

P. Williams (Referee)

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Reviewer P. Williams.- *The author has analysed measurements of NCP/GPP/Resp from a single depth from four N-S/S-N Spanish cruises in the Atlantic for the latitudinal seasonality of these above features of the plankton. This type of study, which takes advantage of the N/S runs of the Antarctic supply cruises, was pioneered by Pablo Serret and Carol Robinson. To my mind the research activities of the two groups complement one another, although the present author has, as far as I can see, makes little attempt to take advantage of this – which is a serious omission. There is a rather unconvincing justification for this (p. 512 line 25 to page 513 line 2) “Here, variability was also observed in the temperate waters sampled, as described in other studies (e.g. Gonzalez et al., 2002), but the variability in the intertropical boundaries was identified here because the study included inter-annual data, and a more detailed sampling spatial resolution than previous studies (e.g. Robinson et al., 2002; Serret et al., 2002, 2006; Gonzalez et al., 2002), as the effort was done at a single layer.” Now the present Latitude 1 apparently comprised 34 stations, the other three cruises 10-13 stations, all at a single depth, giving 67 sets of observations in all. Whereas the AMT cruises sampled 24 stations and in AMT 6 apparently 9-12 depths amassing a data base of some 700 observations – some 10-fold greater. Thus the latter is a substantial and relevant resource, which in my experience, is readily available from the British Oceanographic Data Centre and a Web Site maintained by Carol Robinson.*

Comment: It was not my intention to ignore the merits of the AMT program, which is a continuous program since 1995 that has made great contributions to our understanding of the Atlantic Ocean ecosystem.

As the ATM cruises, the Latitude cruises were a series of opportunity cruises but didn't represent a coherent program, since they were conducted under two independent projects. We were offered a few berths and a little time for sampling (except for the Latitude 1 cruise where we were given generous time) to use the transit of the research vessel to Antarctica. So, due to those limitations, for the planktonic metabolism we chose to study a single depth and measured the plankton metabolism at the surface, since it is the layer more directly involved in the exchange of energy, gases, and other substances with the atmosphere.

The patterns observed here for the planktonic metabolism of the surface Atlantic Ocean have not been described before, most probably because the sea surface has not been analyzed separately before. Most reports on plankton metabolism from AMT cruises and other studies in the Atlantic ocean showed the data after been integrated vertically across the water column. The specific variability at the surface water, which is the most sensitive to climate forcing, was probably lost as this layer was subsumed in the integration process.

Action: I changed the paragraph in the new version of the manuscript. Now the paragraph says: “Here, variability was also observed in the temperate waters

sampled, as described in other studies (e.g. Gonzalez et al., 2002; Gist et al., 2009), but the variability in the intertropical boundaries was identified here because the study included inter-annual data of the surface ocean. The surface layer, which exchanges heat, gases and other substances with the atmosphere is more impacted by climatic variability than deeper layers, and water temperature at the seasurface reflects well the changes in climatic variation in the tropical Atlantic (Richardson and Walsh, 1986; Li and Philander, 1997). “

Reviewer P. Williams.- *In relation to this, two significant and relevant papers that derive from the AMT study has not been considered (Gist et al (2009) Seasonal and spatial variability in plankton production and respiration in the Subtropical Gyres of the Atlantic Ocean. Deep-Sea Research II. 56 931-940; Serret et al (2009) Predicting plankton net community production in the Atlantic Ocean. Deep-Sea Research II. 56 941–953) There are other papers, that perhaps are not so directly relevant, that have also not been discussed (Serret et al (2001) Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. Limnol. Oceanogr., 46(7), 1642–1652; Arístegui & Harrison (2002) Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquat Microb Ecol. 29: 199–209).*

Action: I agree, and will follow the suggestions of the reviewer in discussing the results and will cite most of the references suggested in the revised manuscript.

Reviewer P. Williams.- *Figure 5 illustrates that the whole latitudinal sector from 30N to 40S must be, in the balance, net heterotrophic – just reaching balance at times - that's the conclusion we draw from the fitted line. As this paper only has data from one depth it is not possible to determine the scale of the imbalance but it will call for a substantial input of organic material to feed the deficit. Whereas in the discussion the author considers the dynamics of the plankton in some detail I can find no discussion of how these inputs needed to sustain the heterotrophy come about. That this is left hanging is a serious omission to me.*

Comment: I agree. The surface is particularly affected by atmospheric exchange. The heterotrophic metabolism may be increased at the surface waters due to a variety of processes, which are much more intense at the surface layer, as the inputs of organic compounds from the atmosphere associated with long-range atmospheric transport of different substances, and by processes mediated by the intense solar radiation received at this layer, which results in photochemical reactions that may increase the availability of dissolved organic matter to bacteria.

Action: The new version of the manuscript will include the following paragraph: “ ..the lack of coupling between NCP, GPP and Chl a strongly suggests the possibility that inputs of organic matter from sources other than phytoplankton production may be received at the surface of the Atlantic Ocean, influencing the metabolic balance of the community. The surface ocean receives significant inputs of organic carbon from the atmosphere (Dachs et al., 2005; Jurado et al. 2008) that may be used by heterotrophic bacteria. The intense solar radiation

received at the surface ocean, could be also a source of organic matter to heterotrophic plankton, since the photochemical reactions mediated by solar radiation increases the availability of dissolved organic matter to heterotrophic bacteria (e.g. Obernosterer et al., 1999)“.

Reviewer P. Williams.- *There is a statement in the Introduction (p.508, line,14) “Consumption should exceed respiration in unproductive areas . . . “, it may be choice of word but I would contest the word “should” as it’s not a given to my mind. Agreed it is observed in in vitro studies, but it is not seen in in situ studies. Thus, I think “has been observed” is more appropriate than “should”*

Comment: I agree.

Action: I changed “should” and use “has been observed” in the revised version of the manuscript.

Reviewer P. Williams.- *With these various above omissions, I think at this stage the author should be asked to rewrite the paper taking the recent omitted work into consideration and her findings in relation these published findings. Then we’ll have a better idea whether her claim in the Abstract (last line) :” The results showed new spatial and temporal patterns in the pelagic metabolic balance of the surface Atlantic Ocean with consequences for the carbon flux.” is merited. We also need some consideration what drives the heterotrophy — I don’t think you can use the threshold argument as an explanation as it is circular. In essence, heterotrophy has to be driven externally – the community cannot pull in the organic deficit.*

Comment: I thank Dr. Williams for his availability and efforts in reviewing this manuscript, which has greatly benefit from his constructive comments.

Anonymous Referee #2

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This ms describes a dataset collected during 4 quasi-meridional cruises from 1995-1999, bisecting the Atlantic Ocean as part of the LATITUD project. While there were some differences in sampling design, cruises generally followed a diagonal pattern across the Atlantic Basin from the coast of Africa to the coast of South America. Surface waters were sampled at from 10-34 stations per cruise. Incubation assays were done to measure community respiration (R), net community production (NCP) and gross primary production (calculated as NCP+R). R and NCP rates were measured as changes in oxygen concentrations over a 24 h for samples incubated in darkness and natural or simulated sunlight, respectively. Oxygen was measured using a precision Winkler method. The main findings from the study were that NCP and R were very low in these oligotrophic waters, and that R typically exceeded NCP, indicating that much of the open Atlantic ocean is net heterotrophic. The author describes the results using latitudinal plots of Chl a, GPP, and NCP; the latter was further divided into

boreal/austral Spring and Autumn sub-categories. A strong negative relationship was observed between NCP and R. The author discusses the results in the context of prevailing current patterns across the basin and the seasonal temperature regimes, and conclude that understanding the net metabolic balance of large ocean basins require further study of oceanographic, climactic, and micro-heterotrophic processes. This study provides useful data on net metabolism in surface Atlantic waters during different seasons. The author contends that seasonal studies are lacking for this region, therefore this dataset help fills a gap in the literature.

Reviewer #2.- However, I found this to be a very sparse dataset, especially given the sampling design only includes surface waters, traverses such a large geographic range, and transects a diversity of current regimes, each with its own seasonal dynamic. Furthermore, many of the samples were collected from tropical regions where seasonal variation in solar irradiance and temperature are diminishingly small. Therefore, I think it is difficult to resolve meaningful seasonal patterns.

Comment: I agree. The Latitude cruises were opportunity cruises (as the AMT cruises), taking advantage of the N-S transects of research vessels in their way to Antarctica. The opportunistic nature of the cruises implied limitations on the time available to sampling, and on the number of berths available, but offered the opportunity of study large-scale variability in the Atlantic Ocean. Due to these limitations, we chose to focus our efforts on the planktonic metabolism at a single layer, and selected the ocean surface for this purpose, since it is the layer exchanging heat, gases and other substances with the atmosphere, and is of major interest for a range international scientific programs (e.g. WOCE, SOLAS).

Although the subtropical gyres show low seasonal variability, the oceanographic literature describes a large seasonal variability in the intertropical zone, due to seasonal changes in the tropical climate with consequences for the equatorial currents system, characterized by strong currents. The results presented in this manuscript showed that this variability influenced the metabolic balance of the planktonic community at the surface, which resulted in a large variability at the boundaries of the inter-equatorial zone (10°N and 10°S, Fig. 5), switching the communities in these areas from heterotrophic to autotrophic depending on the season.

Action: In the revised version of the manuscript, I included a paragraph describing better the rationale for the focus on the surface layer. The text now reads: “The goal of this study is to analyse the spatial and temporal variability of the metabolic balance of the pelagic communities of the Atlantic Ocean at the seasurface by quantifying the net community production and the community respiration at the surface ocean in a series of oceanographic cruises (LATITUDE cruises) that crossed the Atlantic Ocean from the North Atlantic (from the Canary Islands) to the South Atlantic (to the latitude of Buenos Aires or Montevideo). The ocean surface is the layer directly exchanging heat, gases and other substances with the atmosphere, rendering the evaluation of planktonic metabolism, the key biological process affecting CO₂ and O₂ fluxes, of particular interest “.

Reviewer #2.- *The relationship between NCP and R is interesting, though the implications of this finding could be further explored. Apart from resolving the point at which autotrophic and heterotrophic processes are balanced, are there implications to the slope of the relationship? Similarly, what is the nature of coupling between autotrophic biomass (chl a) and production (GPP). Does a scatter plot of GPP and chl-a show a strong relationship? Why or why not? If so, what does the slope of that relationship suggest?*

Comment: The slope obtained in the relationship of NCP vs R was not significantly different from 1 (SE of the slope = 0.09). There was no relationship between GPP and Chl a concentration as the reviewer suggested, and this is now more clearly indicated in the revised version.

Action: The description of the lack of coupling between GPP and Chl a was modified in the new version of the manuscript: "GPP was not related to chlorophyll a concentration ($P > 0.1$) and the pattern of variability of GPP with latitude differed from that observed for chlorophyll a (Fig. 4), which showed low values at the South Atlantic, with the minimum values around 10° S among the transects, and increasing at the North Atlantic, with maximum chlorophyll a values around the area influenced by the equatorial upwelling (Fig. 4). "

Reviewer #2. *One technical note: The detection limit should be stated explicitly. In other words, what is the minimum difference in dissolved oxygen from initial to 24 h that can be reliably resolved? What proportion of the samples were at or below this detection limit?*

Comment: I agree, we used a high precision microwinkler technique, but I didn't indicate the degree of precision attained. The lowest values were obtained for NCP, but since 0 $\mu\text{molO}_2 \text{ L}^{-1} \text{ d}^{-1}$ means net metabolism in equilibrium, I did not exclude these or any other results.

Action: In the revised version, the following paragraph was added to the methods section: "The average precision of the O_2 concentration measurements was $\%CV = 0.12$, and the mean of the standard errors of the NCP and CR rate measurements were 0.24 and 0.34 $\mu\text{molO}_2 \text{ L}^{-1} \text{ d}^{-1}$, respectively."

Anonymous Referee #3

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The objective of this study is to analyze the variability on the metabolic balance of the pelagic communities of the Atlantic Ocean. To this aim the plankton metabolism (GPP, NCP and R) and chlorophyll a concentration were measured at the surface of the Atlantic Ocean during four latitudinal cruises in spring and autumn. Seasonality

was only found for CR and NCP, not for GPP and chl_a, leading to the conclusion that R explains the net heterotrophic balances and variability of NCP, which are attributed to the influence of temperature on the activity of heterotrophic zooplankton and bacteria.

Reviewer #3.- *I think that the discussion on mesozooplankton should be excluded as the contribution of these organisms to the R rates measured by the author (in 125 mL samples from Niskin bottles) should be negligible compared to those of pro- and eukaryotic microbes. Regarding temperature, although it is certainly an important factor, for sustaining the observed net heterotrophy the critical point is the supply of allochthonous organic matter, which should be discussed in the manuscript. However I will focus my comments here on my main concern, which is not discussion but the data set and its analysis. Reviewing interpretations in Discussion would require resolving these issues first.*

Comment: I agree with the reviewer, that zooplankton is not influencing the NCP and R values measured. The discussion on the zooplankton was included to remark that some biological processes in the Atlantic Ocean showed a lack of coupling with chlorophyll a concentration or GPP, but certainly the sentence was not sufficiently clear. I revised the discussion section to avoid confusion.

Action: The paragraph was modified in the revised version of the manuscript as follows: “The results indicated a lack of coupling between R and NCP and Chlorophyll a concentration during the study, in agreement with studies showing biological variability to be independent of Chl_a in the Atlantic, as found for the reproduction and dynamics of zooplankton (Calbet and Agustí, 1999; Finenko et al., 2003) and bacterial dynamics (Gasol et al., 2009). Although our measurements of community respiration and NCP do not include respiration by metazoans, variability in the ration of Chl *a* to zooplankton biomass has been reported to vary seasonally for the Atlantic inter-equatorial zone (Finenko et al. 2003). This pattern is comparable to the patterns described here for heterotrophic metabolism, showing a prevalence of heterotrophic activity in spring, when the ratio of Chl *a* to zooplankton biomass is lowest.”

Reviewer #3.- *I am disinclined to accept that we can “analyze the spatial and seasonal variability on the metabolic balance of the pelagic communities of the Atlantic Ocean” by measuring GPP and R at one single depth in the water column. As the author states, “the net metabolism of a system is an important descriptor of the role of the biological processes in the carbon flow”; which hence critically requires integrating those processes over the spatial and temporal scales of the system. Commonly accepted scales for integration of trophic processes in planktonic communities in the open ocean are the photic zone, the mixed layer, the compensation or the critical depth, but not the surface of the water column. Two good references here are Smith and Hollibaugh (1993) and Williams (1998), who wrote “I have come to the conclusion that with the data sets of net primary production and respiration currently available to us, generalizations on the regional distribution of carbon balance in the oceans cannot be derived from simple regression analysis of volumetric observations”. Particularly when they*

come from a single depth, disregarding the variability of subsurface processes. Recent evidence and discussion on the issue (e.g. Gist et al. 2009) are based on photic zone integrated data, and hence cannot be compared with the data set presented here. Even within the data set presented here I find it difficult to compare surface P:R balances between systems with such a different vertical distribution, variability and control of physical, chemical and biological properties as the ocean gyres, the Equatorial upwelling, and the NW African upwelling.

Comment: I agree that the vertically integrated metabolic rates are of major interest to characterize oceanographic regions and to formulate regional balances, but there are other aspects of variability of the oceanic processes that also deserve attention. The surface layer is of particular importance since it is the layer of the ocean directly interacting with the atmosphere. The surface layer is the focus of major international programs, such as WOCE and SOLAS, because it is the layer exchanging heat, gases and other substances with the atmosphere. I included in the new version of the manuscript this explanation for the focus in surface seawater that was lacking in the previous version.

Action: I included the following paragraph in the revised manuscript: “The goal of this study is to analyse the spatial and temporal variability of the metabolic balance of the pelagic communities of the Atlantic Ocean at the seasurface by quantifying the net community production and the community respiration at the surface ocean in a series of oceanographic cruises (LATITUDE cruises) that crossed the Atlantic Ocean from the North Atlantic (from the Canary Islands) to the South Atlantic (to the latitude of Buenos Aires or Montevideo). The ocean surface is the layer directly exchanging heat, gases and other substances with the atmosphere, rendering the evaluation of planktonic metabolism, the key biological process affecting CO₂ and O₂ fluxes, of particular interest “.

And new paragraphs in relation with the surface layer are now included in the discussion section, to answer the comments of reviewer P. Williams:
“ ..the lack of coupling between NCP, GPP and Chl a strongly suggests the possibility that inputs of organic matter from sources other than phytoplankton production may be received at the surface of the Atlantic Ocean, influencing the metabolic balance of the community. The surface ocean receives significant inputs of organic carbon from the atmosphere (Dachs et al., 2005; Jurado et al. 2008) that may be used by heterotrophic bacteria. The intense solar radiation received at the surface ocean, could be also a source of organic matter to heterotrophic plankton, since the photochemical reactions mediated by solar radiation increases the availability of dissolved organic matter to heterotrophic bacteria (e.g. Obernosterer et al., 1999)“.

Referee #3. *Inferences on the seasonal variability are based on the combination of all the data from each cruise into a single mean, which is assumed to be the representative value of the corresponding rate for that season in the Atlantic (Tables 1 and 2). However, it is commonly accepted that the study of primary production in the ocean requires a biogeographic partition to accommodate*

regional differences in control and seasonality, and the same necessarily applies to the balances between primary production and respiration. The presented mean of some surface data of P and R from the NAST, CNRY, WTRA, SATL and BRZ (Longhurst 1998) is to me unintelligible. And deriving the seasonality of the metabolic balance in the Atlantic Ocean from the difference between two such means in different seasons, is not possible, especially when different provinces were sampled in different cruises (e.g. Latitude 2 included the NW African upwelling) (see fig.1).

Comment: Climate strongly influences the oceans, and climatic variability is forcing changes in the ocean at the seasonal scale even at the tropical areas (several references provided in the manuscript). Moreover, the influence of climate is expected to be larger at the surface waters, as this is the layer exchanging heat with the atmosphere, and this is well reflected in the results presented here. Of course there are regional differences, but “fall” and “spring” are occurring in all the regions (NAST, CNRY, WTRA, SATL and BRZ). Spring is an astronomically defined concept, and is consistent within hemispheres. Whereas spring occurs in different months in the Northern and Southern hemispheres, both do have a spring season (hence, the table showing the means for Spring and Fall are based on different months for the northern and southern hemispheres). Seawater temperature is consistently higher in all the regions in fall, and consistently lower in spring. As a consequence, at the surface waters, the differences between spring and fall temperature in the results presented here are highly significant.

Referee #3. *Data are presented without their corresponding s.e. or deviation, which makes figures 3 to 5 ineffective, and their interpretation not acceptable. This is an important issue that needs to be revised because the observation of higher across systems variability of R compared to GPP is quite an unusual one, especially when data come from the highly productive NW African upwelling, the equatorial upwelling and the oligotrophic gyres.*

Comment: I agree that this information is important. The SE was added to NCP data of Figure 5, in the new version of the manuscript. This was not possible for Figure 4, since chlorophyll a concentration measurements were not replicated. For Figure 3, the patterns, which are not very strong, were obscured by the error bars, which do not represent well in a log scale. Hence, I chose not include the SE bars in that figure.

Action: The SE was added to NCP data of Figure 5, in the new version of the manuscript. Following reviewer #2, new information on the precision of the method was added in the methods section (see above).

Referee #3. *Interestingly, the highest R data come from Latitude 4 and 1, that did not cross through the NW African upwelling. Similarly unusual is the correlation of NCP with R but not with GPP (e.g, Aristegui and Harrison 2002; del Giorgio and Duarte 2002). The author states that the predominantly “low productivity was expected since the area included the sampling in the ultra oligotrophic waters of*

both North and South Atlantic subtropical gyres" (L5. Discussion). However in a extensive analysis including 6 AMT cruises and the global database at www.amtuk.org/data/respiration.xls, Gist et al (2009) found maxima R rates in photic zone of the N and S Atlantic gyres of ca. 2 and 1.5 mmol O₂ m⁻³ d⁻¹, respectively. In the R data set presented here aprox half of the surface data are > 2 mmolO₂ m⁻³ d⁻¹, with maxima rates of >7 mmolO₂ m⁻³ d⁻¹. The data presented should be accompanied by an estimate of their precision, and the author should explain the high R rates.

Comment: The R values obtained in this study showed a normal distribution, with a similar range to those reported in other studies in the Atlantic Ocean. Gonzalez et al. (2002) reported highest R values in oligotrophic Atlantic waters than those found here, with half of their values exceeding 2 mmol O₂ m⁻³ d⁻¹. Aristegui et al. (2004) and Serret et al. (2001) also reported values of community respiration in the Atlantic Ocean around 7 (and above) mmolO₂ m⁻³ d⁻¹, in areas not associated to the NW African and equatorial upwellings.

The strong relationship between NCP and R, is the consequence of the predominance of a heterotrophic metabolism in the surface layer. Gonzalez et al. (2002) also showed relationships, not as strong as those reported here, between NCP and R. The reason why these relationships have not been shown in other papers are to be provided by the authors of those papers, but it is possible that these relationships are stronger for sea surface waters, than for integrated metabolic rates.