June 27, 2019

Dear Dr Ciavatta,
Associate Editor, Biogeosciences

Please accept our sincere apologies for the mismatch found between the lines indicated in our reply and the manuscript changes, here we are re-submitting our reply and the manuscript "*Rates and drivers of Red Sea plankton community metabolism*" with tracked changes. We have corrected the issue, and now the lines indicating the changes in the new manuscript can be found in the following section and our reply to the reviewers:

1. About the different variables used to explain the changes of planktonic metabolism in the Red Sea (i.e., latitude, water depth and seasonality) and reviewers' suggestion to rewrite the narrative of the manuscript by focussing on one or two variables.

   Reply
   We had modified the text and had mainly focused on the latitudinal and seasonal variability of planktonic metabolism and their relationship with temperature and nutrient availability (both tightly related to the latitudinal gradient that characterised the Red Sea). Although changes throughout the water column are relevant, we agreed with the reviewer that it added an unnecessary complexity to the text.

   Action
   We re-wrote most of the results section (now between lines 254–387 of the new version of the manuscript which includes the track changes), and modified the figures so that Figure 2 describes the latitudinal gradient of variables only in surface waters. Figure 3: we modify the format and the data presented, so we only included data within the photic layer. We removed Figures 4–5, and Figures 1A and 2A. We also removed Table 1, and Table 2. The information from Table 2 is now presented as a figure (now Figure 5) with the overall information and with all the data plotted. The changes in the results are in agreement with changes in the narrative of the discussion section. The main changes in the discussion section can be tracked between lines 447–463 and between lines 550–559.

2. About the methodology chosen and length of the incubations.

   Reply
   The Winkler titration method used in this study, is a methodology extensively used in studies that aim to measure autotrophic planktonic photosynthetic rates (i.e. gross primary production rates) and respiration rates derived from both the autotrophic and heterotrophic plankton community (see e.g., Williams et al., 1979; Duarte and Agustí, 1998; Bender et al., 1999; Robinson and Williams, 1999; Ducklow et al., 2000; Serret et al., 2001; Robinson et al., 2002; Serret et al., 2009; García-Martín et al., 2017). The selected incubation time allows to fully take into account diel changes of both metabolic rates, as community respiration rates occur during day and night.

   Action

We have clarified this point in the methods section 2.3 (between lines 166–174). In addition, we have ensured that the sampling, filling and fixing of the samples is described in sufficient detail. We also clarified how we calculated gross primary production, community respiration and net community production (which is the balance between the autotrophic and heterotrophic metabolism, and not only the result of photosynthetic activity). These calculations can be seen between lines 206 and 216.

3. About the lack of statistical analyses.

Reply
We agreed with the reviewers that a section with a detailed description of all the statistical analyses was missing, and that the statistical analyses mentioned in the results were not properly clarified, hence the reviewers were under the impression that we did not perform any statistics to support our conclusions.

Action
We have included a detailed description of all the statistical analyses done (see section 2.4 between lines 227–253). In addition, the results of each analysis are detailed whenever they are presented. See e.g. line 354 or line 383.

4. We also detected some typos and errors in three figures and one table that have been rectified, yet neither of those changed our main conclusions in any way.

Figures:

- Figure 8C (now Figure 4G) R^2 is 0.38 not 0.39 and, R^2 in Figure 8I is 0.16 not 0.17
- Figure 7A (now Figure 6A), the intercept is 0.73 not 0.74
- Figure 9B (now Figure 7B), the intercept is -0.73 not -0.72

The detailed answer to the reviewers with the updated line numbers is presented in the following section.

I would be grateful if this newly revised version of the manuscript was considered for publication in Biogeosciences.

Sincerely,
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Reply to reviewers

Reviewer 1

2.1.1 General comments

The authors describe a dataset of environmental variables related to the metabolism of planktonic communities along a depth and latitudinal gradient in a seasonal resolution in the Red Sea. The authors conclude that gross primary production relates positively to sea surface temperature and nutrient availability. The dataset is extensive, and the research questions (for this part of the Red Sea), to my knowledge, are novel and worthy of publication. The abstract is clear and reads well, but shows a different narrative than the rest of the manuscript. Thus, I suggest for the authors to consider rewriting the manuscript. As mentioned in the author contributions, the manuscript is written by several people and this is noticeable (see specific comments). The abstract mentions the latitudinal gradient but the ms introduces two more variables, i.e. depth and seasonality. While interesting variables, they make the story confusing at times and harder to disentangle the story the authors want to tell
(according to the abstract). Concerns about the methods used are mentioned in the specific comments and need to be addressed first. Proper description of statistical analyses is lacking.
My recommendation is that the ms needs major revisions, but only if methodological concerns can be addressed adequately. Then, I suggest a complete overhaul of the manuscripts narrative by focusing on 1 or 2 of the 3 major variables (latitude, water depth and seasonality) and stick with these in the entire narrative. Also, there needs to be a clear description of used statistics in the M&M section and figures and tables should be cut back and/or improved. Consistency in the presentation of the results (including the statistics) and the use of abbreviations (as well as changing them) is recommended

Reply to general comments

We sincerely appreciate the thorough revision, comments and the time devoted to review our manuscript in such a rigorous manner, as it helped us to greatly improve our manuscript. We have addressed all the reviewer's comments, and significant changes were done to the manuscript, figures and tables. Also, we have included a detailed description of the statistical analyses.

Action

The changes can be tracked in the new version of the manuscript in the Results section between lines 254–387 of the new version of the manuscript with track changes. We modified the figures according to the new narrative of the results as such that Figure 2 now only describes the latitudinal gradient of variables in surface waters. In Figure 3, we modified the format and the data presented, so now we only focus on data within the photic layer. We removed Figures 4–5, Figure 1A and 2A, as well as Table 1 and Table 2. The information from Table 2 is now presented as a figure (now Figure 5) with the overall information and with all the data plotted. The changes in the results are in agreement with changes in the narrative of the discussion section. The main changes in the discussion section 447–463 and between lines 550–559.

2.1.2 Reply to specific comments

Reviewer comment 1
Title: Says Red Sea but Gulfs are not included.

Reply

We agree with the reviewer that our study does not include data from the Gulf of Aqaba nor does it include the western half of the Red Sea. However, this detail is carefully described in the Introduction (line 123) and Methods sections (between lines 139–140) and in Figure 1, so the reader will not be misled.

Action

We, preferred to leave the title as it is, since we provided sufficient detail in the manuscript on which areas were sampled.

Reviewer comment 2
Abstract: Line 10: Mentioning "Low productive waters" immediately brings down the importance of the story.

Action

We modify the text accordingly and deleted "low productive waters" (see line 10)

Reviewer comment 3
The first paragraph is loaded with self-referencing while many others are not or less.

Reply

There is no intent to load the paper unnecessarily with self-references, but it turns out that the co-authors of this paper have published a large number of relevant articles on the topic. We have now, however, added additional works, by other researchers.

Action

These new references can be tracked between lines 39–44 and between 103–104.

Reviewer comment 4
Page 2, line 4-5 and 11: Introduce abbreviations once (see technical corrections) and use them consistently throughout the ms.

Reply

Thank you for your comment. We have modified the text accordingly.

Action

Abbreviations were introduced between lines 13 and 14 and subsequently used consistently.

Reviewer comment 5
Page 2: The abbreviations of GPP, CR and NCP are presented with units of daily oxygen produced or used. However, these abbreviations are normally used for daily production and use of carbon. I suggest the authors change the abbreviations for these processes and/or use a conversion factor to present daily carbon production and use.

Reply

This and other comments from the reviewer, led us to believe that there is a misunderstanding as they seem to suggest that our work was focused on primary production, which is performed by the photosynthetic components of the plankton community during the daytime and that has gross and net components (as phytoplankton excrete and respire carbon). However, our paper focuses on the entire plankton community, both photosynthetic and heterotrophic (e.g. bacteria), where the net community production (NCP) represents the organic matter remaining after consumption of the GPP through respiration by plants (autotrophs), microbes (either autotrophs or heterotrophs), and animals (heterotrophs) (Ducklow and Doney 2013). Hence, it is the balance of the photosynthetic processes (GPP) and respiratory activity of the entire plankton community (not just phytoplankton) measured during 24 h periods. Studies that focus on the photosynthetic component of the plankton community (e.g. Net Primary Production, NPP) report values for the daylight period only whereas studies such as this, report (24 h) rates. For instance, published syntheses of community metabolism rates report values per day (24 h), e.g., Robinson and Williams 2005, Regaudie-de-Gioux 2012, 2013).

Reports of daily GPP, NCP and CR rates in oxygen units has remained the case since Haaken H. Gran used the light and dark bottle method in combination with the Winkler method to report community metabolic rates (Gaarder and Gran 1927; Gran 1927). The reviewer can find other examples in Mclntire et al. 1964; Williams et al. 1979; Williams et al. 1983; Owens and Crumptom 1995; Robinson and Williams 1999; López-Urrutia et al. 2006; Stanley et al. 2010; García-Martín et al. 2017. The use of 24 h to report rates is indeed not just a tradition but is justified as the metabolic budget needs be resolved over 24 h to be completed. For photosynthesis this does not apply as it is a light-dependent process, but respiration, which is necessary to define net community production, occurs at night as well. Moreover, all of the above papers report rates based on oxygen units since this is the property measured, and converting these to C requires some assumptions, such as a theoretical PQ value. However, to allow comparisons with another component of carbon cycling, we have provided an estimate of what, for example, the mean GPP reported here represents in terms of carbon production, assuming a PQ=1.

Action

We have clarified this point in the Methods section 2.3 (between lines 166–174). In addition, we clarified how we calculated gross primary production, community respiration and net community production (which is the balance between the autotrophic and heterotrophic metabolism, and not only the result of photosynthetic activity). These calculations can be seen between lines 206 and 216. The average GPP rates in carbon units can be tracked between lines 302–303. We have also included the equivalent of CR in carbon units (assuming a RQ=1) in line 305.

Reviewer comment 6

Page 4, line 7-8: There are plenty of references that describe metabolism in the northern part of the Red Sea (e.g. Rahav et al. 2015 MEPS, Tilstra et al 2018 Frontiers, Levanon-Spanier et al 1979 Deep Sea Res.)

Reply

Thank you for the references, we have included them in our manuscript.

Action

Please find the suggested references and others more between lines 103–104.

Reviewer comment 7

Page 5-6: Silicate is measured, mentioned in the results and in many figures/tables (with significant interactions) but nowhere mentioned in the Discussion. If not important, mention briefly in Discussion. Page 6-7, line 20 and 1 (resp.): Was NH4 determined? If not, then you have NOx values, not DIN.

Reply

Thank you for pointing this out. Regarding the lack of discussion about the specific relationship between metabolic rates and silicates, we would like to mention that we did not discuss in detail the relationship between metabolic rates and any of the inorganic nutrients measured, as we aimed to discuss the overall patterns found among all variables (i.e., nutrients, temperature, autotrophic biomass).

Action

We have replaced DIN with NOx throughout the manuscript. Please see lines 261 and 306, as well as Figure 3, and Table 1.

Reviewer comment 8

Page 7, line 10: provide actual depths of PAR measurements. Also, I am confused about the use of 100%, 60-20 and 8-1 as table 1 and 2 give different ranges. Is the data comparable if different depths of sampling were used?

Reply

The reviewer is absolutely right, and we understand the reviewer's confusion. During our surveys, the samples to quantify planktonic metabolic rates were consistently taken within the first optical depth (ζ), towards the bottom of the photic layer, and one intermediate sample was either taken where we found the max. Chl-a fluorescence, or in case the Chl-a max was at the surface or the bottom layers, the intermediate sample was collected towards the middle of the euphotic layer (approx. 2.3 ζ). Therefore, our measurements are comparable. We chose the sampling based on the optical depths instead of physical depths (i.e., depth in m) as they are biologically relevant to describe metabolic processes such as GPP.

Action

This has been clarified in the manuscript between lines 175–188

Reviewer comment 9

Page 7: Were samples for metabolic rates filtered? Does the planktonic community include both single and multicellular organisms? Were the optodes adjusted for salinity? A major, potential, flaw in the methods used for metabolic rates is that it appears as though net photosynthesis was measured for 24h. If correct, this includes an approx. 12-hour period of darkness and thus results in data that cannot be used for calculations for gross photosynthesis, i.e. O2 measurements will be severely lower due to dark respiration. net photosynthesis should have been measured only during daylight and respiration rates should have been measured in 2 phases; during the daytime and during nighttime, so approximately 12:12 h as respiration rates can have a diurnal rhythm. So

extrapolating these data to daily rates could result in a wrong estimation of gross photosynthesis Also, how was O2 production data extrapolated to per day? I suggest authors stick to hourly values for oxygen rates. If methods are used correctly, carbon budgets can be calculated using a conversion factor. If net photosynthesis was measured during daylight and respiration for 24 hours, the authors need to state assumptions of the values to their manuscript (potential over- or underestimation of rates)

Reply

We agree with the reviewer that to measure net photosynthesis (i.e., the net organic carbon production in the light), a 24-h incubation can carry potential bias. However, in our study, we are neither measuring nor reporting net photosynthetic rates. As clarified in our reply to specific comments (5) and also stated in our introduction and methodology, our goal was to quantify the daily net community production. Therefore, we aimed to estimate the metabolic contribution not only from the autotrophic community but the entire planktonic community (i.e., the balance between the production and respiration of organic material). The selected methodology to quantify planktonic metabolism is based on the extensively used dark and light method in combination with the Winkler titration method (as mentioned in our reply AC5) and not optodes (as mentioned by the reviewer), in a 24 h incubation period, hence we report our results as daily rates.

Action

We have clarified why we used this methodology, and supported with references that the methodology chosen is largely used for the goals of this manuscript. These points can be seen in the methods section 2.3 (between lines 166–174)

Reviewer comment 10
Page 9, statistics: Need to be expanded with actual models used.

Reply

We agree with the reviewer that a section with a detailed description of all the statistical analyses was missing.

Action:

We have included a detailed description of all the statistical analyses done (see section 2.4 between lines 227–253) and in addition the results of each analysis are detailed whenever they are presented. See e.g. line 354 or line 383.

Reviewer comment 11
Page 9, line 11: NOx, not DIN.

Action

We modified the text accordingly, as seen now in line 261.

Reviewer comment 12
Page 10, line 17: 56% of heterotrophs suggests dominance of this trophic strategy

Reply

We agreed with the reviewer

Action

We have modified the results section and we no longer describe by depths the autotrophic or heterotrophic status of the communities

Reviewer comment 13
Page 11, line 4: What models were used to test this?

Reply

We determined if plankton metabolism and nitrite and nitrate were correlated by using a Pearson's correlation

Action

We re-analysed the data and the results are shown between lines 306–309

Reviewer comment 14
Page 11, line 8: Which analysis?

Reply

We evaluated the relationship between GPP with CR and NCP by performing an OLS linear regression.

Action

This information has now been clarified in the statistical analyses section (between lines 234–249) and in the associated figure (Figure 6).

Reviewer comment 15
Page 11, line 11: Introduction of this statistical method should be in the appropriate section

Reply

We agree with the reviewer and have included it in the statistical analyses.

Action

Please refer to line 234–249, the rationale behind the Arrhenius plots was already described in section 2.3. This information can now also be found between lines 218–226.

Reviewer comment 16
Page 11: How were AE values calculated? - Page 11: AE are presented as negatives, are they? Next page the authors mention a positive value.

Reply

The procedure to obtain the activation energies were explained in the methods section 2.3 (page 8 between lines 16–21, now between lines 218–226). That being said, we determined the activation energies by fitting an OLS linear regression to the relationship between the natural logarithm of Chl-a specific metabolic rates and the inverse of the absolute temperature.

The slopes of these so-called Arrhenius plots represent the average activation energy. The negative values seen in Figure 10 (now figures 7 and 8), resulted from the way we plotted the normalised metabolic rates against the inverse of the absolute temperature multiplied by the Boltzmann's constant (from 38 to 39.5 eV^{-1}, lower x-axis), the slope of the resulting relationship is negative. However, please note that the relationship with temperature (upper x-axis) would yield a positive slope if plotted from 20.7 to 32.3 ºC.

Reviewer comment 17
Page 13, line 14: GPP is said to be low, compared to what?

Action

We clarified this point in the new version of the manuscript, please see in line 483.

Reviewer comment 18
Page 15, line 18: How was AE standardized to Chl-a?

Reply

We understand the confusion; the sentence was poorly written. We aimed to described the activation energies obtained from the relationship between the Chl-a specific GPP data and temperature.

Action

We completely changed this section of the discussion, please refer to lines 550–559.

Reviewer comment 19
Page 16, line 2: What is "the ocean"?

Action

We modified this noun, as we meant open oceanic waters. Please see lines 556–559.

Reviewer comment 20
Page 16: Opens with "Surprisingly" and a discussion, then the next paragraph mentions a contradiction that is not surprising. What is the contradiction exactly the authors mean?

Reply

AC22: Thank you for highlighting this point

Action

We deleted this adverb as it is misleading

Reviewer comment 21
RC23 Page 16, line 6-7: Authors compare results with other references but need to mention
actual values.

Reply

We added the requested information

Action

The changes can now be tracked between lines Please see lines 556–559.

Reviewer comment 22
Figure 3: Thickness of the pink or green seems to say something about how significant it is but this is said nowhere. In line with this, the diagonal dark green lines seem to signify extreme significance instead of same variable and thus not tested. DIN is NOx. Are variables tested at different depths than metabolic rates of plankton? If so, how can you relate the 2?

Reply

We agree with the reviewer's comments.

Action

We modified this graph to present information relevant to the depths where we analysed metabolic rates (i.e., only photic layer). In addition, we modified the way the results are presented, and we explained the color code in figure 3.

Reviewer comment 23
Figure 4-6: Lots of white space and hard to see with tiny colored dots anyway. Revise these figures. I suggest to distill from them the most important results you want to show and add the rest to the supplementary section.

Action

We decided to remove the figures in this new version of the manuscript

Reviewer comment 24
Figure 7: could be mentioned with text in the results section. Suggest moving figure to supplements.

Reply

The information regarding this figure is mentioned in the results, but as it also provides information to derive the GPP threshold, we prefer to keep it.

Reviewer comment 25
Figure 9: Same as Figure 7, B is missing a parenthesis on the y-axis - Figure 10: Same as Figure 7.

Reply

Since figure 9 and 10 are both explaining one of the main results (i.e. the metabolic response of metabolic rates to temperature) we prefer to keep them as main figures.

Action

We added the missing parenthesis to the y-axis of the figures.

Reviewer comment 26
Please use continues line numbers for the manuscript

Reply

We followed the format and template designated by the journal.

Action

However, in the new version of the manuscript we changed to continuous lines as suggested by the reviewer.

Reviewer comment 27
Page1, line 8-9: Please rewrite, it reads as if you want to understand their variability and their present and their future but you want to understand their variability in the present and the future

Action

This has been modified as suggested, please refer to line 9

Reviewer comment 28
Page 2, line 4-5: Add community

Action

Done as suggested, please see in line 38

Reviewer comment 29
Page 2, line 11: First mention of NCP, introduce abbreviation.

Reply

NCP was mentioned for the first time on Page 1 line 14

Reviewer comment 30
Page 3, line 1: “The Red Sea is a semi-enclosed”

Action

We modified the text, please see line 67

Reviewer comment 31
Page 3, line 3-5: Consider merging this sentence with the previous one

Action

Please see the changes between lines 68–70

Reviewer comment 32
Page 3, line 9: “throughout the year”

Action

Changed as suggested, see line 75

Reviewer comment 33
Page 3, line 10: Delete the dot before the references

Action

Noted, see line 76

Reviewer comment 33
Page 4, line 12: Add “relatively” to “unproductive waters”

Action

Done as suggested, see line 107

Reviewer comment 34
Page 4, line 18: Add “latitudinal gradient” to the sentence

Action

Done as suggested, see line 112

Reviewer comment 35
Page 10, line 8-10: I suggest to start the Results section with this sentence

Reply

Thank you for the suggestion but we prefer to keep the sentence as a closing sentence

Reviewer comment 36
Page 10, line 16: net autotrophic?

Reply

This entire section of the discussion was modified

Reviewer comment 37
Page 12, line 8: Please stay consistent, use R2.

Reply

This section was modified

Reviewer comment 38
Page 13, line 9: Heterotrophic suggest no autotrophs, add “net”

Reply

This section was modified

Reviewer comment 39
Page 15, line 6-9: Please rewrite.

Reply

Modified as indicated, please see lines 540–544

Reviewer comment 40
Page 16, line 4: Add i.e. or parentheses after 2.5 _C

Action

We modified the text in the section but indicated the range inside a parenthesis (line 554)

Reviewer comment 41
Page 19, line 6: Heterotrophic

Action

Typographical error corrected, see line 666

Reviewer comment 42
Figure A1: Add axis titles to every part of the figure, having double axes without titles is confusing, especially since the 27 _N axis title (Temperature) is not on any axis.

Action

We are not including this figure in the new version of the manuscript

Reviewer comment 43
Table 1: Add Silicate to the table description. Also, it is unclear which header belongs to which environmental variable. Also, I fail to see the benefit of the min and max values

Action

We are not including this table in the new version of the manuscript

Reviewer comment 44
Present data as mean +/- SE

Action

We clarified this point in line 253. Whenever we presented mean values, we added the standard error of the mean

Reviewer comment 45
Table 2: N does not need decimals

Action

We are not including this table in the new version of the manuscript

Reviewer comment 46
What does “rank” mean? % PAR differs from Table 1

Action

We are not including this table in the new version of the manuscript. Data from table 2 are now being presented in a figure (new figure 5) with the overall information by seasons, but with all the data points included in the study.

Reviewer comment 46

Table 3: Upper part are, what seems to be, Pearson rank coefficients, not the units given in the description. The lower part seems to be p-values, mention this in the description. A hyphen is not the same as a blanc.

Reply

Thank you for pointing this out. It is indeed a correlation matrix.

Action

We modified the table (now Table 1) and only presented the correlation of metabolic rates with main explanatory variables.

Reviewer 2

2.2.1 General comments

The authors quantified plankton metabolic rates along the Red Sea. They have shown that Chla and planton community metabolism (GPP and CR) increase with temperature. Contrary to previous results they have observed a higher Activation Energy for GPP than for CR showing a positive relationship between NCP and Temperature. These results have been explained by the authors as a consequence of the high nutrient availability in warmer waters and the lack of external organic carbon sources to sustain a heterotrophic metabolism constraining the CR.
The dataset are very interesting and merit been published, however, the way how the results have been presented, the lack of statistical analyses and the methodology proposed
are not the most suitable to achieve the main goal proposed in the manuscript.
Therefore, I consider the ms still needs major revision in order to be published and providing the authors follow the reviewers recommendations.

2.2.2 Reply to general comments

Reply

Thank you for your comments and suggestions. We have addressed the changes and recommendations of the reviewer and provide a detailed answer to each of the points made in the following section. First, we completely agree with the reviewer that a detailed description of the statistical analyses performed was missing in the methodology section. We have included a detailed description of the statistical analyses in a new section (2.4), and this change can be tracked now between lines 227–253 in the latest version of the manuscript. Regarding the primary concern of Reviewer 2, which was also pointed out by the first referee, related to the methodological approach we used to quantify planktonic metabolic rates, we think, there is a misunderstanding. The methodology used to quantify planktonic metabolism is based on the extensively-used dark and light method (in combination with the Winkler titration method). The reviewer indicated that the methodology used was not suitable, and suggested that a shorter incubation period (6 –12 h) was more appropriate to quantify NCP. We want to point out that NCP represents the organic matter remaining after consumption of the GPP through respiration by plants (autotrophs), microbes (either autotrophs or heterotrophs), and animals (heterotrophs) (Ducklow and Doney 2013), and to account for those process, the standard incubation time for *in vitro* incubations is 24 h. This incubation length is needed because contrary to photosynthesis, which can be resolved during daylight, the losses due to respiration (which are necessary to define NCP) also occurs at night.

Action

We have clarified this point in the methods section 2.3 (between lines 166–174). In addition, we made sure that a detailed description of the sampling, filling and fixing of the samples was provided. We also clarified how we calculated gross primary production, the community respiration and the net community production (which is the balance between the autotrophic and heterotrophic metabolism, and not only the result of photosynthetic activity). These calculations can be seen between lines 206 and 216.

2.2.2 Specific comments

Reviewer comment 1
First, according to the title and the abstract the authors consider as drivers of the plankton community metabolism in the Red Sea, the Chla and temperature. However, other important parameters such as, temporal and spatial variability, salinity and nutrients seem to govern the plankton community metabolism within this particular ecosystem
and are not included in the abstract. Therefore, this lack of agreement between the ms, the consclusion and the abstract. is confusing. In my opinion, there is a large floor in the experimental design proposed and it is difficult to resolve.

Reply

We appreciate the reviewer's comment, and agree that the abstract highlighted our main findings and did not detail all the results. The abstract was indeed mostly orientated towards the effect of temperature and nutrient availability on metabolic rates as we found that those were the main controlling drivers. That was consistently explained in our results, discussion and conclusion; therefore, we do not find disagreement in our statements. However, following the suggestion of referee #1, we changed the narrative of the text to focus only on the variables highlighted in the abstract (i.e., temperature and nutrient availability; which are tightly related to the latitudinal gradient that characterises the basin) leaving aside the changes of planktonic metabolism throughout the water column.

Action

The changes can be tracked in the new version of the manuscript in the result section between lines 254–387. We have modified the figures accordingly so that Figure 2 now describes the latitudinal gradient of variables only in surface waters. In Figure 3 we have modified the format and the data presented, so now we only centre on data within the photic layer. We removed Figures 4–5, Figure 1A and 2A. We also removed Table 1, and Table 2. The information from Table 2 is now presented as a figure (now Figure 5) with the overall information and with all the data plotted. The changes in the results are in agreement with changes in the narrative of the discussion section. The main changes in the discussion section can be tracked between lines 447–463 and between lines 550–559

Reviewer comment 2
All samples included the deepest ones have been incubated on deck with surface water. During some of the surveys there is an important thermal variability. The authors have attempted to mitigate the issue by including just those samples above the thermocline. However, Material and Methods mention that changes in temperature and PAR in the incubation tanks were recorded with HOBO data loggers. Therefore, those data should be shown in a table in order to select objectively the samples for the analyses. Hence, eliminating those samples that register thermal differences above 2_C with the in situ temperatures. In addition, samples adapted to cool temperatures such as those at the bottom will respond more drastically to artificial increments of temperature than surface ones (for example. Apple et al. 2006. AME. 43: 243–254) resulting in erroneous conclusions. Therefore, Figure A1 is important and should be
included in the Ms.

Reply

As mentioned in our previous answer, after careful consideration, we decided to focused on the overall patterns observed in planktonic metabolism leaving aside the variability that takes place through the water column.

Action

We removed Figure A1 from the current version of the manuscript; however, all metabolic rates are now shown in the newly generated Figure 5.

Reviewer comment 3
Other figures such as 4-6 do not show crucial information in the current format. Figure 3 and Table 3 to me are redundant

Action

We removed Figures 4–6 from the current version of the manuscript, and the overall results are now presented as a new figure (Figure 5). We modified Table 3 (now Table 1) to only show complimentary information to Figure 3.

Reviewer comment 4
The paragraph 10-15 page 6 the authors should indicate if samples were collected before sunrise (to avoid any light on the samples) and if the incubation started at the sunrise to estimate the full light period. The authors say, the samples were colleted between 7 to 9 and to me this sounds very late to incubate and obtain the full light period nor precisely.

Reply

The samples were incubated for 24-h, covering an entire dark-light period, thus there is no need to estimate the light period.

Reviewer comment 5
In The net community metabolism..... page 7, NCP should be estimated during the light period (NCP 6 to 12 hours).

Reply

We believe that there is a misunderstanding regarding the process we measured. The reviewer's comment seemed to suggest that our work was focused on primary production, which is performed by the photosynthetic components of the plankton community during the daytime and that has gross and net components (as phytoplankton excrete and respire carbon). However, our paper focuses on the entire plankton community, both photosynthetic and heterotrophic (e.g. bacteria), where the net community production (NCP) represents the organic matter remaining after consumption of the GPP through respiration by plants (autotrophs), microbes (either autotrophs or heterotrophs), and animals (heterotrophs) (Ducklow and Doney 2013). Studies that focus on the photosynthetic component of the plankton community (e.g. Net Primary Production, NPP) report values for the daylight period only. Whereas studies, such as this, report (24 h) rates. For instance, published syntheses of community metabolism rates report values per day (24 h), e.g., Robinson and Williams 2005, Regaudie-de-Gioux 2012, 2013). The use of 24 h to report rates is justified as the metabolic budget needs be resolved over 24 h to be completed, not required for

photosynthesis as it is light-dependent, but respiration, which is necessary to define net community production, which occurs both during day and at night.

Reviewer comment 6
The authors should show, the variation coefficient of the pool data and also the original CR, NCP and GPP data including their SE.

Action

The data are now shown in Figure 5, with a detailed description of the statistical analyses. In addition, the relevant information regarding the mean and the standard error of the mean are shown. See e.g., lines 351, 352, 359.

Reviewer comment 7
Because, In these oligrotrophic areas the metabolic rates are very low and can be difficult to detect. Therefore, the methodology needs to be very precise in the processesof filling, incubating and fixing the bottles.

Reply

We agree with the reviewer, however, the information about filling the bottles and all special cares during the sampling was detailed in methods section 2.3 (Page 7: lines 11–15). Now between lines 188–194.

Reviewer comment 8
The paragraph 20 in page 8 It should be indicated the Arrhenius plots the authors Mention

Reply

The Arrhenius plots were described in the methods section 2.3 (P8, between lines 13 and 20) and additionally explained in the results section 3.3 (P11: lines 16 and P12 lines 1–3) and Figures 9 and 10.

Action

The temperature-dependence of planktonic metabolism explained with the Arrhenius plots can now be seen between lines 379–387 and in Figures 7 and 8.

Reviewer comment 9
The paragraph 10 in page 10 should be transfered from the Results to the Discussion.

Reply

The sentence on P10, between lines 8–10 is a closing statement with the main results shown in previous paragraphs, we are not discussing any results. Therefore, we prefer to keep it as it is.

Reviewers comment 10
And also the first paragraph of the 3.2 Variability of plankton : : :. Is already mentioned in M and M.

Reply

We agree with the reviewer's comment and have modified the text accordingly

Action

We have deleted this sentence

Reviewers comment 11
The name of the KAUST is excessive. I would use just one larger map with different colours or shapes to show the stations at each survey or season.

Reply

We decided to not modify the figure as some of the stations were sampled in the same location more than twice, and different shapes or points overlap

Action

We did remove the name of the university to leave it only in one panel

Reviewers comment 12
Figure 2. I consider in this figure is difficult to detect the thermocline and the vertical profiles of Chla and salinity. I consider that nutrient profiles should also included

Reply

It was not possible to determine the depth of the thermocline in Figure 2, and it was not intended to do so. The figure summarises the main characteristics along the latitudinal axis that we sampled (i.e., the increasing temperature and phytoplankton chlorophyll-a toward the southern region with an increasing salinity towards the north).

Action

We modified Figure 2, so that now it only shows the variability of temperature, salinity and chlorophyll-a in surface waters.

Reply to reviewer 13
Figure 8, 9 and 10. To test one of the main conclusions, if AE is higher for GPP than for CR, authors should test statistically if the slopes are different. I would test also the slopes for the figures 9 and 10 explaining the consequences of the statistical differences in the cases observed

Reply

We performed an analysis of covariance (ANCOVA)

Action

We have mentioned this in section 2.4 between lines 249–251 and described the results between lines 382–387.

Reply to reviewer 14
In the figure 9, the RMA analyses have been included but it is not necesary in this case because temperature is not a rate. In addition, the authors have not explained when the RMA or OLS should be used in M and M.

Reply

We agree with the reviewer that it is not necessary to provide the results of the RMA analyses

Action

We removed these analyses and their results from our manuscript.

Rates and drivers of Red Sea plankton community metabolism

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Abstract

Resolving the environmental drivers shaping planktonic communities is fundamental to understanding their variability, in the present and the future, across the ocean. More specifically, resolving the temperature-dependence of planktonic communities is essential to predict the response of marine ecosystems to warming scenarios, as ocean warming leads to oligotrophication of the subtropical ocean. Here we quantified plankton metabolic rates along the Red Sea, a uniquely oligotrophic and warm environment, and analysed the drivers that regulate gross primary production (GPP), community respiration (CR) and the net community production (NCP). The study was conducted on six oceanographic surveys following a north-south transect along the Saudi Arabian coast. Our findings revealed that GPP and CR rates increased with increasing temperature (R^2 = 0.41 and 0.19, respectively, $p < 0.001$ in both cases), with a higher activation energy (Ea) for GPP (1.2 ±0.17 eV) than for CR (0.73 ± 0.17 eV). The higher Ea for GPP than for CR resulted in a positive relationship between NCP and temperature. This unusual relationship is likely driven by 1) the relatively higher nutrient availability found towards the warmer region (i.e., the South of the Red Sea), which favours GPP rates above the threshold that separates autotrophic from heterotrophic communities (1.7 mmol O_2 m^{-3} d^{-1}) in this region. 2) Due to the arid nature, the basin lacks riverine and terrestrial inputs of organic carbon to subsidise a higher metabolic response of heterotrophic communities, thus constraining CR rates. Our

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study demonstrates that GPP increases steeply with increasing temperature in the warm ocean when relatively high nutrient inputs are present.

1 Introduction

The balance between gross primary production and community respiration, which involves both autotrophic and heterotrophic metabolic activity (Williams, 1993; Cullen, 2001; Ducklow and Doney, 2013), sets the metabolic status of an ecosystem by defining the carbon available to fuel pelagic food webs and determining whether plankton communities act as a source or sink of CO_2 (Del Giorgio et al., 1997; Williams, 1998). Whereas GPP typically satisfies the respiratory demands within the food web across productive waters, the oligotrophic ocean often requires allochthonous inputs of organic carbon to meet the metabolic requirements of heterotrophic organisms (Smith and Mackenzie, 1987). Due to comparatively higher carbon consumption, relative to the production, planktonic communities in low productive systems are in close metabolic balance (i.e., the net community production (NCP = 0, or GPP = CR) or experience a net metabolic imbalance (i.e. NCP < 0, GPP < CR) (Smith and Hollibaugh, 1993; Duarte and Agustí, 1998; Duarte et al., 2013).

In tropical and subtropical oligotrophic regions, the high temperatures may amplify the metabolic imbalances in plankton communities, as CR tends to increase faster than GPP (Harris et al., 2006; Regaudie-de-Gioux and Duarte, 2012) if the allochthonous sources of organic carbon are enough to subsidise their carbon demand. These allochthonous inputs may be delivered from land through riverine discharge, from the atmosphere through atmospheric deposition of dust and volatile organic

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carbon (Jurado et al., 2008), or are exported from productive coastal habitats (Duarte et al., 2013; Barrón and Duarte, 2015).

The Red Sea is a semi-enclosed highly oligotrophic basin (Acker et al., 2008; Raitsos et al., 2013). It is known as one of the warmest tropical seas, with maximum sea surface temperatures ranging from 33.0 to 33.9 ºC during the summer period (Chaidez et al., 2017; Osman et al., 2018), and between 34–35 ºC in certain regions (Rasul and Stewart, 2015; Garcias-Bonet and Duarte, 2017; Almahasheer et al., 2018). Due to the prevailing arid conditions, the Red Sea experiences large evaporation rates (nearly 2 cm yr^{-1} of freshwater from the surface layers), while the lack of river runoff and low precipitation rates make this system one of the saltiest seas on the planet (Sofianos, 2002; Sofianos and Johns, 2015; Zarokanellos et al., 2017). Two wind patterns govern the region: in the northern part, the wind coming from the northwest remains relatively constant throughout the year, while in the southern area, the Indian Monsoon system regulates the wind dynamics (Sofianos, 2002; Sofianos and Johns, 2015). During the winter monsoon, the wind changes direction, and this wind reversal along with the thermohaline forces drives the overall circulation and favours the exchange of water with the Indian Ocean (Sofianos, 2002; Zarokanellos et al., 2017).

Due to the almost negligible terrestrial inputs, the intrusion of nutrient-rich waters from the Indian Ocean through the Bab-el-Mandeb Strait (Sofianos and Johns, 2007; Raitsos et al., 2015; Kürten et al., 2016), together with aeolian dust and aerosol deposition (Chen et al., 2007; Engelbrecht et al., 2017), represent the primary sources of nutrients into the basin. Thus, nutrient availability in the Red Sea follows a latitudinal pattern that is opposite to the one of salinity, but parallel to the thermal

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gradient, with nutrient-richer and warmer waters towards the Southern Red Sea compared to the cooler and more oligotrophic Northern Red Sea (Sofianos, 2002; Raitsos et al., 2015).

Studies based on ocean color data revealed that chlorophyll-a (Chl-a) concentrations decline from the Southern Red Sea to the Northern Red Sea (Raitsos et al., 2013; Kheireddine et al., 2017; Qurban et al., 2017) and depict a clear seasonality. During winter time, when the maximum exchange of water with the Indian Ocean takes place, Chl-a concentration peaks, decreasing towards the summer period when the water column is mostly stratified (Sofianos, 2002). Measurements of primary production also revealed that phytoplankton photosynthetic rates follow the same south to north gradient as Chl-a and nutrient concentration (Qurban et al., 2017). However, reports regarding the metabolic balance of the plankton communities are scarce, mostly focus on the contribution of the autotrophic community via photosynthetic processes (Levanon-Spanier et al., 1979; Qurban et al., 2014; Rahav et al., 2015), or are restricted to specific regions (Tilstra et al., 2018).

Based on available evidence, we hypothesise that the high gross primary production expected in the Southern Red Sea may be counterbalanced by a higher respiratory demand in these warm waters, and that NCP might decline towards the relatively unproductive waters of the Northern Red Sea. With the expected decrease in GPP towards the northern region, planktonic metabolism might be driven mainly by heterotrophic communities (Duarte and Agustí, 1998; Duarte et al., 2013). However, the absence of significant allochthonous subsidies in the basin may hamper the metabolic response of the heterotrophic plankton communities. Hence, it remains unclear what the metabolic balance of plankton communities is and whether a south to north latitudinal gradient in NCP exists in the Red Sea.

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Here we report the variability of plankton community metabolism (GPP, CR and NCP) along a latitudinal gradient in the Red Sea, and examine if the temperature-dependence of planktonic metabolic rates in this basin are consistent with those reported for the global ocean (López-Urrutia et al., 2006; Regaudie-de-Gioux and Duarte, 2013; Garcia-Corral et al., 2017). We did so by measurements conducted as part of six surveys along the south-north latitudinal gradient in the Saudi Economic Exclusive Zone in Red Sea waters. We determined plankton metabolic rates between winter 2016 and spring 2018, thus allowing us to 1) delineate the seasonal variability of the gross primary production and community respiration along the Red Sea, 2) quantify changes in the metabolic balance (net community production) and 3) test the hypothesized roles of productivity gradients and temperature in driving NCP.

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2. Material and Methods

2.1 Field Sampling

We conducted six oceanographic surveys: two during autumn (October and November 2016), two during winter (February 2016 and January 2017), one in summer (August 2017), and one in spring (March 2018) on board the R/V *Thuwal* and R/V *Al Azizi*. Sampling was conducted following a latitudinal transect along the Red Sea within a region limited by coordinates 17.25 °N to 27.82 °N and 34.83 °E to 41.39 °E (Figure 1). At each station, vertical profiles of temperature and salinity were obtained with a Sea-Bird SBE 911 plus CTD profiler (Sea-Bird Electronics, Bellvue, WA, USA), equipped with additional sensors to measure the attenuation of photosynthetically active radiation (PAR) (Biospherical/Licor PAR/Irradiance Sensor), *in vivo* fluorescence (WetLabs ECO FL fluorometer), and dissolved oxygen concentration (Seabird SBE 43 Dissolved Oxygen Sensor). Water samples for chemical and biological measurements were collected between 7:00 and 9:00 am local time, using a rosette sampler equipped with 12 Teflon Niskin bottles (12 L) that were provided with silicone O-rings and seals.

2.2 Inorganic nutrients and chlorophyll-a concentration

Water samples for nutrient analyses were collected in 50 mL polyethene bottles and kept frozen (-20 ºC) until determination. Inorganic nutrient concentration was determined with a SEAL AA3 Segmented Flow Analyzer (SEAL Analytical Inc., WI, USA) using standard methods (Hansen and Koroleff, 1999). The detection limits were 0.05 µM for nitrate, 0.01 µM for nitrite, 0.01 µM for

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phosphate and 0.08 µM for silicate. For the chlorophyll-a analysis, 200 mL samples were taken at ten discrete depths (between 5 and 200 m) and filtered through Whatman GF/F filters. The filters were kept frozen (-20 ºC) until further analysis. Pigments were extracted for 24 h using 90 % acetone and left overnight in the dark at 4 ºC. Chl-a concentration was estimated with the non-acidification technique using a Trilogy Fluorometer equipped with CHL-NA module (Turner Designs, San Jose, USA), previously calibrated with pure Chl-a.

2.3 Net community metabolism, community respiration and gross primary production

Plankton metabolic rates were determined *in vitro* by measuring the changes in dissolved oxygen concentration after 24 h light-dark bottle (Winkler) incubations (Carpenter, 1965). This methodology, commonly used to determine plankton metabolic rates (Williams et al., 1979; Duarte and Agustí, 1998; Bender et al., 1999; Robinson and Williams, 1999; Ducklow et al., 2000; Serret et al., 2001; Robinson et al., 2002; Serret et al., 2009; García-Martín et al., 2017), allows to account for the diel cycle of oxygen and carbon fluxes derived from photosynthetic mechanisms (light-dependent reactions) and also those linked to the acquisition of energy by both autotrophic and heterotrophic microorganisms (light and dark-dependent reactions) (Robinson and Williams, 2005; Williams and del Giorgio, 2005).

Water samples were collected at three different optical depths (ζ) through the water column. One at the surface (100–80 % of incident PAR), another towards the bottom of the photic layer (8–1 % of incident PAR), and one intermediate sample, at a depth of the chlorophyll maximum (Chl-*a* max). In case the Chl-*a* max was sampled at the surface or bottom layers, the intermediate sample was taken

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between 1.5–2.3 ζ (i.e., 22–10 % of incident PAR). Seawater was collected directly from the Niskin bottles to fill a total of 21 (100 mL) Winkler bottles. The bottles were carefully filled using silicone tubing and allowing the water to overflow during the filling, taking special care to avoid the formation of air bubbles. Surface samples were collected in 100 mL quartz bottles. From each depth, seven of the bottles were immediately fixed with Manganese sulfate ($MnSO_4$) and Potassium hydroxide/Potassium iodide solution (KI/KOH) to determine the initial oxygen concentration while the other 14, seven light and seven black bottles, were incubated on deck in surface water flow-through tanks. Due to the difference in temperature between the surface and deep waters, particularly during the summer and autumn surveys, we decided to include in our analyses only those samples collected above the thermocline. Changes in temperature and PAR in the incubation tanks were recorded with HOBO Pendant data loggers (Onset, Massachusetts, USA).

Before the incubation, the bottles were covered with neutral mesh to reduce the incident PAR radiation according to the sampled depth. At the end of the incubation period, light and dark bottles from each depth were fixed to determine final O_2 concentrations. Oxygen concentration was measured by automated high-precision Winkler titration with a potentiometric end-point detection (Oudot et al., 1988) using a Mettler Toledo T50 Titration Excellence auto-titrator attached to an Inmotion autosampler. NCP was calculated as the difference in the oxygen concentration between the light bottles after the 24 h incubation period ($[O_2]_{L\text{-}24h}$) and the oxygen concentration measured before the incubation ($[O_2]_{Tzero}$) (i.e., NCP = $([O_2]_{L\text{-}24h} - [O_2]_{Tzero})$. CR rates (mmol O_2 m^{-3} d^{-1}) were calculated as the difference of the oxygen concentration after the 24 h incubation period in the dark bottles ($[O_2]_{D\text{-}}$

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$_{24h}$) and the initial oxygen concentration ($[O_2]_{Tzero}$) (i.e., CR = $[O_2]_{Tzero}$ - ($[O_2]_{D\text{-}24h}$). GPP (mmol O_2 m^{-3} d^{-1}) was calculated as the sum of NCP and CR.

Due to the consistent relationship existing between plankton metabolism and temperature across diverse marine regions (Regaudie-de-Gioux and Duarte, 2012; García-Corral et al., 2014), we examined how plankton metabolic rates covariate with temperature in the Red Sea, a system whose temperature range is higher than previously encountered in marine planktonic metabolism research. We determined the relationship between metabolic rates and temperature by fitting an ordinary least squares linear regression equation to the relationship between the natural logarithm of the Chl-a specific metabolic rates and the inverse of the absolute temperature * *k*, which is the Boltzmann's constant (8.617734 *10^{-5} eV K^{-1}). In these Arrhenius plots, the slope represents the average activation energy (Ea), characterising the extent of thermal-dependence of metabolic processes.

2.4 Statistical Analyses

Statistical analyses and figures were done using the statistical and machine learning toolbox in Matlab version R2018b (Mathworks Inc, Natick, MA, USA) and with the R statistical computing package using RStudio 1.1419. Pearson correlation tests were used (corrplot function in R) to determine the relationship between environmental variables (temperature, nitrate + nitrite (NOx), phosphate and silicate concentration) and their latitudinal distribution, and to determine the relationship between volumetric measurements of GPP, CR, NCP, and environmental variables (Temperature, NOx concentration, Chl-*a*, and latitude). We used ordinary least squares (OLS) simple regression models (fitlm function in Matlab) to describe the potential relationships between different planktonic metabolic

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rates, between metabolic rates and environmental variables, and to predict the response of the Chl-a normalised GPP (and CR) to temperature (Arrhenius plots described in section 2.3). To test if the activation energies (obtained from the Arrhenius plots) were significantly different, we performed an analysis of covariance (ANCOVA) by using the aoctool in Matlab. The variability of planktonic metabolic rates between cruises was statistically analysed using non-parametric Kruskal-Wallis tests. Mean values and their standard error of the mean (SE) are reported throughout the text.

3. Results

3.1 Latitudinal variability of physico-chemical properties and Chl-a concentration

Hydrographic (temperature and salinity) and chemical variables (nutrient concentrations) depicted a marked latitudinal gradient typical of the Red Sea. At the southern-most area, sea surface temperature (SST) fluctuated between 28 ºC (winter-spring) and 32 ºC (summer), while at the far-northern sampling site SST ranged between 23 ºC (winter) and 27–28 ºN (summer-autumn) (Figure 2). Overall, all macronutrients observed a significant inverse correlation with latitude (Pearson correlation coefficients r <-0.4, p<0.05) (Figure 3). Nitrite+nitrate (NOx) decreased from 6.1 ± 0.9 µM in the southern region to 2.9 ± 0.3 µM towards the northern Red Sea, while on average, phosphate concentration ranged from 0.5 ± 0.01 µM in the south of the Red Sea to 0.1 ± 0.01 µM towards the northern stations (data not shown). Phytoplankton biomass (measured as Chl-a concentration) also decreased significantly towards the north of the Red Sea (Pearson's correlation, r = -0.41, p<0.001) (Table 1). We found the highest autotrophic biomass during the autumn and winter cruises. During this

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period, surface Chl-a ranged from 0.6–0.8 mg m^{-3} in the southern region to 0.2–0.3 mg m^{-3} in the north (Figure 2). In general, our results confirm that all variables correlated significantly with latitude, highlighting the prevalence of the south-north gradient in temperature, salinity, nutrient availability and chlorophyll-a concentration across the Red Sea.

3.2 Variability of plankton metabolism measured along the Red Sea

Analogous to the environmental variability, planktonic metabolism followed the same significant north-south decreasing pattern with latitude (Figure 4). The inverse correlation of GPP rates with latitude was highly significant (Pearson correlation coefficient r = -60, p <0.001) (Table 1), as found for autotrophic biomass, thus, explaining the strong correlation observed between GPP and Chl-a concentration (Pearson correlation coefficient r = 0.69) (Table 1). GPP rates decreased on average by 79%, from 4.1 ± 0.5 mmol O_2 m^{-3} d^{-1} (≈ 49.2 mgC m^{-3} d^{-1}; assuming a photosynthetic quotient, PQ = 1) at the southernmost station of the Red Sea to 0.9 ± 0.1(≈ 10 mgC m^{-3} d^{-1}; PQ = 1) at the northern site, while CR decreased on average by 73 %, from 3 ± 0.4 mmol O_2 m^{-3} d^{-1} (≈ 36 mgC m^{-3} d^{-1}; assuming a respiratory quotient, RQ = 1) in the south to 0.8 ±0.1 in the north (≈ 9.6 mgC m^{-3} d^{-1}; RQ = 1) (Figure 4). We did not find any significant correlation between NOx availability and GPP (Pearson correlation coefficient, r = 0.01, p > 0.05), CR (Pearson correlation coefficient, r = 0.19, p > 0.05) nor NCP rates (Pearson correlation coefficient, r = -0.19, p > 0.05) (Table 1); however, all metabolic rates were positively correlated with temperature (Table 1).

The highest GPP and CR rates measured along the Red Sea came from data collected during the autumn and winter cruises, when GPP and CR rates reached values above 6 and 4 mmol O_2 m^{-3} d^{-1},

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We identified two distinctive patterns portraying nutrient distribution along the Red Sea. Nutrient concentration throughout the water column decreased with latitude (Figure 3), while DIN concentration increased with temperature in the first optical depth (37 % PAR) and at the base of the euphotic zone (1–0.1 % PAR) (Figure 3A and 3B). Phosphate and silicate concentrations were also positive correlated with temperature at the base of the photic layer (Pearson correlation, DIN, r = 0.39, P = 0.01; phosphate, r = 0.48, P < 0.001; silicate, r = 0.42, P< 0.001) (Figure 3B). Below the first optical depth and above the base of the euphotic zone, nutrient availability and temperature were not correlated (data not shown).

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respectively (Figure 5), and when the mean values were the highest ($GPP_{autumn-winter}$ = 2.9 ± 0.3 – 2.3 ± 0.3 mmol O_2 m^{-3} d^{-1}; $CR_{autumn-winter}$ = 2.5 ± 0.3 – 2 ± 0.2) (Figure 5). However, despite the overall variability between autumn-winter and spring-summer, when all data are taken in concert, planktonic GPP and CR rates were not significantly different between seasons (Kruskal-Wallis H test, $\chi^2 = 6.83$, p = 0.08; $\chi^2 = 4.14$, p = 0.25, respectively). Furthermore, the balance between planktonic autotrophic production (GPP) and the respiratory losses (due to the heterotrophic and autotrophic metabolism, CR) (i.e., NCP rates), revealed that NCP rates also decreased towards the northern region (by 94%). From 1.1 ± 0.3 mmol O_2 m^{-3} d^{-1} at the southern stations to 0.1 ± 0.1 mmol O_2 m^{-3} d^{-1} above 26 ºN (Figure 4). The average NCP from our cruises was 0.3 ± 0.1 mmol O_2 m^{-3} d^{-1} (Figure 5), which indicates an overall prevalence of autotrophic communities (Figure 5). However, a closer look to our data revealed that during spring, the mean NCP rate was -0.31 ± 0.24 mmol O_2 m^{-3} d^{-1} (Figure 5), while during the summer, NCP rates in the northern region ranged from -0.64 to -0.09 mmol O_2 m^{-3} d^{-1}, which evidenced that planktonic metabolism was governed by heterotrophic communities during the spring and also during the summer at the northern region.

When we evaluated the relationship of GPP with CR and NCP, the analysis showed that both CR and NCP increased significantly with GPP (R^2 = 0.62 and 0.49, respectively; p <0.001) (Figure 6). From the functional relationships between GPP with CR and NCP, we calculated the threshold of GPP for metabolic equilibrium for the region. By solving for GPP=CR and for NCP = 0 (from the relationship describing NCP as a function of GPP), and by using the slope and intercept shown in figures 6A and 6B, we determined that the GPP threshold that separates autotrophic from heterotrophic planktonic communities in the Red Sea is 1.7 mmol O_2 m^{-3} d^{-1} (range 1.2–1.9 mmol O_2 m^{-3} d^{-1}).

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3.3 Metabolic rates and temperature

Due to the pervasive influence of temperature in regulating metabolic rates, we further explored the temperature-dependence of GPP and CR by analysing the relationship between chlorophyll-a specific metabolic rates and temperature. Our analysis revealed that both GPP and CR tended to increase with temperature albeit with different activation energies (i.e., Ea was significantly higher for GPP (-1.2 ± 0.2 eV) than for CR rates (-0.73 ± 0.2 eV), ANCOVA, F = 3.94, p = 0.04) (Figure 7). We also tested whether the temperature-dependence response was consistent between cruises (Figure 8). Our results indicated a relatively higher activation energy for GPP during the summer cruise (-2.3 ± 0.8 eV) and in spring for CR (-2.6 ± 0.9 eV). However, the observed differences in the activation energies for GPP were not significantly different between seasons (ANCOVA, F = 0.38, p = 0.8).

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4. Discussion

4.1 Variability of plankton community metabolic rates along the Red Sea

Our results demonstrate that planktonic metabolic rates are markedly different between the southern and northern regimes of the Red Sea, with an increase from the southern to the northern regions in the overall mean GPP and CR by a factor of 5 and 4, respectively (i.e., an absolute increase in GPP rates of 3.2 mmol O_2 m^{-3} d^{-1} ≈ 38.4 mgC m^{-3} d^{-1}, and an absolute increase in CR rates of 2.2 mmol O_2 m^{-3} d^{-1} ≈ 26.4 mgC m^{-3} d^{-1}). Although, *sensu stricto*, the overall balance between autotrophic metabolism and planktonic community respiration (i.e. NCP) indicated a prevalence of autotrophic communities during our samplings along the Red Sea, heterotrophic communities prevailed during the spring, and in the northern stations during the summer, which highlights the shift in the trophic conditions in the basin. Consistent with these findings, our data revealed that the GPP threshold that separated autotrophic from heterotrophic communities in the Red Sea (1.7 mmol O_2 m^{-3} d^{-1}) is similar to that reported across oceanic communities elsewhere (Duarte and Agustí, 1998; Duarte and Regaudie-de-Gioux, 2009), agreeing with the oligotrophic characteristics that govern at certain periods or locations the basin. The latitudinal differences depicted in our results mirror the increasing north-south pattern in Chl-*a* concentration and photosynthetic carbon fixation rates previously reported for the Red Sea (Acker et al., 2008; Raitsos et al., 2013; Qurban et al., 2014; Kheireddine et al., 2017), and which are supported by the presence of different planktonic communities (Al-aidaroos et al., 2016; Pearman et al., 2016; Robitzch et al., 2016; Kheireddine et al., 2017; Kottuparambil and Agusti, 2018).

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The lower productivity of the northern section of the Red Sea, explains the dominance of heterotrophic communities therein. Still, sustaining heterotrophy in oligotrophic regions requires an allochthonous source of organic matter (Duarte et al. 2011, 2013). The arid nature of the northern Red Sea, with the watershed consisting mostly of deserts, leads to the absence of rivers and significant organic carbon inputs to the sea. Dust inputs are important, however, and whereas they have shown no effect on primary production (Torfstein and Kienast, 2018), they are a source of organic carbon (Jurado et al. 2009) that can partially supply the organic matter required to sustain heterotrophic communities. Moreover, the Red Sea supports highly productive coral reef, mangrove, seagrass and algal communities in the extensive shallow coastal areas (Rasul et al., 2015; Almahasheer et al., 2016), which may export significant organic carbon to the pelagic compartment, thereby helping to sustain heterotrophic plankton communities in the northern Red Sea.

4.2 Temperature and metabolic balance in the Red Sea

Temperature is a master variable that regulates many components of ocean dynamics, such as vertical stratification, and most aspects of organismal biology, from setting boundaries in the distribution of organisms (Clarke, 1996) to controlling biochemical reactions that constrain the energy for metabolic processes (Gillooly et al., 2001). Hence, temperature is likely a significant driver of metabolic processes in the Red Sea, one of the warmest tropical marine ecosystems (Raitsos et al., 2011; Chaidez et al., 2017). Indeed, our results showed a positive response of planktonic metabolism to temperature. Moreover, the functional relationships between metabolic rates with temperature suggested that both GPP and CR were positively enhanced with increasing temperature; but at a different pace.

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The metabolic theory of ecology (MTE) relates the metabolic rate of an organism with its mass and temperature. This theory hypothesizes that individual metabolic rates relate to temperature with a relatively constant activation energy (Ea ~ 0.63 eV) for a wide range of taxa, from unicellular organisms to plants and animals (Gillooly et al., 2001; Brown et al., 2004). For aerobic respiration, Ea values vary between 0.41 and 0.74 eV at temperatures between 0–40 ºC (Gillooly et al., 2005), while for photosynthetic processes, the predicted Ea is lower, ~ 0.32 eV (Allen et al., 2005). From a thorough compilation of data obtained for a wide range of marine systems (from polar to subtropical and tropical oceanic regions), Regaudie-de-Gioux and Duarte (2012) found that overall, the activation energies for photosynthetic production (GPP) varied between 0.29–0.32 eV, and for respiratory processes (CR) between 0.65 and 0.66 eV.

The Ea for GPP (-1.2 ± 0.17 eV) obtained for the Red Sea was higher than the overall value predicted by the MTE, while the Ea values for CR were below those for GPP (0.72 ± 0.17 eV) unlike observed elsewhere in open oceanic waters (Regaudie-de-Gioux and Duarte 2011, Garcia-Corral et al. 2017). Furthermore, these Ea values imply that GPP rates increased faster (5.1-fold) than CR rates (2.7-fold), in the Red Sea's thermal range (22–32.5 ºC). These findings differ with the expected double increase of heterotrophic respiration (regarding photosynthetic processes) with temperature (Harris et al., 2006), but are closer to results obtained by Garcia-Corral et al. (2017), who recently reported activation energies for GPP of -0.86 , -1.48 and -1.07 for the Atlantic, Indian, and Pacific oceans, respectively, while Ea for CR found in the Atlantic, Indian and the Pacific oceans were -0.77, -0.57 and -0.82, respectively.

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The apparent contradiction between our findings and the general patterns predicted by the MTE is, however, not surprising. In their model, Allen et al. (2005) predict the activation energy of photosynthesis per chloroplast (for temperatures between 0–30 ºC) using the temperature dependence parameters obtained by Bernacchi et al. (2001) for RuBisCO carboxylation rates in one species (tobacco leaves). Although the temperature range selected by Allen et al. (2005) comprises the optimum temperatures of growth rates for a wide range of functional groups of marine primary producers (Chen, 2015; Thomas et al., 2016), the temperature observed in the Red Sea exceeded this range. Due to the fast generation times of microbes (Collins, 2010), we can expect that photosynthetic planktonic communities are acclimated or even locally adapted to the thermal conditions they experience. So by favouring certain photosynthetic or thermal traits, they can enhance their metabolism and growth to the temperatures they experience, up to their thermal optimum (Galmes et al., 2015; Thomas et al., 2016). Therefore, it is likely that the acclimation or local adaptation (in the long term) of photosynthetic traits in Red Sea plankton optimises the metabolic response at the high-temperatures reached, resulting in a steeper response to temperature than predicted by the MTE. Moreover, as the trait responses to temperature vary among phylogenetic groups (Galmes et al., 2015; Galmés et al., 2016; Thomas et al., 2016), we anticipated a certain degree of discrepancy if we characterise the photosynthetic response (GPP) of planktonic communities forming an ecosystem, by considering only one trait (i.e., RuBisCO carboxylation) of one species.

However, we must bear in mind that the metabolic response of individuals is not only temperature-dependent, and that resource supply also plays an essential role (Brown et al., 2004; Allen and Gillooly, 2009). Our results evidenced that the increased response of planktonic metabolism

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towards warmer temperatures was mostly confined to the southern half of the Red Sea, a region that receives the direct inflow of the enriched Intermediate Water coming from the Gulf of Aden during the winter monsoon (Raitsos et al., 2015; Wafar et al., 2016). Recent findings have demonstrated that mass-specific carbon fixation rates of phytoplankton communities can be enhanced with temperature when nutrients are not limiting their growth (Marañón et al., 2014; Marañón et al., 2018). Therefore, it is likely that the intertwined effect of both the warmer temperatures and the larger nutrient availability towards the south of the Red Sea are key drivers regulating the metabolic response of planktonic communities. Thus, unlike the global ocean, where nutrient concentration is inversely correlated with temperature (e.g., Agawin et al. 2000), in the Red Sea nutrient concentration and temperature are positively correlated. This anomaly may explain the steep Ea for GPP, as primary producers in the warmer region are being supported by the inflow of the nutrient-enriched waters from the Indian Ocean.

The elevated Ea for GPP compared to CR in Red Sea plankton is also an anomaly, likely associated with the lack of allochthonous nutrient supply due to the absence of rivers and vegetation in the arid watershed of the Red Sea. The warm oligotrophic ocean is characterised by plankton communities that are in metabolic balance or net metabolic imbalanced (Duarte and Agusti 2008, Duarte et al. 2013). In contrast, the warm Southern Red Sea tends to support autotrophic metabolism, sustained by the input of nutrient-enriched waters while low allochthonous carbon inputs may constrain CR. As a result, NCP tends to increase, rather than decrease with increasing temperature (Regaudie-de-Gioux and Duarte 2011, Garcia-Corral et al. 2017). These patterns in plankton metabolism in the oligotrophic and warm Red Sea deviate from those characterising the subtropical and tropical gyres of the open ocean, but it provides an opportunity to explore the mechanistic basis for the global patterns in

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plankton metabolism with temperature, which would otherwise remain obscured by the underlying prevalent negative relationship with nutrient concentrations.

5. Conclusions

Our results show that plankton metabolism in the Red Sea presents a remarkably different pattern compared to other warm and oligotrophic marine systems (e.g., the subtropical and tropical gyres). In this region, autotrophic plankton communities prevailed and are supported by relatively high GPP rates; above the threshold separating heterotrophic low-productivity communities from autotrophic ones. Metabolically-balanced or net heterotrophic plankton communities dominated in the Northern Red Sea, whereas autotrophic communities, supported by nutrient inputs from the Gulf of Aden, were predominant in the south. Elevated temperatures contributed to an enhanced metabolic activity of planktonic organisms due to the increase in kinetic energy (favouring enzymatic reactions) with temperature. Plankton communities in the Red Sea, however, displayed activation energies for GPP that were higher than those for CR, resulting in a positive relationship between NCP and temperature. Those findings represent anomalies in the relationship between metabolic rates and temperature compared to the warm, oligotrophic open ocean. These anomalies are likely related to the higher nutrient supply from nutrient-rich Indian Ocean waters in the warm Southern Red Sea, suggesting that GPP can respond strongly to the temperature in the warm ocean when supported by high nutrient inputs, relative to those in the subtropical gyres.

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Author Contributions

DCL-S, CMD, and SA designed the study; KR and PCdA obtained the data and provided technical support; DCL-S analysed the data; DCL-S wrote the article with a substantial contribution of CMD, and SA; all authors discussed the results and commented on the manuscript.

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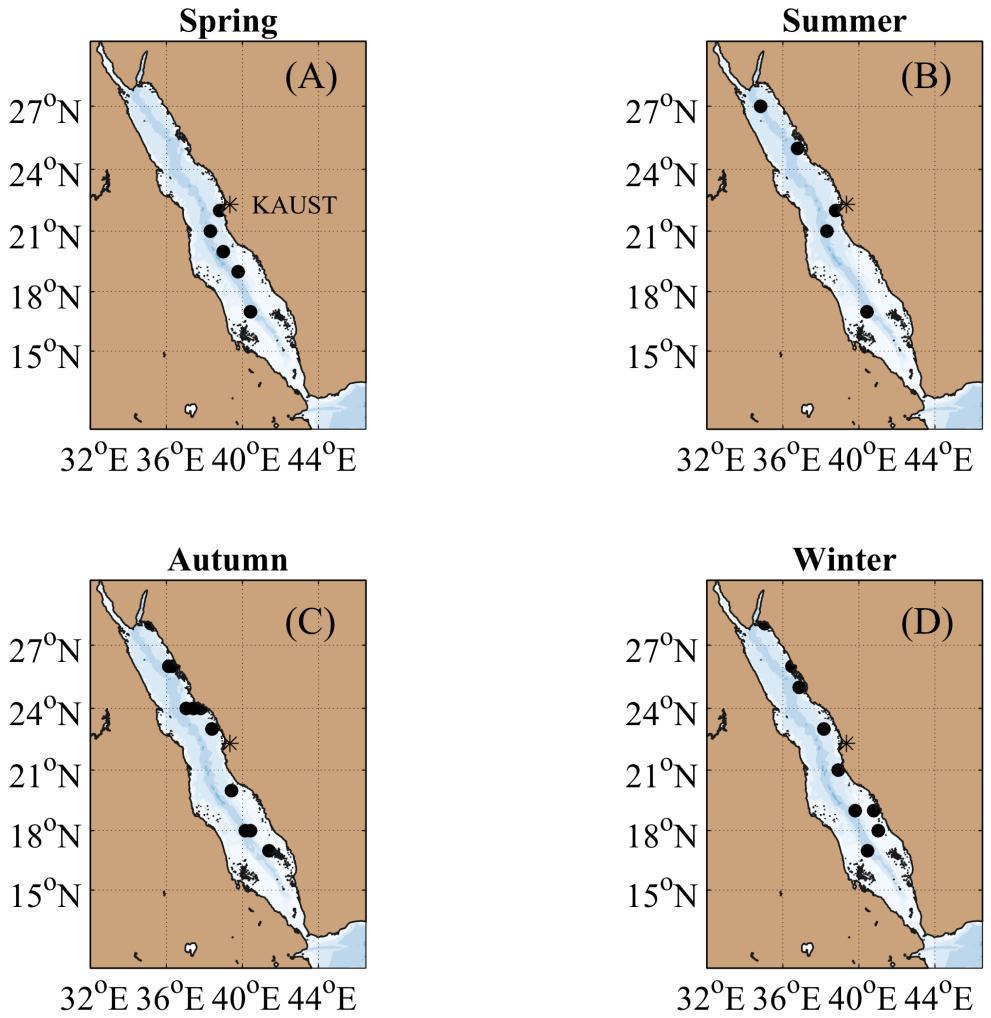

Figure 1: Stations sampled along the Red Sea during (A) spring (2018), (B) summer 2018, (C) autumn (2016) and (D) winter 2016 and 2017

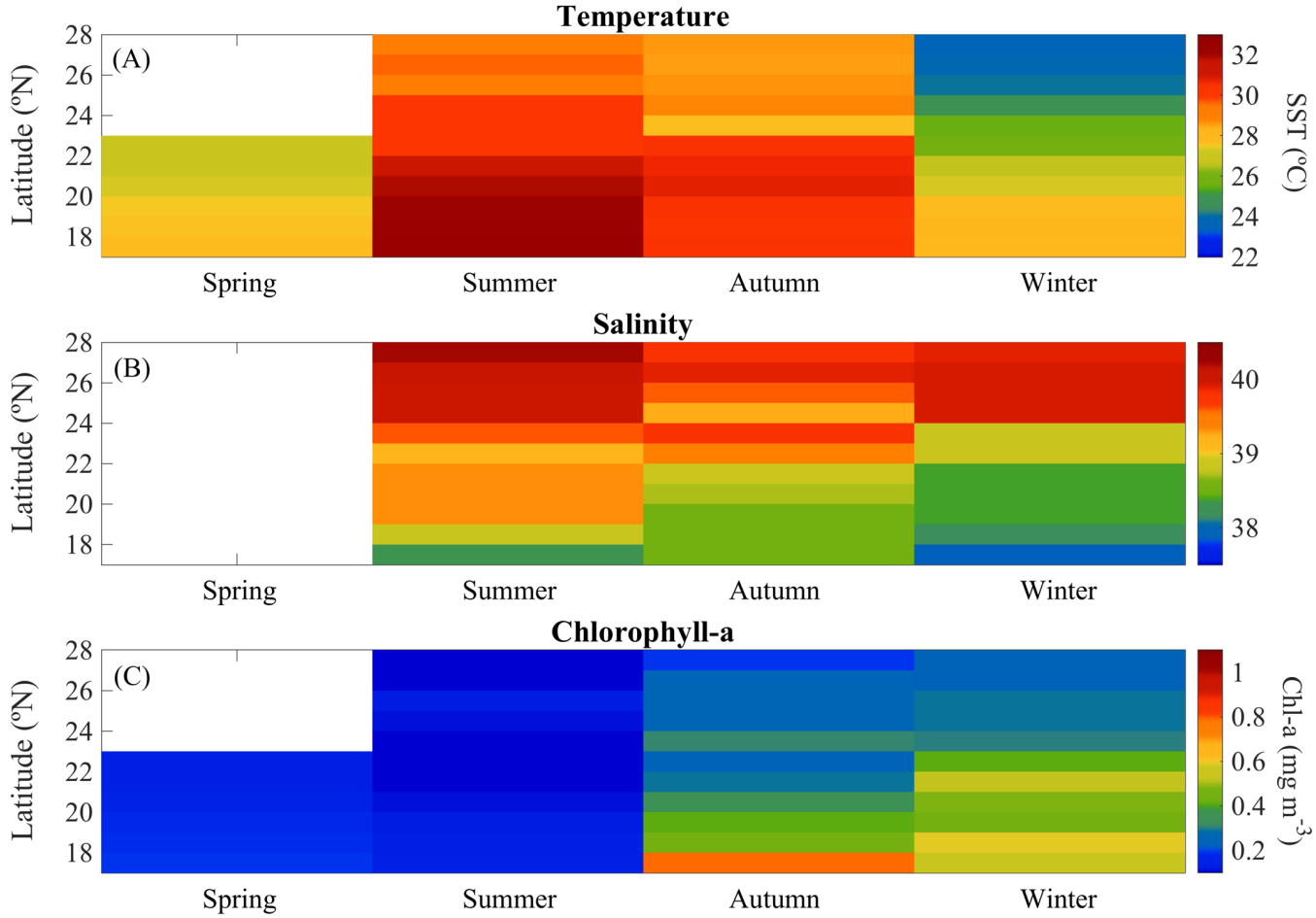

Figure 2: Overall seasonal and latitudinal variability of surface (A) temperature (SST), (B) salinity (C) and chlorophyll-a concentration (Chl-a) measured during spring (2018), summer (2017), autumn (2016) and winter (2016 and 2017) cruises along the Red Sea (~ 100 % of incident Photosynthetically Active Radiation, PAR).

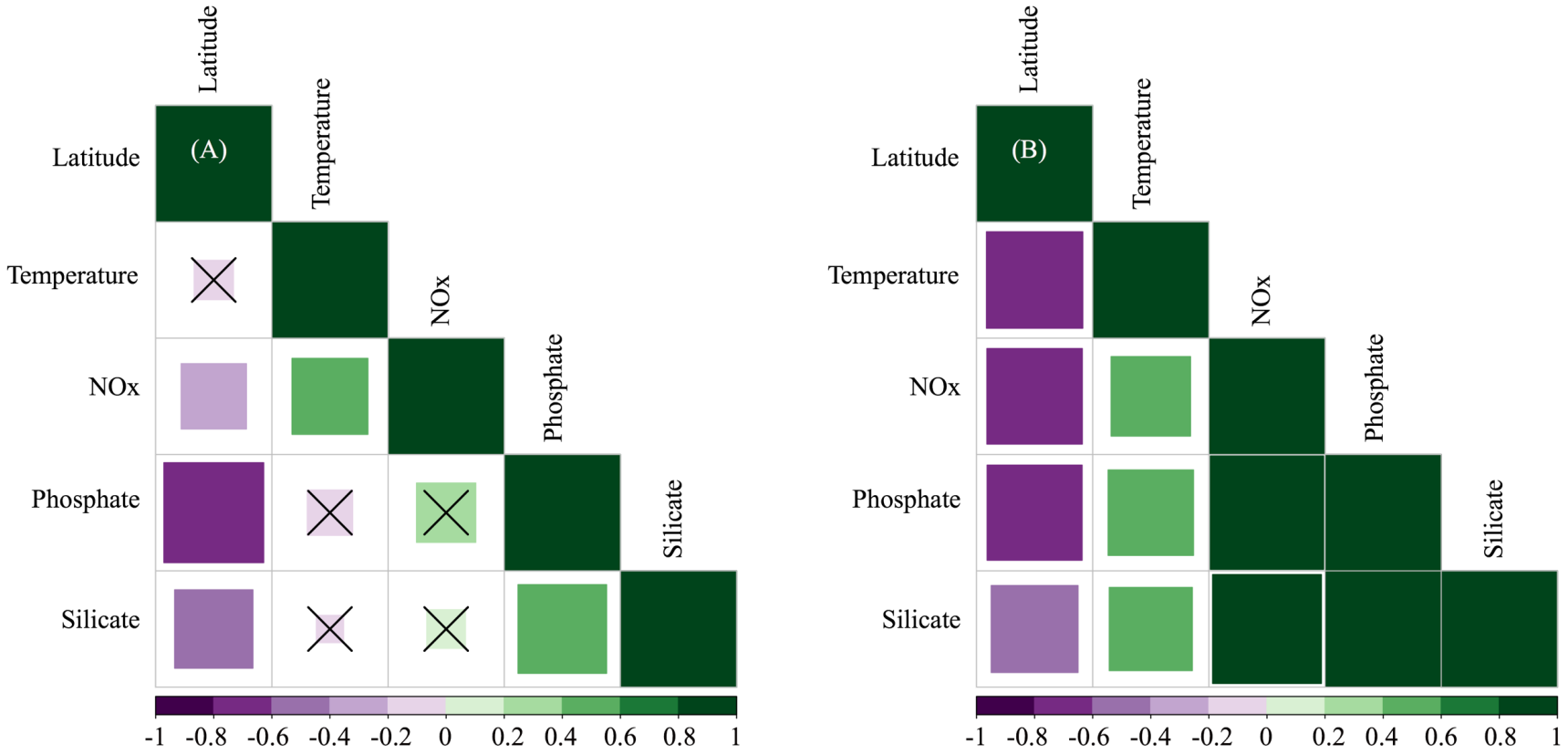

Figure 3: Pearson correlations between environmental variables (temperature and the concentrations of nitrate+nitrite [NOx], phosphate and silicate) and their latitudinal distribution measured at selected depths: (A) the first optical depth (from the surface down to 37% of incident PAR) and (B) at the bottom of the photic layer (between 1–0.1 % of incident PAR values). The size of the squares is the magnitude, the color indicates the direction (green for positive correlations, purple for negative correlations). The value of the correlation coefficient (r) is shown in the color bar below the graphs. Non-significant correlations are denoted with a ×.

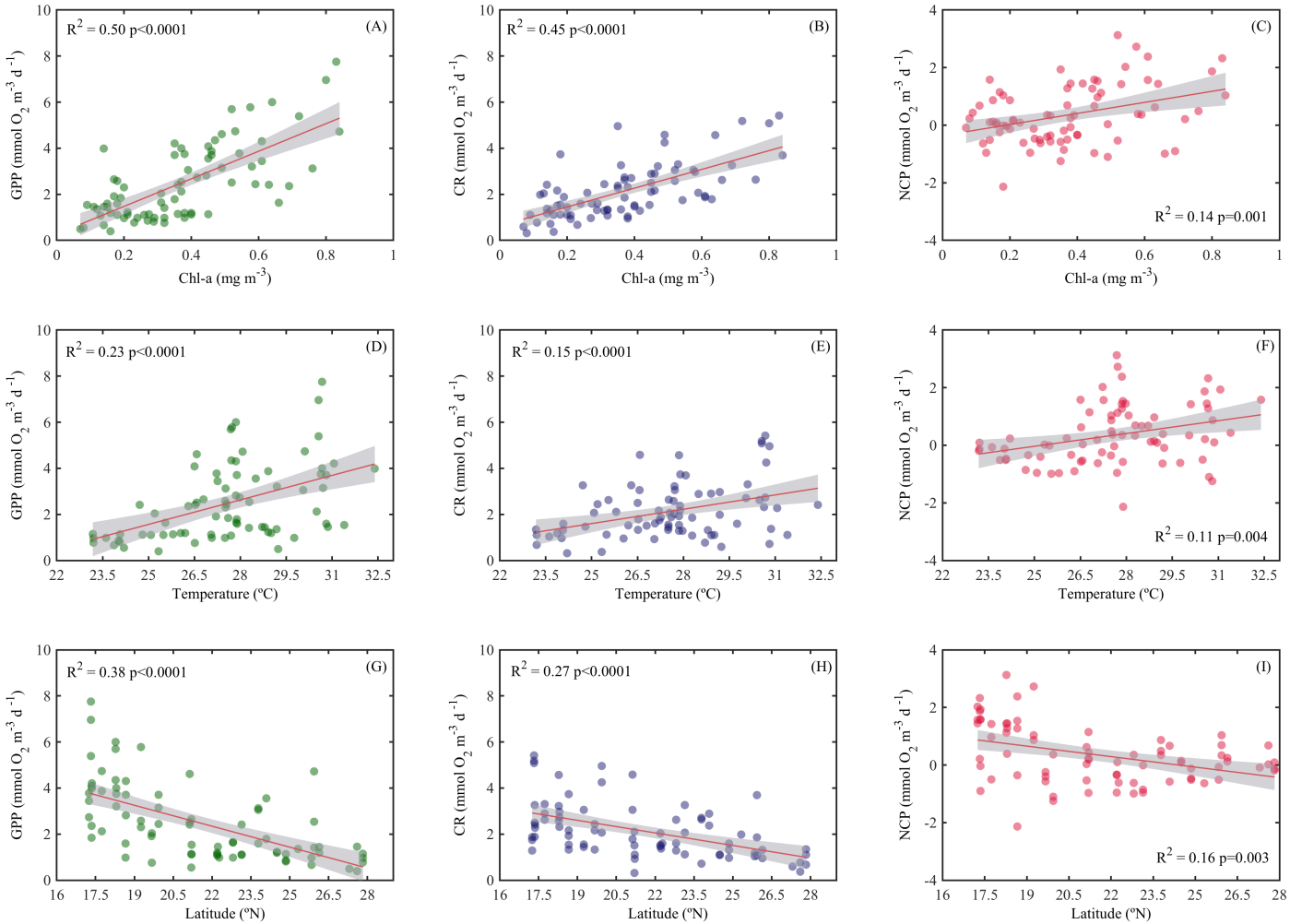

Figure 4: Ordinary least squares linear regression between gross primary production (GPP), planktonic community respiration (CR) and net community production rates (NCP) with (A, B, C) Chlorophyll-a concentration (Chl-a), (D, E, F) temperature and (G, H, I) latitude. The solid red line is the linear least square fit, while the shaded grey area represents the 95% confidence intervals. The coefficient of determination and the statistical significance are indicated for each regression.

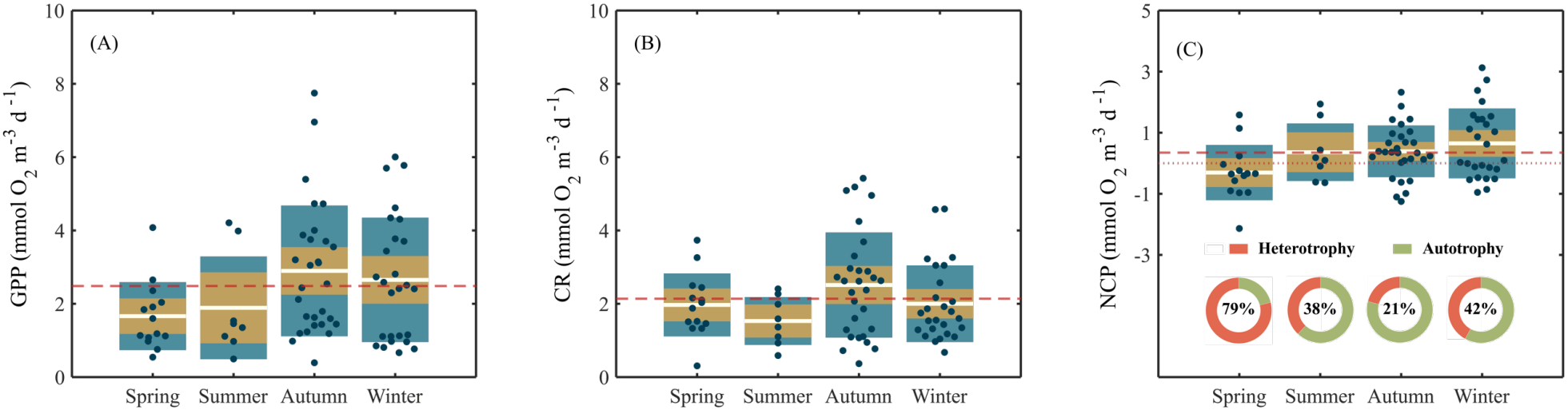

Figure 5. Box plots illustrating the seasonal variability of (A) gross primary production (GPP), (B) community respiration (CR), and (C) net community production (NCP) measured along the Red Sea. On each box are the data layed over a 95% confidence interval (shaded in lighter color), and ± 1 SD (shaded in grey). The central horizontal white lines in the box mark the mean value for each season. The red dashed lines represent the overall mean while the red dotted line in (C) defines the limit between autotrophic from heterotrophic communities (NCP=0). Values inside the donut plots (C) indicate the percentage of heterotrophy (NCP<) for each season.

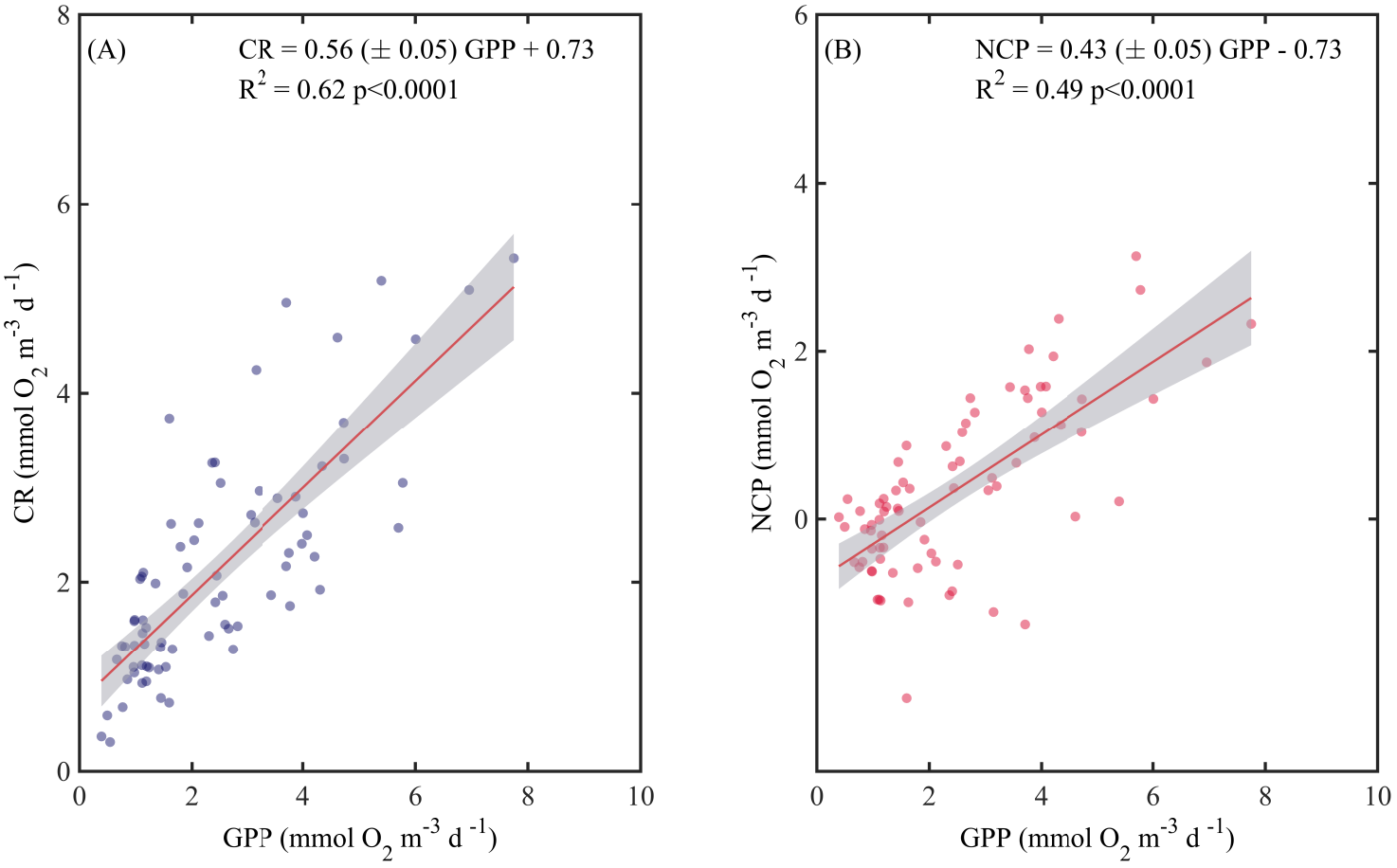

Figure 6: Ordinary least square linear regression between (A) planktonic community respiration and (B) net community production (NCP) with gross primary production (GPP) rates measured along the Red Sea. The ordinary least square regression parameters (slope and intercept) and the statistical significance of each regression are indicated. The solid red line represents the linear least square fit, the shaded grey area represents the 95% confidence interval.

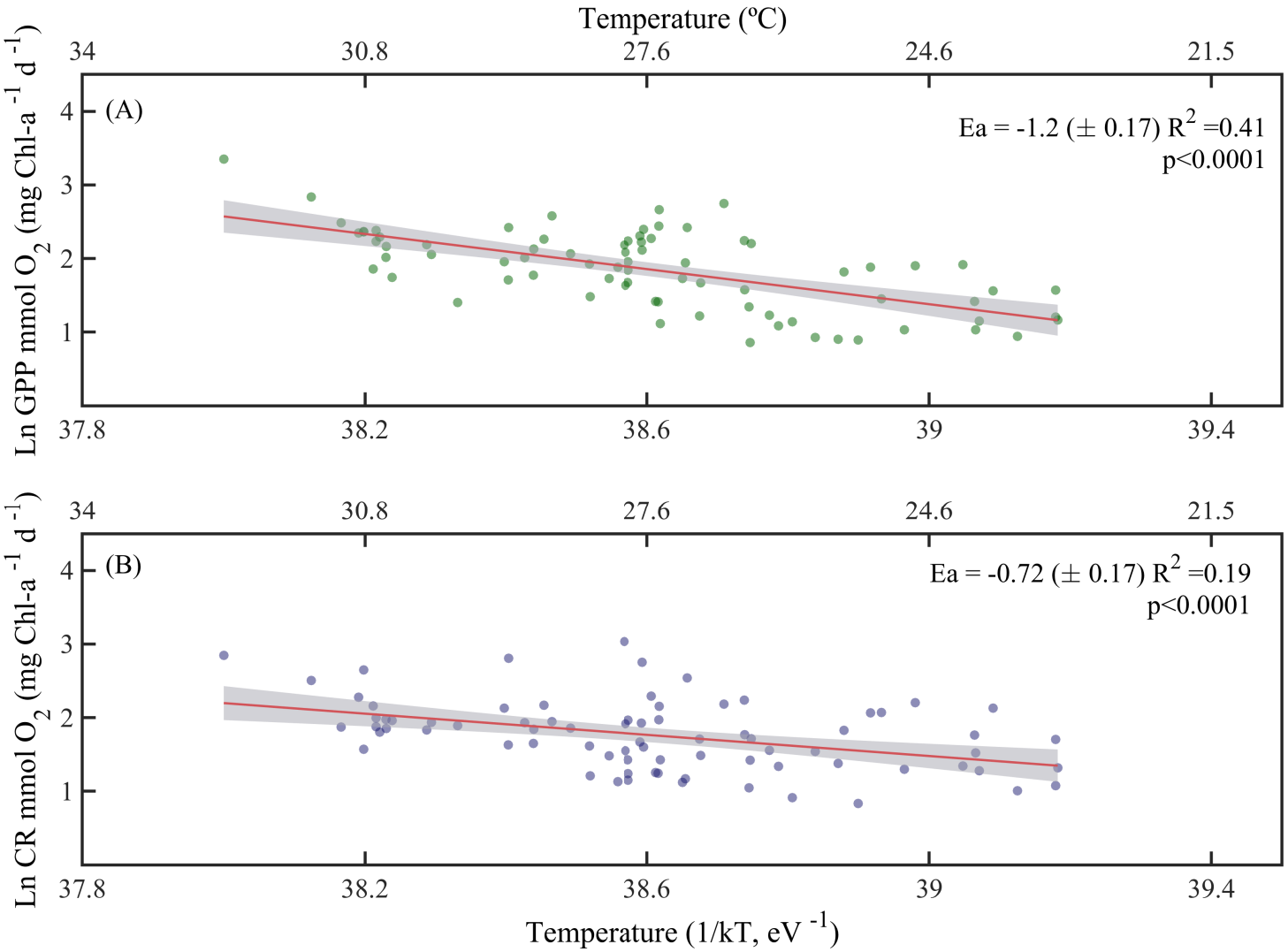

Figure 7: Arrhenius plots indicating temperature dependence of planktonic metabolic rates plotted as the relationship between the natural logarithm of (A) chlorophyll-a normalised gross primary production, and (B) chlorophyll-a normalised planktonic community respiration with temperature as a function of 1/kT (lower axis), where k is the Boltzmann's constant (8.2 x 10^{-5} eV K^{-1}), and T denotes the absolute temperature (K). The corresponding temperatures in degree Celsius are shown in the upper axis for each graph. The solid red line is the linear least square fit, the shaded grey area represents the 95% confidence interval. Ea is the slope of each plot and represents the activation energy.

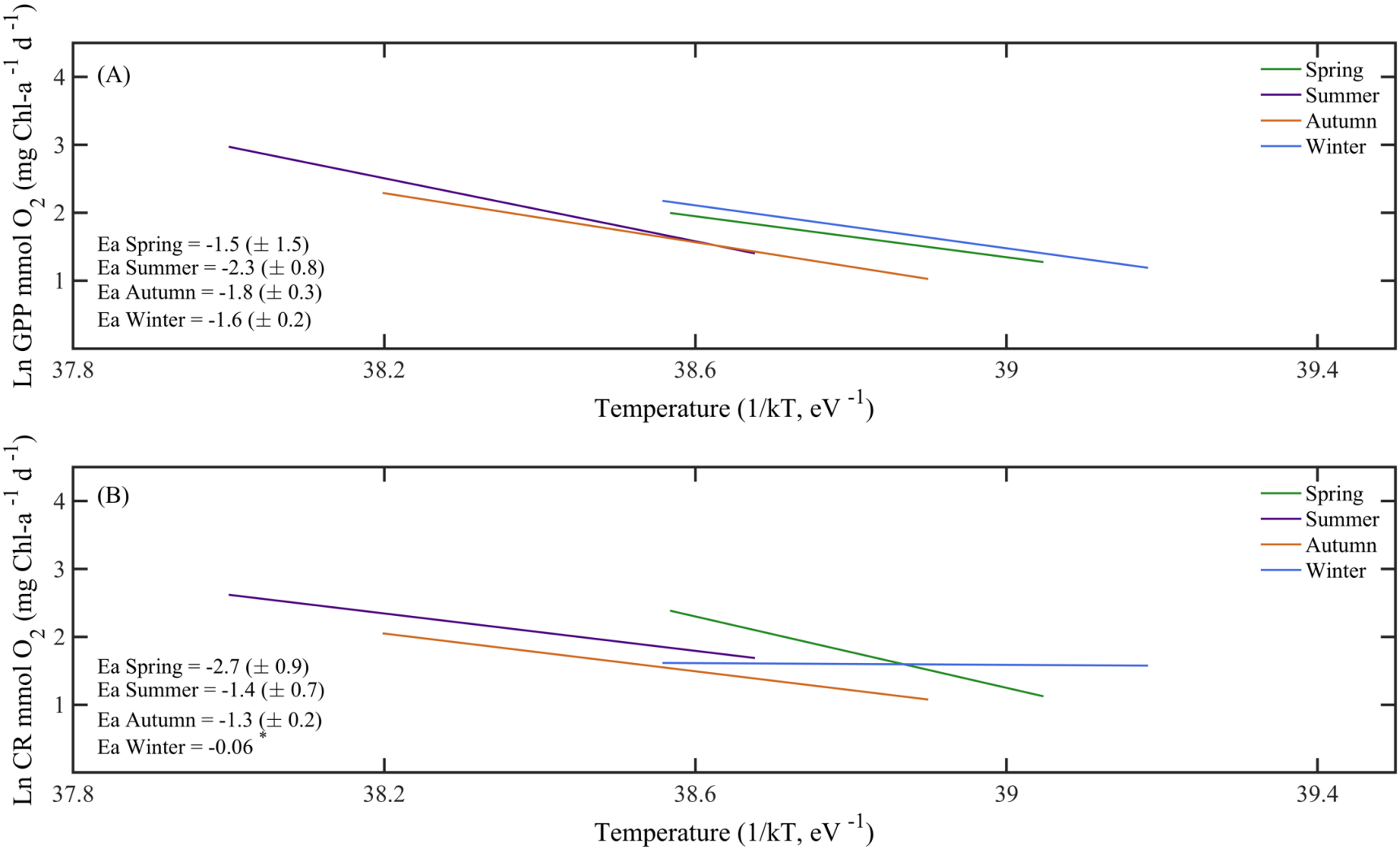

Figure 8: Arrhenius plots indicating the seasonal temperature dependence of planktonic metabolic rates plotted as the relationship between the natural logarithm of (A) chlorophyll-*a* normalised gross primary production, and (B) planktonic community respiration with temperature as a function of 1/kT (lower axis), where k is the Boltzmann's constant (8.2 x 10^{-5} eV K^{-1}), and T denotes the absolute temperature (K). Each line represents the linear least square fit. Ea is the slope of each regression line and represents the activation energy.

Table 1. Pearson correlation matrix between volumetric gross primary production (GPP), planktonic community respiration (CR) and net community production (NCP) with environmental variables (temperature; latitude; nitrite+nitrate, NOx; and Chlorophyll-a concentration, Chl-*a*). Bold numbers indicate significant relationships and the significance level is indicated with *: $p<0.05$*, $p<0.01$** and $p<0.001$***.

	Temperature	**Latitude**	**NOx**	**Chl-*a***	**GPP**	**CR**	**NCP**
GPP	**0.41****	**-0.60*****	0.01	**0.69*****		**0.73*****	**0.70*****
CR	**0.40****	**-0.37***	0.19	**0.61*****	**0.73*****		0.02
NCP	0.19	**-0.49*****	-0.19	**0.37*****	**0.70*****	0.02	
Chl-*a*	0.1	**-0.41*****	**0.29***		**0.71*****	**0.67*****	**0.37****