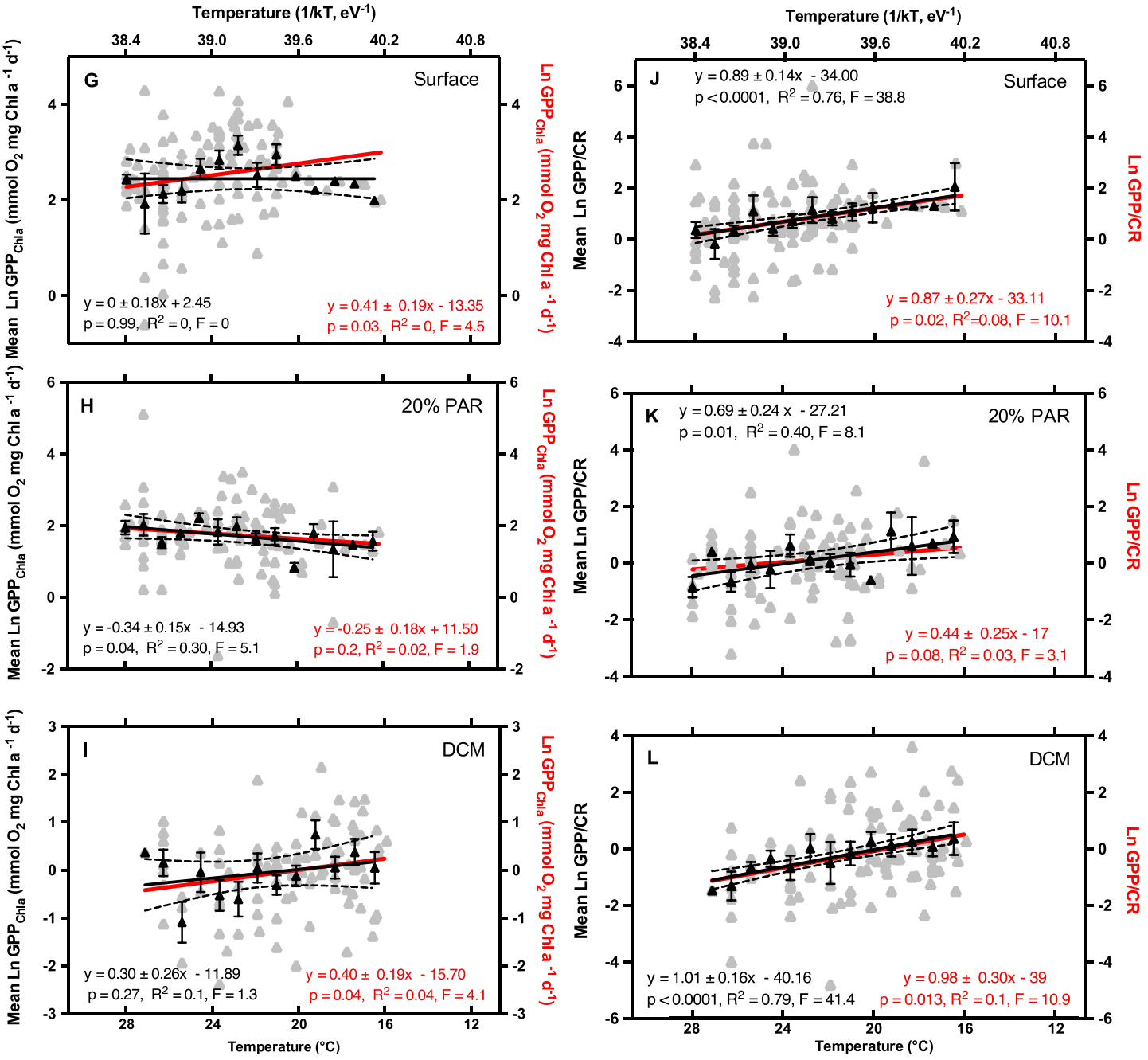

Figure 4. (continued)

MTE and supporting studies is also confirmed by our data; however, our analyses argued a decrease in surface GPP with warming and UVB impact, rather than a higher response of CR compared to GPP (see discussion below).

For the first time, the temperature dependence of metabolic rates in tropical and subtropical plankton communities has been assessed, distinguishing by depth, within the euphotic layer. As temperature varies with depth within the water column, it is reasonable to expect different temperature dependences of metabolic processes at the different sampled depths. The deepest samples measured at the DCM showed no significant relationship between GPP_{Chla} and CR_{Chla} and temperature, probably meaning that at this depth, other factors than the temperature such as light or nutrients might control the temperature dependence

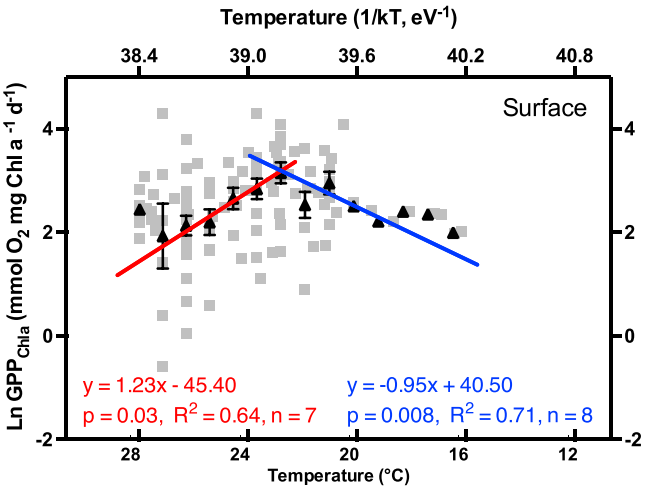

Figure 5. The temperature dependence of GPPChla for surface waters represented by the Arrhenius equation and plot. The red and blue lines indicate the linear regression Type I for the increase with temperature up to 23°C (blue) and the declining trend with increasing temperature (red). The grey squares indicate raw data and the black triangles the averaged data binned by 1°C.

of plankton metabolism. Although a weak but significant relationship was observed for CR_{HPA}, suggesting that the CR is dominated by heterotrophic biomass in the deep oligotrophic waters [*Dortch and Packard*, 1989; *Gasol et al.*, 1997; *Biddanda et al.*, 2001] with a microbial community composition different than within the euphotic layer [*Treusch et al.*, 2009]. Nevertheless, a very strong and significant correlation appeared between GPP/CR ratio and temperature at the DCM, confirming a heterotrophic trend in this layer with water warming.

On the other hand, at the intermediate depth receiving 20% of PAR, all metabolic rates measured showed a significant correlation with temperature. The stronger correlation between CR_{Chla} and CR_{HPA} and temperature at the depth receiving 20% of PAR was associated with higher E_a (1.03 ± 0.19 and 1.13 ± 0.30 eV, respectively) than the E_a of 0.6 eV for community respiration predicted by the MTE. However, the weakest relationship of GPP_{Chla} with temperature resulted in an E_a of 0.34 ± 0.15 eV, similar to that assumed by the MTE (GPP E_a = 0.3 eV). Hence, community respiration is more sensitive to temperature than GPP in communities receiving 20% PAR.

Finally, at surface waters, we found a different response of GPP_{Chla} with temperature. GPP_{Chla} increases significantly as temperature rises to 23°C, whereas, above the threshold of 23°C, GPP_{Chla} declines as

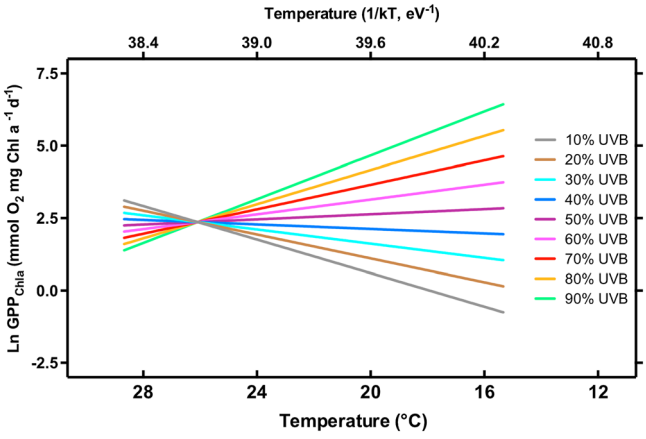

Figure 6. The fitted least squares regression equations showing the relationship between Ln GPP_{Chla} and $1/kT$ across the different percentage of incident UV-B radiation observed in surface waters along the expedition.

temperature increases further. *Regaudie-de-Gioux and Duarte* [2012] found that heterotrophic communities dominated above 21°C; however, the difference in the temperature threshold could be due to the broader range of temperatures (−1 to 29°C) that they considered. Additionally, when the E_a of GPP_{Chla} at surface waters (0.95 ± 0.25 eV in the temperature range where it increases, from 16–23°C) is compared to the E_a of CR_{Chla} (0.89 ± 0.22 eV) and CR_{HPA} (0.99 ± 0.22 eV), no significant difference (*t* test, $p < 0.05$) appeared between them. We ascribed the different response of surface GPP_{Chla} with temperature to the fact that, at least partially, other factors such as the high percentage of UVB radiation received at surface waters in the tropical and subtropical oceans can be affecting the temperature dependence of planktonic primary production. Indeed, the two contrasting E_a values for increasing and decreasing GPP_{Chla} with temperature can counteract and result in the lower E_a found in the previous works, where GPP_{Chla} was measured using materials that exclude UVB radiation [*López-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012; *Yvon-Durocher et al.*, 2012].

Our results showed that UVB radiation affects the temperature dependence of GPP_{Chla}, so that it decreases, rather than increases, in warmer waters under high UVB levels. This observation is consistent with (a) the inhibition of photosynthesis by UVB in open ocean waters [*Li et al.*, 2011] dominated by picoautotrophs, which represent 50% or more of the total autotrophic biomass in the warm oligotrophic waters [*Agawin et al.*, 2000]; (b) the observation that UVB radiation induces high mortality in picophytoplankton organism in oligotrophic waters [*Agusti and Llabres*, 2007] as vulnerability to UV radiation is suggested to be size dependent [*Boelen et al.*, 2000]; and (c) the experimental demonstration of a synergy between temperature and UVB radiation on the community production in oligotrophic waters [*Garcia-Corral et al.*, 2015].

Hence, the model presented here (Figure 6) suggests that the optimum temperature for GPP declines with increasing incident UVB, so that GPP rather than increasing declines at warmer temperatures in the surface layers of the subtropical and tropical oceans. The oligotrophic gyres are expanding in the oligotrophic ocean [*McClain et al.*, 2004; *Polovina et al.*, 2008; *Irwin and Oliver*, 2009; *Jena et al.*, 2013], with the areas of low surface chlorophyll waters outside the equatorial zone expanding at average annual rates from about $-1.3\%yr^{-1}$. The fastest expansion rate was reported for the Atlantic Ocean [*Polovina et al.*, 2008; *Gregg and Rousseaux*, 2014; *Signorini et al.*, 2015], and a decreasing trend has been described for primary production from −3 to -7 mg C m^{-2} d^{-1} yr^{-1} in all subtropical gyres [*Signorini et al.*, 2015]. These trends have been indeed associated with ocean warming, consistent with the results presented here [*Signorini et al.*, 2015]. As subtropical gyres become more oligotrophic and larger, they are expected to allow a deeper penetration of UVB radiation [*Morel et al.*, 2007, 2010; *Smyth*, 2011], affecting vulnerable picocyanobacteria and reducing gross primary production in surface waters. The interaction between ocean warming and UVB in affecting gross primary production found here (Figure 6) implies that ocean warming, which causes stratification of the water column and oligotrophication of the subtropical and tropical oceans [*Signorini et al.*, 2015], may lead to further reduction in GPP as a result of increased penetration of UVB radiation in surface waters.

Moreover, our results confirm the existence of differences in the temperature sensitivity of plankton communities in different ocean basins. We found that plankton communities in the Indian Ocean showed the strongest temperature dependence of metabolic rates, consistent with similar findings by *Regaudie-de-Gioux and Duarte* [2012], suggesting a robust result, while those in the Atlantic Ocean showed the lowest activation energy. Thus, the difference between our findings of higher temperature dependence of plankton metabolic processes and previous assessments might be partially explained by the fact that data sets from previous meta-analyses [e.g., *López-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012] are dominated by data from Atlantic communities. The underlying causes for such variability in the temperature sensitivity of plankton communities in different ocean basins are, however, unknown and likely reflect differences in temperature sensitivity of the species dominating these processes in the different basins.

Hence, the fact that the overall GPP had a higher E_a value than the overall CR at each ocean basin when both rates were standardized per unit of chlorophyll *a* might be due to the higher temperature effects on production rather than in respiration, as chlorophyll *a* production is also affected by the depleted nutrients in oligotrophic waters [*Longhurst et al.*, 1995]. However, heterotrophic prokaryotic respiration represents ~50% of total community respiration [*Rivkin and Legendre*, 2001; *Del Giorgio and Duarte*, 2002; *Robinson and Williams*, 2005] and has been shown to be strongly temperature dependent. Therefore, the E_a value for CR was similar to that for GPP when CR was standardized to heterotrophic prokaryotic abundance and GPP by chlorophyll *a*. However, heterotrophic prokaryotic production is mainly

dependent on resource availability, being the organic matter produced by phytoplankton the limiting factor [*Li et al.*, 2004]. Low nutrient concentration causes low primary production rates in oligotrophic waters [*Longhurst et al.*, 1995] and thus less organic matter produced or excreted by phytoplankton. Additionally, the low allochthonous organic material from land and river discharge [*Williams et al.*, 2013] results in low CR rates and, consequently, lower temperature dependence for this metabolic process compared to the GPP rates.

Indeed, the steeper E_a obtained here for the temperature dependence of the metabolic rates of subtropical and tropical plankton communities is consistent with recent findings [*Dell et al.*, 2011] showing systematic deviations from the E_a predicted by the MTE [*Gillooly et al.*, 2001; *Brown et al.*, 2004]. Particularly, the E_a have been found to increase with the level of organization, with the E_a for populations being higher (0.98 eV) than those for individual organisms (0.54 eV) [*Dell et al.*, 2011], suggesting that community-level E_a may be even higher than those expected for individual organisms or populations, as found here. Previous studies also showed a weaker predictive power of the MTE compared to other models [*Cyr and Walker*, 2004; *Brauer et al.*, 2009; *White et al.*, 2012] because the MTE does not consider important variables, such as solar radiation that affects metabolic rates, particularly so for phytoplankton primary production [*De Castro and Gaedke*, 2008].

The results presented here help to explain the observed low production of the oligotrophic subtropical and tropical oceans with current warming [*Signorini et al.*, 2015] and provide a robust basis to assess the response of plankton metabolism to future increased warming. Indeed, previous studies have shown that E_a estimates derived from comparative analyses across plankton communities are consistent with those derived experimentally [*Garcia-Corral et al.*, 2014], supporting their use to formulate predictions on the effect of warming on plankton metabolic rates. This study is further strengthened by its global nature, encompassing communities across the Atlantic, Indian, and Pacific Oceans, addressing the hitherto poor coverage of estimates of plankton metabolism in the subtropical and tropical oceans [*Regaudie-de-Gioux and Duarte*, 2013] with the added benefit of the use of consistent methods that minimized measurement variability and associated error. However, large variability in the relationship between standardized metabolic rates and temperature remains, which suggests that factors, such as community structure, other than those included here affect the metabolic rates for a given temperature in the oligotrophic ocean. Moreover, the models used do not consider other environmental factors, such as nutrient availability that may affect metabolic rates, also contributing to the variability observed here. Identifying additional community and environmental drivers governing the response of plankton community metabolism to temperature is essential to support reliable predictions of its response to future warming.

Hereby, we conclude that the E_a for plankton metabolic rates in the subtropical and tropical oceans are steeper than that predicted by the MTE [*Gillooly et al.*, 2001; *Brown et al.*, 2004] and that reported for the global ocean [*Regaudie-de-Gioux and Duarte*, 2012], with GPP rates more sensitive to warming than CR, partially due to the high UVB radiation that reaches these areas of the ocean. Our results, and the results from experimental manipulations reported by [*Garcia-Corral et al.*, 2014], show that the metabolic rates of plankton communities in the subtropical and tropical oceans have a steeper dependence on temperature than those in the temperate ocean and suggest more acute impacts of warming of the subtropical and tropical oceans on plankton metabolism than previously assessed. The tendency for plankton communities in a warmer oligotrophic ocean to be heterotrophic is enhanced further, by the increase in the penetration of UVB with oligotrophication and the associated decline in GPP.

In summary, the results presented here are relevant as they support the notion that ocean warming should be leading to a shift in the metabolic balance of plankton communities toward increased heterotrophy [*Harris et al.*, 2006; *López-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012; *Garcia-Corral et al.*, 2014], changes in the size structure of plankton communities toward an ecosystem dominated by picoautotrophs [*Morán et al.*, 2010] and prokaryotes [*Karl et al.*, 2001] parallel to the expansion [*McClain et al.*, 2004; *Polovina et al.*, 2008; *Irwin and Oliver*, 2009], and oligotrophication of the subtropical gyres [*Duarte et al.*, 2013], resulting in additional changes in biogeochemical dynamics. Hence, plankton communities in the subtropical and tropical oceans might shift toward acting more as a source of CO_2 with warming. Because these waters represent over 40% of the Earth's surface, the metabolic shifts with warming reported here are of consequence for the global carbon and oxygen budgets.

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