Depth Dependent Relationships between Temperature and Ocean Heterotrophic Prokaryotic Production

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Marine prokaryotes play a key role in cycling of organic matter and nutrients in the ocean. Using a unique dataset ($>$14,500 samples), we applied a space-for-time substitution analysis to assess the temperature dependence of prokaryotic heterotrophic production (PHP) in epi- (0–200 m), meso- (201–1000 m) and bathypelagic waters (1001–4000 m) of the global ocean. Here, we show that the temperature dependence of PHP is fundamentally different between these major oceanic depth layers, with an estimated ecosystem-level activation energy (E_a) of 36 ± 7 kJ mol^{-1} for the epipelagic, 72 ± 15 kJ mol^{-1} for the mesopelagic and 274 ± 65 kJ mol^{-1} for the bathypelagic realm. We suggest that the increasing temperature dependence with depth is related to the parallel vertical gradient in the proportion of recalcitrant organic compounds. These E_a predict an increased PHP of about 5, 12, and 55% in the epi-, meso-, and bathypelagic ocean, respectively, in response to a water temperature increase by 1°C. Hence, there is indication that a major thus far underestimated feedback mechanism exists between future bathypelagic ocean warming and heterotrophic prokaryotic activity.

Keywords: prokaryotic production, activation energy, open ocean, global warming, Arrhenius law

INTRODUCTION

Marine bacteria and archaea, here collectively termed prokaryotes, are central components of marine food webs and play a key role in controlling ocean biogeochemistry. The surface ocean, also known as the epipelagic zone (here considered as the 0–200 m depth range) receives sufficient light to support photosynthesis, while the dark ocean (below 200 m depth) is characterized by the absence of light. The dark ocean constitutes the largest habitat of the biosphere, comprising about 95% of the global ocean volume. This part of the ocean is subdivided into the mesopelagic zone (201–1000 m depth) with water mass renewal times of decades and the bathypelagic (1001–4000 m depth) and abyssal zones ($>$4000 m depth) with water mass renewal times of centuries to millennia (Matsumoto, 2007). Organic matter produced in the ocean is the main substrate for prokaryotic growth and several fractions of this organic matter are recognized to have decreasing

availability to prokaryotes: a biologically labile fraction which can be processed within hours to days, a semi-labile fraction with turnover times from weeks to months, a semi-recalcitrant fraction that can persist for decades, a recalcitrant fraction with lifetimes of thousands of years, and an ultra-recalcitrant fraction that is resistant to removal for tens of thousands of years (Hansell, 2013). Microbial growth in the dark ocean is mainly supported by the dissolved semi-labile, suspended and sinking particulate organic matter exported from the epipelagic zone and most of this organic matter is degraded in the mesopelagic zone (Arístegui et al., 2009; Herndl and Reinthaler, 2013). Considering that the dark ocean contains around 75% of all pelagic prokaryotic biomass and a large fraction of the global ocean's removal of organic matter occurs below 200 m depth (del Giorgio and Duarte, 2002; Arístegui et al., 2009), minor changes in prokaryotic activity due to climate change could have a large impact on ocean functioning, atmospheric CO_2 concentrations and the Earth climate system.

Human activities have elevated atmospheric greenhouse gas concentrations leading to increases in global temperatures, with the ocean storing more than 90% of the extra heat (Collins et al., 2013). Since the beginning of the twentieth century, global average sea surface temperatures has increased by 0.6°C, with model predictions suggesting a further increase of between 1 and 3°C by the end of this century (Collins et al., 2013). Global warming will thereby change biological, chemical and physical processes in the ocean and affect ecosystem functioning and biogeochemical fluxes. As temperature is an important regulator of most biological processes including the metabolic activity of prokaryotes (White et al., 1991; Pomeroy and Wiebe, 2001; López-Urrutia and Morán, 2007; Calvo-Díaz et al., 2014), accurate knowledge on the impact of rising ocean temperatures on biological rates is pivotal for predicting the biosphere's feedback to these changes and how this will impact the global carbon cycle.

In this article, we compiled a unique global dataset of prokaryotic heterotrophic production (PHP) and temperature measurements from all major oceans and depths to assess the temperature dependence of PHP within the ocean. We here hypothesize that, the temperature dependence of PHP might vary between the epipelagic, mesopelagic and bathypelagic zone.

METHODS

Data Collection

Data on seawater temperature and prokaryotic heterotrophic production (PHP) were compiled from the literature, mainly from original articles and databases available online, resulting in a total of 14,552 data pairs (Supplementary Table S1). Single-data observations were excluded and no data from manipulated experiments were used. The PHP estimates used in this study are based on two methods: incorporation of ^{3}H-thymidine (TdR) and ^{14}C- or ^{3}H-leucine (Leu) into bacterial DNA and protein, respectively. In only a few cases (42 data points in total), Leu and Tdr incorporation obtained in the same sample exhibited a more than 25-fold difference in the PHP estimate. These data points were removed from further analyses and reduced our dataset to

a total of 14,510 data pairs. Leucine incorporation was used in 47% ($n = 6819$) of the data extracted and TdR incorporation was used in 53% ($n = 7691$). To show the implications of the PHP temperature relationships, we converted the raw data to common carbon units. In order to avoid artifacts due to selection of different carbon conversion factors (CF), all PHP data were converted using a factor of 1.95 kg C mol^{-1} leucine incorporated (Calvo-Díaz and Morán, 2009; Alonso-Sáez et al., 2010), 1.63×10^{18} cells mol^{-1} thymidine incorporated (Carlson et al., 1996) and assuming a carbon conversion factor of 12 fg C cell^{-1} (Fukuda et al., 1998). In the cases where only prokaryotic production estimates were reported we back calculated these to obtain raw values, and thereafter applied our average conversion factors. Multiple CFs have been measured in the past with values ranging widely, 0.13 and 3.62 kg C mol^{-1} leucine, and 0.2–5.60 $\times 10^{18}$ cells mol^{-1} thymidine (Carlson et al., 1996; Calvo-Díaz and Morán, 2009; Alonso-Sáez et al., 2010; Baltar et al., 2010), with no clear trends with depth layers of the measured values (e.g., compare the studies of Alonso-Sáez et al., 2007; Baltar et al., 2010 both in the same oceanographic area). A recent study covering the global subtropical and tropical ocean furthermore does not support any clear geographic effect on CFs (Teira et al., 2015), and based on these studies, it cannot be concluded whether deep waters have different CFs than surface waters. The values we use in this study are averages of the most commonly used CFs; had we used lower or higher factors it would not have influenced the slope of the observed relationships between PHP and temperature, but only the origin intercept, i.e., the data position in the plots.

To refine our analysis, we should have used variable conversion factors measured specifically for each ocean region, depth range, and season sampled. But given the lack of empirical CFs reported in the vast majority of the studies included, we can only ignore the potential differences in conversion factors between different oceans and depth ranges as no coherent trends in CFs emerge from the published CFs (Baltar et al., 2010).

Using these conversion factors, a linear relationship was found between Leu and Tdr incorporation in the samples where a dual label approach was used ($R^2 = 0.56$, $n = 2848$, $p < 0.0001$), with a slope of 0.97 ± 0.03 suggesting that the PHP estimates obtained with either method are not statistically different. Furthermore, we also performed a control analysis of the temperature relationships of the Leu and Tdr estimates separately, showing that our conclusions are not biased by the method used to assess the PHP (Supplementary Figure S1). Although, Leu to TdR ratios provide valuable information in regional studies (e.g., Chin-Leo and Kirchman, 1990; Franco-Vidal and Morán, 2011) for basin-scale to global ranges such as those shown here there is little doubt that both substrates are equally valid for estimating production of heterotrophic prokaryotes.

The data were split according to depth corresponding to the epipelagic (here considered as the depth range from 0 to 200 m), mesopelagic (201–1000 m depth) and the bathypelagic (1001–4000 m depth) layer and thereafter grouped and averaged within data bins covering 1°C (Supplementary Table S2). The data binning step was used to provide an average ocean PHP at a given temperature and the size (1°C) of these bins was chosen

to ensure that multiple measurements (average 220) were present in each bin and depth layer. This procedure also forces that all bins have the same weight in the subsequent statistical analyses independently of the number of data that they initially contain. In the abyssal zone (>4000 m) temperature typically varies between 2 and 3°C. It is therefore not possible to obtain PHP estimates over a wide temperature range, which is a prerequisite to calculate E_a. Thus, data from these depths were not included in our analyses. We applied a space-for-time approach, which assumes that the measurements over multiple environmental gradients can be used to predict ecological responses to climate change (Blois et al., 2013; Lester et al., 2014).

Arrhenius Law

The relationship between temperature and biological rates has been modeled in various ways (Ratkowsky et al., 1983; Ahlgren, 1987), while an Arrhenius-type relationship (linearity of a natural logarithm vs. inverse absolute temperature), assuming that chemical kinetics controls the observed rates, is the most widely applied approach (Westrich and Berner, 1988; Middelburg et al., 1996). According to the Arrhenius law, the temperature sensitivity of PHP is defined by:

$$PHP = A \cdot e^{-E_a/R \cdot T} \tag{1}$$

Where A is the theoretical PHP in the absence of E_a; E_a is the energy barrier to be surpassed in order for the reaction to take place (in J mol^{-1}); R is the universal gas constant (8.314 J mol^{-1} K^{-1}); and T is the temperature in Kelvin (K). The factor $e^{-E_a/R} \cdot T$ is proportional to the fraction of substrate molecules with kinetic energies in excess of E_a (Arrhenius, 1889). An estimate of E_a can be derived from the slope of an Arrhenius plot of ln PHP against the inverse absolute temperature (1/T). The E_a can thereafter be calculated by multiplying the regression slope by R, the universal gas constant. Strictly, the Arrhenius law should be applied to a well-defined enzymatic reaction with a constant E_a and with temperature as the only factor affecting the rate. Furthermore, as heterotrophic prokaryotes are highly diverse and they degrade organic matter that consists of myriads of compounds, the temperature response measured is in reality the sum of all processes involved and therefore the calculated E_a should be seen as an apparent or ecosystem-level E_a (Westrich and Berner, 1988; Middelburg et al., 1996). Although, this is not the classical definition of E_a (Arrhenius, 1889) it seems appropriate to use the term apparent activation energy to refer to these values.

The temperature sensitivity of biological rates is normally expressed as an increase ratio following a 10°C increase (Q_{10}) in temperature. As the ocean will most likely experience temperature increases of a few (1–4°C) degrees Celsius over the next decades, we calculated the increase in PHP compared to a water temperature increase of 1°C (Q_1) instead of 10°C using the following formula:

$$Q_1 = e^{\frac{E_a}{R} \frac{1}{T_1 T_2}} \tag{2}$$

Linear regression analyses were used for the Arrhenius plots. Prior to regressions, normality was checked and the confidence level was set at 95%, with all statistical analyses conducted in R version 3.1.0 (Development core team R, 2014).

RESULTS

We have compiled and harmonized a total of 14,510 pairs of concurrent measurements of open ocean water temperature and prokaryotic heterotrophic production rates to test, using a space-for-time substitution analysis, the *in situ* response of prokaryote activity to temperature in epi-, meso-, and bathypelagic waters of the world ocean. The individual depth layers contained data from each major ocean. In the epipelagic layer most (51%) data points were collected in the Atlantic Ocean, followed by the Pacific Ocean (15%) and Arabian Sea (13%). In the mesopelagic layer the Atlantic Ocean contributed again with the largest fraction (51%), followed by the Arabian Sea (12%), Cariaco Basin (14%), Pacific Ocean (12%), and Ross Sea (10%), which contributed almost equally. In the bathypelagic layer the data points were dominated by measurements from the Atlantic Ocean (40%), Arabian Sea (30%), and Pacific Ocean (26%). Most of the data pairs corresponded to the epipelagic (77%), followed by the mesopelagic (15%) and bathypelagic (8%) layers (**Table 1**). In this study we aggregate data from regions that have different environmental conditions, which could potentially bias our dataset. To test if the PHP varied systematically between areas, we plotted all PHP and temperature data in the epi-, meso-, and bathypelagic layers from each region using box-and-whiskers plots (Supplementary Figure S2). These plots show that the variability in the PHP is large, but that no systematic bias is apparent between regions or studies (Supplementary Figure S2).
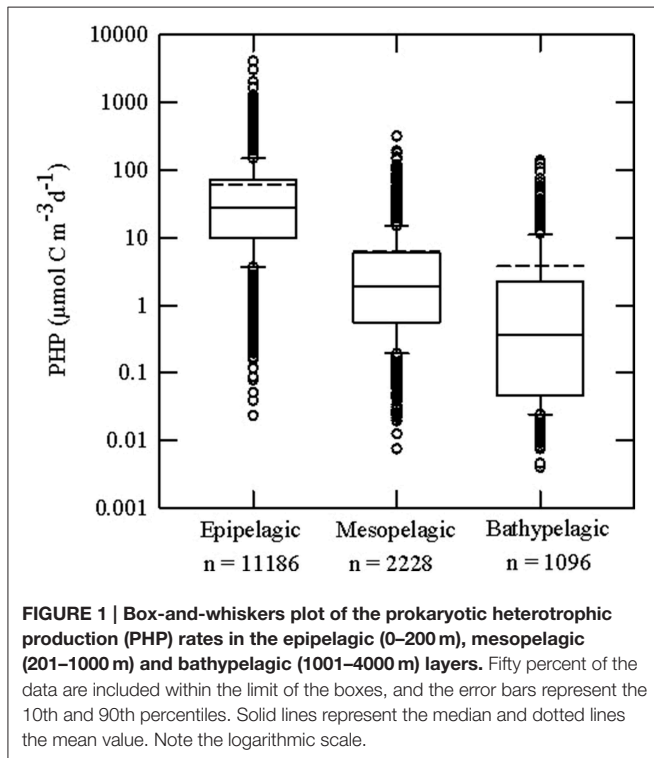
The average seawater temperature was 17.8 ± 8.8°C (range: −1.9–31.1°C), 11.5 ± 6.3°C (−2.0–19.0°C), and 3.1 ± 1.8°C (−0.4 and 9.1°C) in the epi-, meso-, and bathypelagic waters, respectively (**Table 1**). Globally, the average PHP in the epipelagic (61 ± 110 μmol C m^{-3} d^{-1}) was about 10 times larger than in the mesopelagic (6 ± 15 μmol C m^{-3} d^{-1}), which in turn was around 1.7 times higher than in the bathypelagic layer (4 ± 11 μmol C m^{-3} d^{-1}). This approximate 10-fold average decrease in the PHP from the epipelagic to the bathypelagic layer (**Table 1**, **Figure 1**), follows closely the decrease in temperature, average temperature difference between the epi- and bathypelagic ocean is about 15°C (**Table 1**), and the decreasing organic matter supply and bioavailability (Herndl and Reinthaler, 2013; Reinthaler et al., 2013).

After grouping the data of each depth layer by temperature bins of 1°C, we analyzed the temperature dependence of PHP using Arrhenius plots and observed significantly different linear regressions between *ln*PHP and 1/T ($p < 0.001$) for the three layers (**Figure 2**). The apparent activation energies (E_a) derived from the regression slopes of the Arrhenius plots were 36 ± 7 kJ mol^{-1} in the epipelagic, about half in the mesopelagic layer (72 ± 15 kJ mol^{-1}), which in turn was about 4.5 times lower than for the bathypelagic layer (274 ± 65 kJ mol^{-1}). These numbers were significantly different among them: T-Student was 2.167 ($p < 0.1$)

TABLE 1 | Summary of data used with the temperature and prokaryotic heterotrophic production (PHP) ranges and averages (± standard deviations) reported for the epipelagic (0–200 m), mesopelagic (201–1000 m) and bathypelagic (1001–4000 m) zones of the global ocean.

Layer	Temp. Range (°C)	Temp. Avg (°C)	PHP Range (μmol C m^{-3} d^{-1})	PHP Avg. (μmol C m^{-3} d^{-1})	E_a (kJ mol^{-l})	Q_1	N
Epipelagic	[−1.9, 31.1]	17.8 ± 8.8	[0.02, 4042]	61 ± 110	36 ± 7	5 ± 1%	11,186
Mesopelagic	[−2.0, 19.0]	11.5 ± 6.3	[0.008, 315.1]	6 ± 15	72 ± 15	12 ± 3%	2228
Bathypelagic	[−0.4, 9.1]	3.1 ± 1.8	[0.004, 138.3]	4 ± 11	274 ± 65	55 ± 16%	1096

The apparent or ecosystem level activation energy, E_a obtained applying the Arrhenius law to PHP rates from each layer is also reported. Q_1 represents the relative increase of PHP in response to a 1°C increase around the average temperature (Temp. Avg) of each layer and N is the number of data points in each depth layer.

FIGURE 1 | Box-and-whiskers plot of the prokaryotic heterotrophic production (PHP) rates in the epipelagic (0–200 m), mesopelagic (201–1000 m) and bathypelagic (1001–4000 m) layers. Fifty percent of the data are included within the limit of the boxes, and the error bars represent the 10th and 90th percentiles. Solid lines represent the median and dotted lines the mean value. Note the logarithmic scale.

when comparing the epi- and mesopelagic layers and 3.003 ($p <$ 0.01) when comparing the meso- and bathypelagic layers. These E_a translate into relative increases of PHP in response to a 1°C increase of 5% for the epipelagic, 12% for the mesopelagic and 55% for the bathypelagic zone (**Table 1**).

DISCUSSION

Application of Ecosystem Level Activation Energies in Earth Sciences

The Arrhenius law has previously been used in marine sciences for calculating the apparent E_a of the ocean's metabolic balance and explaining its temperature dependence under its recent reformulation within the metabolic theory of ecology (MTE) (Brown et al., 2004; López-Urrutia et al., 2006). The MTE scales the metabolic rates by combining the effects of body size and temperature, suggesting that autotrophic and heterotrophic

processes in marine systems will react differently to ocean warming, thus possibly changing the metabolic balance leading to a more heterotrophic ocean (Yvon-Durocher et al., 2012). In soils the temperature sensitivity of microbial organic matter degradation has been studied extensively (Davidson et al., 2000; Davidson and Janssens, 2006), demonstrating that increasing ambient temperature preferentially stimulates the microbial degradation of the more recalcitrant organic matter fractions. These results led to the formulation of the carbon quality temperature (CQT) hypothesis (Davidson et al., 2000; Davidson and Janssens, 2006; Kleber, 2010), which is based on the principles of enzyme kinetics combined with the Arrhenius law. According to the CQT hypothesis, substrate quality can be defined by changes in E_a, which is the energy barrier to be surpassed for substrate degradation to take place. Thus, the more recalcitrant the substrate, the higher its E_a and, following the Arrhenius law, the higher its temperature sensitivity to microbial degradation (Bosatta and Ågren, 1999; Sierra, 2011).

The CQT hypothesis has not been tested yet in the dark ocean, where most of the organic matter consists of recalcitrant compounds (Hansell, 2013). The E_a of the epipelagic and mesopelagic zones found in this study were similar to values found for organic matter degradation in marine sediments and soils (Middelburg et al., 1996; Craine et al., 2010), while the bathypelagic was similar to an E_a recently proposed ($\sim$200 kJ mol^{-1}) for the degradation of recalcitrant organic matter in marine sediments (Burdige, 2011). The increase of apparent E_a with depth that we report here (**Table 1**) agrees with the predictions of the CQT hypothesis, suggesting that marine microbes degrading more recalcitrant compounds with higher E_a have higher temperature sensitivity (Bosatta and Ågren, 1999; Sierra, 2011). Although it should be kept in mind that PHP in the deep ocean is not only fuelled by recalcitrant compounds since sinking particles and physical transport can export labile compounds to the ocean interior (Carlson et al., 2010; Follett et al., 2014). Furthermore, the E_a for the epipelagic layer was somewhat below the E_a value of 62.7 kJ mol^{-1} that has been predicted by recent theories for overall heterotrophic organism metabolism, suggesting that factors other than temperature (e.g., substrate) also limit the PHP in this layer (Brown et al., 2004; López-Urrutia and Morán, 2007). In the mesopelagic zone the E_a of 72 ± 15 kJ mol^{-1} was very close to the theoretical value, suggesting that temperature is one of the main limiting factors for the PHP in this layer. However, the E_a for the bathypelagic
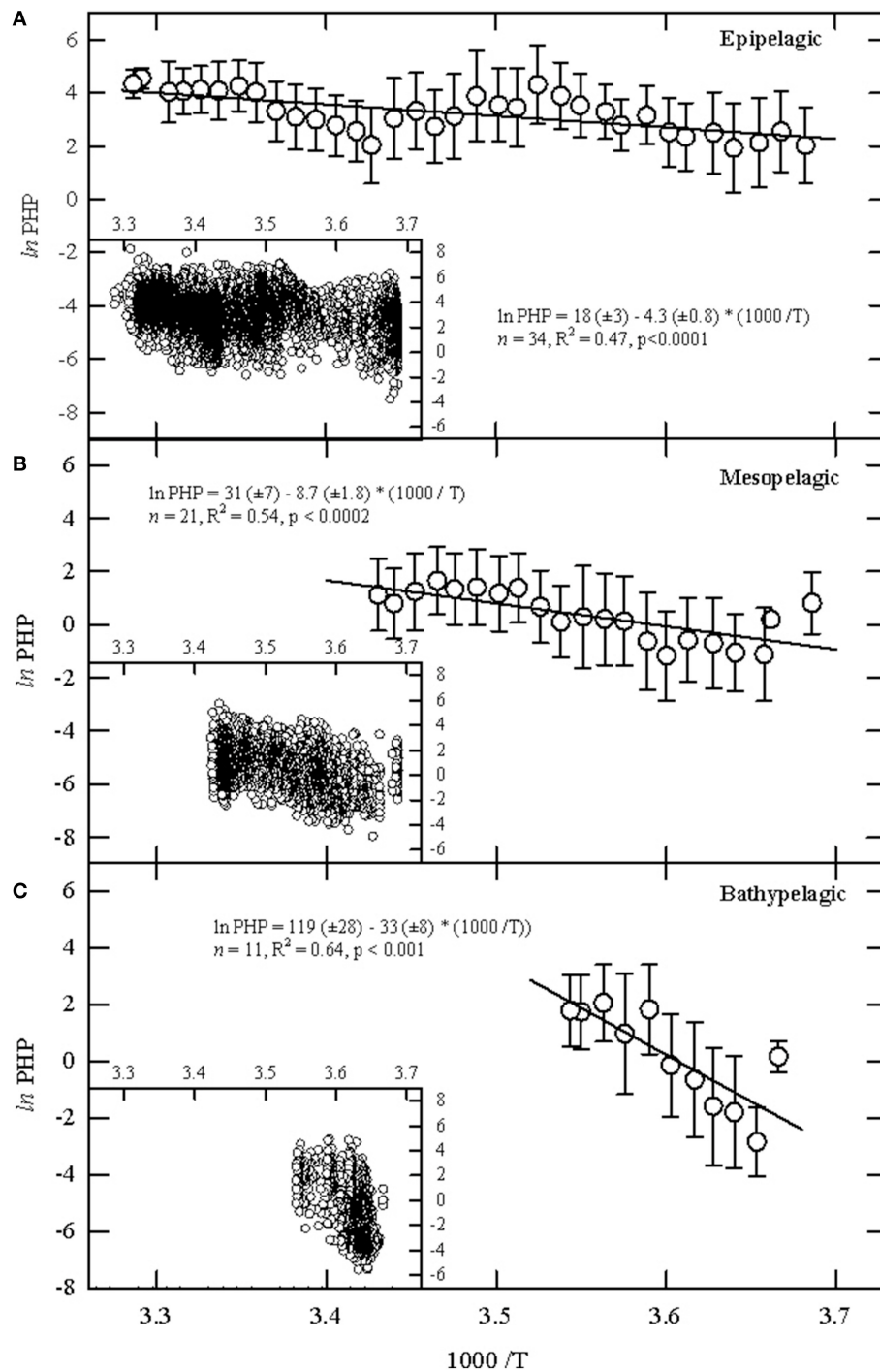
FIGURE 2 | Arrhenius plots of the natural logarithm of the prokaryotic heterotrophic production (*ln* PHP) against the inverse absolute temperature (1/T) for the (A) epipelagic (0–200 m), (B) mesopelagic (201–1000 m), and (C) bathypelagic (1001–4000 m) sets of samples. The error reported for the PHP grouped samples by 1°C bins represent the standard deviation. Solid lines represent the corresponding regression lines with the origin intercept and slope of the regression equations and their corresponding standard errors; R^2, coefficient of determination. The inset in each graph shows the raw data for each depth layer.

is approximately 3 times larger than the theoretical value, which might reflect fundamental differences in either prokaryotic physiology, organic matter supply, organic matter composition or a combination of these, compared to the shallower depth layers (Brown et al., 2004; López-Urrutia et al., 2006; López-Urrutia and Morán, 2007; Yvon-Durocher et al., 2012).

Other Factors Affecting the Prokaryote Production to Temperature Relationship

The varying relationship between PHP and temperature between depth layers could also be constrained by factors such as varying cell abundance and size, inorganic nutrient concentrations, dissolved oxygen, UV-light exposure, taxonomy/genomic potential, decompression effects, and the amount, bioavailability or extreme dilution of individual organic substrates (Benner, 2002; Mopper and Kieber, 2002; Kattner et al., 2011). Prokaryotic cell abundances were reported in a subset of the dataset included in our analysis ($n = 7597$). Cell-specific PHP rates and the corresponding E_a, ranging between 38 ± 8 kJ mol^{-1} (epipelagic) and 228 ± 45 kJ mol^{-1} (bathypelagic layer) (Supplementary Figure S3), showed a similar pattern compared to the whole dataset and the bulk PHP rates ($n = 14,510$). This suggests that varying cell abundances were not a major factor for the differences in E_a among depth layers. The MTE predicts that cell size should decrease with increasing temperatures thereby affecting the organism metabolism and resulting in a higher E_a, as shown for phytoplankton communities (Gillooly et al., 2001). For heterotrophic prokaryotes most studies have focused on the impact of temperature on metabolic rates. Generally, these studies indicate an increase in specific growth rate, PHP, and respiration with elevated temperatures (White et al., 1991; López-Urrutia and Morán, 2007; Vázquez-Dominguez et al., 2007), and even suggest that heterotrophic prokaryotes might have the ability to adjust their body size (Morán et al., 2015). We unfortunately do not have data on cell size distribution in the different depth layers and, therefore, cannot judge how this might impact the observed temperature-PHP relationships. PHP has also been shown to depend on the concentrations of inorganic nutrients (Gasol et al., 2009), likely influencing our PHP rates in the epipelagic, but not in the meso- and bathypelagic zones, where inorganic nutrient levels are well above limiting concentrations. Low dissolved oxygen concentration has been shown to impact the metabolic pathways and taxonomic composition of prokaryotic communities, and anaerobic degradation of organic matter is generally assumed to be slower than aerobic degradation (Lee, 1992; Quiñones et al., 2009). The dataset presented here includes sites with occasionally very low oxygen concentrations in mesopelagic zones such as in the Arabian Sea and the Cariaco Basin. As the PHP rates and temperatures found in these areas were similar to values found in other ocean regions, we considered the influence of low oxygen on our apparent E_a values negligible. UV-radiation is known to influence PHP both directly and indirectly through e.g., photochemical induced transformation of organic matter (Herndl et al., 1993; Mopper and Kieber, 2002; Ruiz-González et al., 2013). Most of the measurements included in this study were conducted in the dark, thus it is not possible to assess how direct or previous sunlight exposure in the photic zone might have influenced the rates measured. The ocean's prokaryotic community composition has been shown to vary both with depth and over spatial and temporal scales, with potential impacts on the PHP rates (DeLong et al., 2006; Sunagawa et al., 2015). We do not have prokaryote diversity estimates available

for our dataset and we can therefore not judge how changes in the community composition might impact our apparent E_a values. Future studies, combining PHP measurements with diversity estimates over large temperature and depth ranges will be needed to address these relationships. All our mesopelagic and bathypelagic samples were decompressed prior to measuring PHP. Whether, decompression of deep sea samples lead to an increased or decreased prokaryotic activity is still a major unknown (Tamburini et al., 2013). In order to estimate the effect of decompression on the E_a we subdivided our mesopelagic and bathypelagic data into two depth intervals and found that the apparent E_a values were constant between these depth layers (Supplementary Figure S4). This suggests that while the overall PHP rates might have been different under *in situ* and decompressed conditions, the obtained temperature relationships are independent of the pressure effect. Our estimated E_a might also be influenced by the amount, bioavailability or extreme dilution of individual organic substrates. Recently, it has been argued that the dark ocean organic matter pool contains hundreds of thousands of individual compounds at extremely dilute concentrations (Kattner et al., 2011; Arrieta et al., 2015). Thus, molecular diffusion of individual compounds could be the limiting factor for prokaryotic growth. It is well known that increasing temperature impacts the molecular diffusion of organic molecules, however, the E_a for diffusion about 15 kJ mol^{-1} (Oelkers, 1991), is too low to explain the extremely high ecosystem-level E_a in the bathypelagic realm. Alternatively, it could be argued that prokaryotic cells may switch to a maintenance mode by down-regulating their enzymatic activity when the diffusive substrate encounter rate is energetically unfavorable (Egli, 1995). This suppression of enzymatic activity would lead to an increased E_a. Previous works have also suggested that planktonic communities growing at lower temperatures will have a steeper response to increased temperature, which has been linked to a covariation between temperature and substrate availability (see review by (Pomeroy and Wiebe, 2001) for further information and references). For the epipelagic samples an argument could be made that there are two different temperature gradients (**Figure 2A**), so that microbes living in warm and cold environments would response differently to increasing temperatures. Whether similar covariations between temperature and substrate exist for our mesopelagic and bathypelagic samples is not clear from the available data and further studies are therefore needed to elucidate such relationships.

Implication for an Ocean under Global Warming

Our analysis of the temperature dependence of PHP using an Arrhenius type relationship has shown that the resultant apparent activation energies (E_a) are fundamentally different between the epi-, meso-, and bathypelagic ocean layers (**Table 1**). Since the E_a is particularly high in the bathypelagic layer compared with the epi- and mesopelagic layers, it suggests that dark ocean microbes are the most sensitive to global warming.

Over the last years it has become evident that the rate of upper-ocean-warming has leveled off, showing only a modest warming over the last decade (Meehl et al., 2011; Balmaseda et al., 2013). This has been mainly explained by the gradual heat absorption of the dark ocean, with approximately 30% of the ocean warming occurring below 1000 m depth and an average increase of 0.003°C year^{-1} (Meehl et al., 2011; Balmaseda et al., 2013). Accordingly, this temperature increase would stimulate the dark ocean PHP more than the PHP of their epi- and mesopelagic counterparts. The apparent E_a we obtained would predict an increased PHP by about 5, 12, and 55% in the epi-, meso- and bathypelagic ocean in response to an increase in water temperature of ∼1°C. Thus, global warming could cause a non-steady state condition to which the microbes may acclimatize, reaching a new equilibrium over time. Whether increasing temperatures have long-lasting and major impacts on the prokaryotic community, indicating a progressive acclimation of the prokaryotic community, or whether they quickly adapt to the elevated temperatures, remains to be seen. Long term (years) heating experiments in soils have shown that microbial activity returns to pre-warming values within a few years, likely due to a depletion of labile organic matter pools and/or thermal adaptation of the microbial community to the increased temperatures (e.g., Bradford et al., 2008; Rousk et al., 2012). Microbial temperature adaptation has also been demonstrated in lakes (Hall and Cotner, 2007; Hall et al., 2008) and similar mechanisms could also be at play in the ocean, but experimental data to support this are still missing.

Considering that heterotrophic prokaryotes play key roles in the oceanic carbon cycle, minor changes in their productivity due to increased temperature could have major impacts on the ocean carbon fluxes. It must be noted that our analysis uses only biomass production by heterotrophic prokaryotes, not the total consumption of organic matter (PHP plus respiration (PHR)). Hence a differential growth efficiency (PHP/(PHP+PHR)) with depth, related to changes in temperature (Rivkin and Legendre, 2001) or in the quality and availability of the organic matter consumed (López-Urrutia and Morán, 2007; Vázquez-Domínguez et al., 2007; Alonso-Sáez et al., 2008) could also play an important role in determining the impacts of the observed responses. As prokaryotic respiration measurements are scarce, especially in the deep ocean, future studies to resolve the interactions between prokaryotes carbon cycling and climate change could benefit from combining the field estimates with global biogeochemical models (e.g., Bendtsen et al., 2002; Hasumi and Nagata, 2014).

CONCLUSIONS

We suggest that (1) the assumption that prokaryotes in the ocean will uniformly react to increasing temperature is not valid along the depth gradient; and (2) the empirically estimated E_a values indicate that increasing ocean temperature will enhance prokaryotic production in the deep realm of the ocean more than in surface waters. This differential behavior of the dark ocean might have far reaching consequences for the overall carbon balance of the global ocean.

AUTHOR CONTRIBUTIONS

CL, LC contributed equally to the data survey. TR, GH, XM, and JG provided raw data. CL, XA analyzed the data, devised the research and wrote the first draft of the manuscript. LC, TR, GH, JG, XM, and NB commented and discussed on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00090

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