

Interactive comment on "Temperature-dependence of planktonic metabolism in the Subtropical North Atlantic Ocean" by L. S. García-Corral et al.

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Dear Professor G. Herndl,

I am writing to submit our response to reviewers comments, along with a revised version of the manuscript "Temperature-dependence of planktonic metabolism in the Subtropical North Atlantic Ocean," where we have incorporated the concerns and comments of the reviewers, to be reconsidered for publication in Biogeosciences (BG).

We thank the reviewers for the helpful comments made, which we have considered while thoroughly revising the manuscript, and which we believe have aided in greatly improving the manuscript relative to that originally submitted. The actions taken to C2895

accommodate the reviewer's comments are described in detail below.

We hope that, as a result of the improvements made, you will now find the revised version acceptable for publication in Biogeosciences.

Sincerely,

Lara S. García-Corral

Actions taken in response to the comments by the Anonymous Referee#1

Reviewer #1:

General comments: While the above arguments might be true, I am not convinced that the data presented is able to suggest such conclusions. The main reason being the missing explanation on how the data were treated for statistical analysis and the data presentation itself. Much of the results and discussion seems to deal with chlorophyll a concentrations, which to my mind is not substantially adding to verify the conclusions reached. On the other hand the important data GPP, CR, NCP etc. are not sufiňĄ-ciently discussed in the context of the temperature dependence.

Comment: We agree that the paper needed to be strengthened.

Action: We have addressed the problem of missing information about data analyses in the revised version of the manuscript. See details below.

SpeciiňĄc comments Reviewer #1:

Introduction: Page 3243, line 21-22: What do you mean by stating 'the metabolic balance of plankton communities is ...'?

Comment: 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.

Action: We have changed the text to " The metabolic status of plankton communities is..."

Methods: I feel that the methods section needs to be rearranged. I would place the paragraph on measuring chl a concentration after the section "study area", which I would call sampling sites and study area.

Action: Done. Paragraph and the title of the section have been changed.

Somewhere in the paragraph on the community metabolism I would expect a better description of the Winkler approach. Particularly I miss the mention of the chemicals used.

Comment: We agree that additional information is needed. The Winkler technique has been describe since the 1960s (Carpenter,1965; Carritt &Carpenter 1966); it has subsequently been used and its accuracy has often been validated (Williams & Jenkinson, 1982; Williams & Purdie 1991). We performed the Winkler titrations with the reagents recommended by Carritt & Carpenter (1966) using a 0.01 N sodium thiosulfate solution. As the "Material and methods" section it is extensive already and the exact reagents and methodology can be referred to in the previously published literature, we do not consider it necessary to explain in an explicit way the technique and methodology followed in this study.

Action: We have revised the "Methods" section, "Community metabolism" subparagraph to include the following line: "We used 0.01 N (S.D \pm 0.000141) thiosulfate solution and the reagents recommended by Carrit and Carpenter 1966."

I could not see what the use of the satellite derived data for the study is, so I would delete this paragraph plus the iňĄgure.

Comment: We believe that the satellite images help the reader to assess the distribution of chlorophyll a concentrations and temperature for each of the cruises, which are important elements to consider the results described. The other reviewer and the

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editor did not recommend that the figure be removed and we, therefore, opt to leave it in the manuscript.

You need to add a short paragraph on data treatment and statistics (what test has been used under which conditions etc). Where the data generally normally distributed? Using t-tests e.g. is valid if the data are normally distributed.

Comment: We agree that the statistical information should be provided in greater detail.

Action: We have assessed the normality of the data and where the data were not normal a non-parametric comparison between cruises was used. This is now indicated in the "Material and methods", which reads: "Volumetric metabolic rate estimates (GPP, CR and NCP) for the three different cruises were tested for normality before statistical analysis via Shapiro-Wilk tests with a 0.05 significance level, and homogeneity of variances was tested using the Levene test. When GPP, CR and NCP estimates deviated from a normal distribution (p>0.05), a Kruskal-Wallis test was used to compare variables. The Kruskal–Wallis test is a non-parametric equivalent to a one-way analysis of variance by ranks. It tests the null hypothesis that 3 or more groups all come from the same distribution. It uses the ranks of data and is therefore resistant to outliers". Consequently, the "Results" section now reads: "NCP did not differ significantly among cruises (Kruskal-Wallis test, p = 0.5), whereas CR and GPP were significantly higher for the spring cruise (Kruskal-Wallis test, p < 0.0001)".

I also miss a note on how the integrated rates were calculated.

Comment: The calculation of the integrated rates was explained in the text, page 3247 lines 16-18. However, reviewer #2 suggested to use the depth-averaged rate rather than integrated rates as a basis for comparisons. We agreed with that suggestion and while reporting integrated rates, we base all comparisons on the depth-averaged rate as suggested by reviewer #2.

Action: The "Material and methods" section now reads: "Integrated metabolic rates

were calculated by adding up the weighted-average rate between consecutive sampling depths from the surface layer to the DCM (1%PAR), and standard errors were calculated using error propagation. Because the depth of integration differed, for comparisons we used the depth-averaged rate, calculated as the ratio between the mean integrated rate and the depth of integration". Integrated rates were changed throughout the text and in table 2.

Page 3246, line 4: Is there a citation for the claim that the incubation bottles themselves reduce incident radiation by 8-12% or did you measure this for a batch of bottles?

Comment: Yes, the citation is Agustí et al. (2014), as we used the same bottles.

Action: We have now added the citation Agustí et al., 2014 to the reference list: Agusti, S., Regaudie-de-Gioux, A., Arrieta, J.M. and Duarte, C.M.: Consequences of UV-enhanced community respiration for plankton metabolic balance. Limnol. Oceanogr, 59, 5–15, 2014.

Page 3247, line 22: Did you calibrate the sensor yourself (with which solution) or did the company do it?

Comment: The sensor was calibrated by the company, but the absolute values are not used in any step (only the calculation of the titration end point, inferred from the slope of change in redox vs. volume of titrating solution).

Figure 1: Indicate the biogeographical provinces you mention in the text. A shape iňĄle can be found at http://www.marineregions.org/sources.php Longhurst biogeographical provinces.

Comment: We appreciate the link provided.

Action: We added the Longhurst Provinces to the figure 1 of the sampled stations. Also, in the new map (figure 1), one station (number 26) has changed its classification, from NATR Trades - N. Atlantic Tropical Gyral Province to NASE Westerlies - N. Atlantic Subtropical Gyral Province (East) and the correspondent changes have been made in

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the Table 3.

Results: Generally the results are confusing and need extensive editing. The long sentences including many brackets and detailed numbers should be shortened. See as a prime example page 3250 line 21-24.

Comment: We agree.

Action: We have thoroughly revised the results section to improve clarity, using shorter sentences.

Particularly the different sampling depth should either be simpliiňAed (it does not matter whether you sampled at 23.49 m or at 23.5 m depth) or referred to in a table.

Action: Done. We reduce all depth descriptions to one digit after decimal point instead of two for ease of reading.

It is not adequate to use a simple t-test when comparing the means of 3 or more samples, particularly without any mention of the data distribution. I suggest you to use ANOVA analysis (if the data conforms to the assumptions) plus the appropriate post hoc tests, including a correction for multiple signiin Acance testing, to detect differences of means between Leg 1, 2 and 3.

Comment: We agree.

Action: See explanation above on changes in statistical tests, and see newly re-written results section for results of these tests.

Instead of using Leg 1, 2 and 3 it would be more intuitive to substitute these for the season names winter, spring and summer.

Comment: We agree.

Action: To make the comparison between cruises easier we have change leg 1 to winter, leg 2 to spring and leg 3 to summer in most of the descriptions.

Figure 2 is too small, particularly the labels can hardly be read. In the text you explain temperature iňĄrst, thus put temperature here as iňĄrst row too. In the row showing chl a concentrations I suggest you to indicate the DCM. The legend is incomplete: what are the black dots and lines?

Action: The Figure 2 has been made larger and labels more legible. Temperature chart has been changed into the first row and the legend has been completed, indicating that black lines and points showed the profile and the sampled depths.

I would prefer to see GPP, CR and NCP as well as the GPP/CR ratio in a graphical form while table 1 could be showing temperature and chlorophyll a.

Comment: We agree that a figure will improve the presentation of these important data.

Action: We have now added a figure (figure 6) showing the mean \pm SE of the rates for each of the cruises and depths.

Page 3252, line 14: I did not understand what the use of Chl a standardized CR or GPP rates should be. A one liner in the text explaining this would be nice.

Comment: Previous examinations of the temperature-dependence of metabolic rates have demonstrated that bulk rates (i.e. mmol O2 m-3 d-1) are dependent on both community biomass and temperature, with the biomass-specific rate being the component that is temperature-dependent and conforming to the temperature-dependence expected by the Arrhenius law and metabolic theory (e.g. Regaudie-de-Gioux and Duarte, 2012). Metabolic theory states that metabolic rates are a function of biomass and temperature (Brown et al., 2004) whereas biomass is not necessarily temperature dependence, so that use of bulk rates conceal the role of temperature. Moreover, previous research on the temperature-dependence of metabolic rates shows that the most effective metric to standardize for community biomass is chlorophyll a concentration both for GPP and CR (Regaudie-de-Gioux and Duarte, 2012).

Action: We now provide the rationale in the "Material and methods" section, which now

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reads: "Whereas the experimental assessments use the same community, the evaluation of the temperature-dependence of metabolic rates across stations is confounded by the changes in community. Indeed, previous examinations of the temperaturedependence of metabolic rates have demonstrated that bulk rates (i.e. mmol O2 m-3 d-1) are dependent on both community biomass and temperature, with the biomassspecific rate being the component that is temperature-dependent and conforming to the temperature-dependence expected by the Arrhenius law and metabolic theory (e.g. Regaudie-de-Gioux and Duarte, 2012). Metabolic theory states that metabolic rates are a function of biomass and temperature (Brown et al., 2004) whereas biomass is not necessarily temperature dependence, so that use of bulk rates conceal the role of temperature. Moreover, previous research on the temperature-dependence of metabolic rates shows that the most effective metric to standardize for community biomass is chlorophyll a concentration both for GPP and CR (Regaudie-de-Gioux and Duarte, 2012). Hence, we standardized the rates per unit chlorophyll a to allow for cross-station comparison of temperature-dependent metabolism and comparisons of experimental assessments with previous assessments".

Page 3251 paragraph 2: I am sure that your data on GPP is not accurate to the second digit after the decimal point (including all the errors of calculation and integration). Thus I guess integers will do.

Comment: We have changed the method of integrated rates calculation as suggested by reviewer #2, ("depth- averaged" values, dividing the integrated value with the deepest sampling) and the new values are accurate to the second decimal point.

Action: We modify the paragraph 2 and 3 of page 3251 and the table 2, to describe the new calculated depth-averaged integrated metabolic rates, leaving the two decimal points.

Discussion:

Page 3253, line 13-17: The authors state at length that the eastern and western basin

are different to highlight the uniqueness of their western basin data. If this is so, it would be consequent to desist from comparing the overall average of chl a concentrations with and average of the eastern basin from a former study by Teira et al.

Comment: We agree that the comparison is not entirely appropriate.

Action: We removed from the discussion the following sentence: "Mean surface chlorophyll a concentration (0.16 \pm 0.02 mg chl a m-3) for the three cruises was higher than the 0.09 \pm 0.01 mg chl a m-3 reported by Teira et al., (2005) for the Eastern basin of the Subtropical North Atlantic".

Page 3253, line 18-19: Isn't it trivial to report that chl a concentrations sampled in the oligotrophic gyre are representative of oligotrophic waters?

Comment: Yes, we agree.

Action: We have removed the sentence.

Page 3253, line 25: Do you mean phytoplankton community structure here? In any case, I suggest to discuss more in depth how the various factors you mention inïňĆuence the variability of the measured rates.

Comment: Yes, we referred to phytoplankton community structure in this sentence. For a better explanation of the variability found in the metabolic rates showed in this study, we explain in more detail the factors that can influence the metabolic rates at large scales.

Action: We have now included more details in the explanation, beginning with the new paragraph: "Here we report a high temporal and spatial variability of metabolic rates in the Subtropical North Atlantic Ocean. Such variability can be due to atmospheric forcing (i.e. North Atlantic Oscillation), as interannual variability in pCO2 correlated with temperature and mixed-layer depth anomalies, can affect the nutrient supply to the euphotic zone (Gruber et al., 2002). Physical forcing mechanisms such as mesoscale instabilities can act as important sources of organic carbon (González et al., 2001)

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and nutrients (Garçon et al., 2001) to the pelagic ecosystems in oligotrophic areas. Also, intrinsic factors, such as changes in phytoplankton community structure and trophic dynamics (Serret et al., 2009) can influence the variability of plankton community metabolic rates".

Page 3254, line 8-24: The issue on heterotrophic versus autotrophic subtropical regions made quite some buzz in the past. Here the authors iňĄnd that the subtropical Atlantic seems to be primarily autotrophic. Thus I suggest to discuss this topic in more detail, and at least speculate on the carbon sources in the western basin.

Comment: We agree that some additional discussion is needed.

Action: The paragraph now reads:" The Subtropical North Atlantic Ocean showed a net metabolic balance in this study, with a prevalence of autotrophy in 66% of the communities. The prevalence of autotrophic conditions in the three cruises conducted is in contrast to previous reports of a prevalence of heterotrophy in oligotrophic gyres (del Giorgio et al., 1997, Duarte and Agustí 1998, Duarte et al., 2013) and for the North Atlantic Subtropical Ocean (Duarte et al., 2001, González et al., 2002, Serret et al., 2002, 2006, Morán et al., 2004, Aranguren-Gassis et al., 2011). However, some studies have also shown balanced metabolism (Williams 1998, Aranguren-Gassis and Serret, 2012) or a prevalence of autotrophic communities (Kähler et al., 2010), leading to challenges in the view that oligotrophic regions of the ocean support heterotrophic plankton communities (Williams et al., 2013). These contrasting results maybe due to interannual variability in ocean metabolism, which has not been assessed as of yet but has been shown to be important in driving variability in satellite-based primary production estimates (Behrenfeld and Falkowski, 1997) and in the inorganic carbon cycle (Gruber et al., 2011). Alternatively, previous assessments were all based on the Eastern basin of the North Atlantic Subtropical Ocean which suggests possible differences across basins. The Eastern basin of the North Atlantic receives allochthonous organic carbon inputs, both as production exported from the North African upwelling (Pelegri et al., 2005) and atmospheric inputs (Dachs et al. 2005), which must, therefore, support balanced or autotrophic metabolism. Sources of allochthonous organic carbon and nutrients into the Western basin, are less evident, but mainly come from large rivers as the Amazon and Orinoco that discharge 70,140 km3 yr-1 of freshwater into the Atlantic Western basin (Franzinelli and Potter 1983; Lewis et al. 1990). An autotrophic status suggests either enhanced GPP or reduced inputs of allochthonous organic carbon (reduce CR), both contributing to positive NCP.

Somewhere in the methods I read about Q10 values but these are not discussed. Why?

Comment: We agree this part was omitted in the discussion.

Action: We excluded Q10 values and references from the whole work (Material and methods and Table 4) because is not relevant for our aim and conclusions.

Page 3255, line 23-29: The content of what the authors want to state is somehow clear, but this paragraph need extensive editing.

Comment: We agree.

Action: We have modified the sentence: "North Atlantic Ocean constitutes the largest ocean sink for atmospheric CO2 in the Northern Hemisphere (Gruber et al., 2002) storing 23% of the global oceanic anthropogenic CO2, despite covering only 15% of the global ocean area (Sabine et al., 2004). Long-term trends indicate that the subtropical gyre of the North Atlantic Ocean is, at present, acting as a significant sink for anthropogenic CO2 (Bates et al., 2002). However, the results presented here show that the metabolic balance of the Subtropical North Atlantic Ocean may be highly sensitive to warming. Assuming the forecasted ocean warming of 1-3°C by the end of the century (IPCC, 2007), our finding of an increase in respiration rates with warming suggests that the role of plankton communities in the Subtropical North Atlantic communities as significant CO2 sinks may be weakened substantially or even revert to become CO2 sources to the atmosphere in the future."

Technical corrections: Page 3244, line 1: Recent analysis suggested seawater temper-

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ature as a driver ... Page 3245, line 1: ... regional variability of plankton metabolic Page 3247, line 4: Incubation tubes were ... Page 3247, line 6: ... holding the temperature within \pm 0.5âUę C of the in situ temperature ... Page 3249, line 22: ... showed a similar range for... Page 3254, line 28: ... show a clear temperature-dependence ...

Comment: We thank the reviewers for paying attention to the details of the composition and apologize for the grammatical errors found.

Action: All technical corrections were made.

Page 3255, line 24: Something went wrong here by copy pasting.

Comment: We agree there were editing errors.

Action: We have modified the sentence: "However, the results presented here show that the metabolic balance of the Subtropical North Atlantic Ocean may be highly sensitive to warming. Assuming the forecasted ocean warming of 1-3°C by the end of the century (IPCC, 2007), our finding of an increase in respiration rates with warming suggests that the role of plankton communities in the Subtropical North Atlantic communities as significant CO2 sinks may be weakened substantially or even revert to become CO2 sources to the atmosphere in the future."

The ïňAgures need letters to distinguish the different panels that are described in the legend (e.g. A, B, C)

Comment: We agree with the comment.

Action: Figure 2 has been labelled as: first row A) indicating in the legend it shows measured in situ temperature, second row B) Chlorophyll a concentrations and third row C) Salinity for each cruise. Also, figure 3 has been labelled, as A) Chlorophyll a concentrations and B) Surface Temperature measured by satellite derived data. Figure 4 and 6 have also been labelled.

Actions taken in response to the comments by the Anonymous Referee#2

General Comment Reviewer #2:

I have to agree with the comments from reviewer #1 that the iňAeld data should be reanalyzed with clear statistical description.

Comment: We agree.

Action: We have described in greater detail and improved the statistical analysis of the data. In particular, we have assessed the normality of the data and where the data were not normal a non-parametric comparison between cruises was used. This is now indicated in the "Material and methods", which reads: "Volumetric metabolic rate estimates (GPP, CR and NCP) for the three different cruises were tested for normality before statistical analysis via Shapiro-Wilk tests with a 0.05 significance level, and homogeneity of variances was tested using the Levene test. When GPP, CR and NCP estimates deviated from a normal distribution (p>0.05), a Kruskal-Wallis test was used to compare variables. The Kruskal–Wallis test is a non-parametric equivalent to a one-way analysis of variance by ranks. It tests the null hypothesis that 3 or more groups all come from the same distribution. It uses the ranks of data and is therefore resistant to outliers". Consequently, the "Results" section now reads: "NCP did not differ significantly among cruises (Kruskal-Wallis test, p = 0.5), whereas CR and GPP were significantly higher for the spring cruise (Kruskal-Wallis test, p < 0.0001)".

The authors should justify the physiological and ecological implications of the positive temperature responses of GPPChI-a and CRChI-a derived from this study. Living organisms live on materials but not temperature, temperature is a physical factor that may elevate the reaction rates (by lowering down the activation energy) only when the supply rates of materials are not limiting. Therefore, positive temperature responses (as shown in Figs. 4 &5, and Table 4) can occur only when other factors, such as light and nutrient supply (for GPPChI-a) as well as organic substrate supply (for CRChI-a), are not limiting. Is this true for the systems that the authors studied?

Comment: We agree and now discuss this question in more detail.

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Action: We have inserted the following sentence in to the discussion to capture this argument: "Metabolic responses to temperature are dependent on the availability of other resources, such as light, nutrients or organic matter, to support autotrophic or heterotrophic metabolism (López-Urrutia and Morán 2007). Our results show that about 50% of the variability in respiration rates among plankton communities in the subtropical Atlantic Ocean can be accounted for by temperature differences, confirmed by the results of our experimental temperature manipulations. This suggests that whereas other resources may contribute to explain the 50% of the variability in respiration rates that cannot be accounted for by temperature differences, the availability of resources is still sufficient to leave scope for metabolic control by temperature."

I am a little bit concern about using the "integrated" values to make comparison (page 3251, paragraphs 2 & 3). It would be more subjective to use the "depth- averaged" values. That is, dividing the integrated value with the deepest sampling depth of that station

Comment: We agree with the comment and agree that depth-averaged values would provide a better basis for comparison.

Action: The "Material and methods" section now reads: "Integrated metabolic rates were calculated by adding up the weighted-average rate between consecutive sampling depths from the surface layer to the DCM (1%PAR), and standard errors were calculated using error propagation. Because the depth of integration differed, for comparisons we used the depth-averaged rate, calculated as the ratio between the mean integrated rate and the depth of integration". Integrated rates were changed throughout the text and in table 2.

SpeciiňĄc comments Reviewer #2:

1. The authors mentioned that they did 13 manipulation experiments in Leg 2 (spring season), but showed only one equation and one Q10 value in Table 4. Please explain.

Comment: We performed 13 experiments, incubating the diverse communities at different temperatures, to assess changes in community respiration (see Material and Methods, section "Experimental assessment of the temperature-dependence of community respiration rates"). All data were used to make an Arrhenius plot, which shows the relationship of the natural logarithm of Chl a-standardised rates with inverted water temperature (1/kT). The activation energy (Ea) was derived from the slope of the Arrhenius linear equation.

Action: We have removed the references to Q10 and associated references from the revised version (Material and methods and Table 3) as Q10 values were not reported or used.

2. For readers' convenience, the panels in Figs. 2 & 3 should be marked with capital A, B, C. . .etc.

Comment: We agree with the comment.

Action: Figure 2 has been labelled as: first row A) indicating in the legend it shows measured in situ temperature, second row B) Chlorophyll a concentrations and third row C) Salinity for each cruise. Also, figure 3 has been labelled, as A) Chlorophyll a concentrations and B) Surface Temperature measured by satellite derived data. All the references in the text have been checked and modified.

Fig. 2 showed the patterns of salinity, but the authors did not give any description in the text.

Comment: We agree.

Action: After the temperature and chlorophyll a descriptions we added the following paragraph about salinity values: "Sea surface salinity showed significant differences (Kruskal-Wallis test, p < 0.0001), between seasons, with lower values during spring (mean \pm SE; 36.5 \pm 0.06) and higher values during summer (36.8 \pm 0.08) and winter (37 \pm 0.03). The lowest value was found at the Caribbean Province (35.9 \pm 0.13), prob-

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ably due to equatorial water that carries a summer seasonal Amazon signal (Dessier and Donguy, 1994) while the high evaporation and lack of riverine inputs close to the NATR Province, resulted in higher salinity (37 \pm 0.03) for the open ocean region (Fig.2C)".

3. For better presentation, the authors may consider revising Table 4 to show their own Ea/Q10 values and the values published by other studies.

Comment: We agree.

Action: Activation energy values are now compared with other values from previous studies in the discussion. Q10 values and discussion have now been removed from the manuscript, as they do not add anything beyond the more robust information contained in activation energy values.

References:

Agusti, S., Regaudie-de-Gioux, A., Arrieta, J.M. and Duarte, C.M.: Consequences of UV-enhanced community respiration for plankton metabolic balance. Limnol. Oceanogr, 59, 5–15, 2014.

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Fig. 1. Map showing the stations occupied in Leg 1-winter (full circles), Leg 2-spring (open circles) and Leg 3- summer (open squares) during the Malaspina 2010 Expedition and the Longhurst Provinces crossed.



Fig. 2. Contour plots for A) temperature (°C), B) chlorophyll a (mg Chla m-3) and C) salinity of the profiles sampled (black lines) in Leg 1-Winter, Leg 2-Spring and Leg 3-summer. Black points indicated the t

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Fig. 3. : Satellite images showing 8 day-average chlorophyll a (A) and surface water temperature (B) from the date of the central station sampled in winter, spring and summer cruise



Fig. 4. Arrhenius plots showing the relationship between chl a-specific average rates A) CRChla) and B) GPPChla within 1° C bins and the inverted water temperature (1/kT, where k is the Boltzmann's constant,

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Fig. 5. Arrhenius plots showing the relationship between chl a-specific average rates A) CRChla) and B) GPPChla within 1° C bins and the inverted water temperature (1/kT, where k is the Boltzmann's constant,



Fig. 6. : Arrhenius plot showing the relationship between average chl a-specific respiration rate within 1°C bins and the inverted water temperature (1/kT, where k is the Boltzmann's constant, 8.617 10-5 eV k

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Fig. 7. Mean \pm SE for A) community respiration (CR), B) gross primary production (GPP) and C) net community production (NCP) (mmol O2 m-3 d-1) for each season (winter, spring and summer) at the three sampled