Bio-optical provinces in the eastern Atlantic Ocean and their biogeographical relevance

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We thank Dr. Gerhard Kattner and the two anonymous referees for their positive and thorough evaluation and their valuable suggestions to improve our manuscript. To the best of our knowledge we have modified the manuscript according to all suggestions made by the referees. Below we answer each comment individually.

1 Handling Editor's comment (Dr. Gehard Kattner)

We tried to reduce the references where it was possible, although some new references have been added through the anonymous referees' comments.

2 Anonymous Referee #1

RC: *Section 2.1.3 – If radiometric data were checked according to the procedures of Wernand 2002, what was the outcome? What proportion of the readings was discarded?*

AC: The processing routines for the radiometric measurements were also written for other cruises besides the cruise ANT-XXV/1. These routines include tests for precipitation and minimum solar radiation according to Wernand (2002) to check automated measurements. During this particular cruise, all measurements were conducted during relatively clear sky and calm sea conditions around noon. Precipitation or limited light conditions did not occur and thus the tests according to Wernand (2002) did not exclude any measurement. The respective section 2.1.3 of the manuscript has been revised accordingly.

RC: *Section 2.1.4 – The choice of Fo as a parameter for measuring chlorophyll seems odd, since (a) it is difficult to measure accurately and (b) it represents the state of maximum quenching. This probably explains why multiple recalibrations against HPLC data were required.*

AC: The reviewer is correct that the accuracy of F0 measurements is lower compared to Fm. We used the F0 values because the method to apply the quenching corrections has been developed with a standard fluorimeter setup which measures F0. We also performed the analysis with Fm data. The respective results using Fm or F0 can be seen in the plot below where chl-a derived from either Fm or F0 is plotted against the latitude. The differences are marginal, and can only be seen in areas with very high Chl-*a* concentrations (Fig. 1_rev1). The uncertainties given below are much better (5-20%) for the F0 analysis in the regions IVb, V and VI and only slightly (1-2%) better for the Fm analysis in the regions III and IVa. Therefore, we used the F0 as the parameter for measuring Chl-*a*. We added two sentences explaining why we used F0 instead of Fm in section 2.1.4.

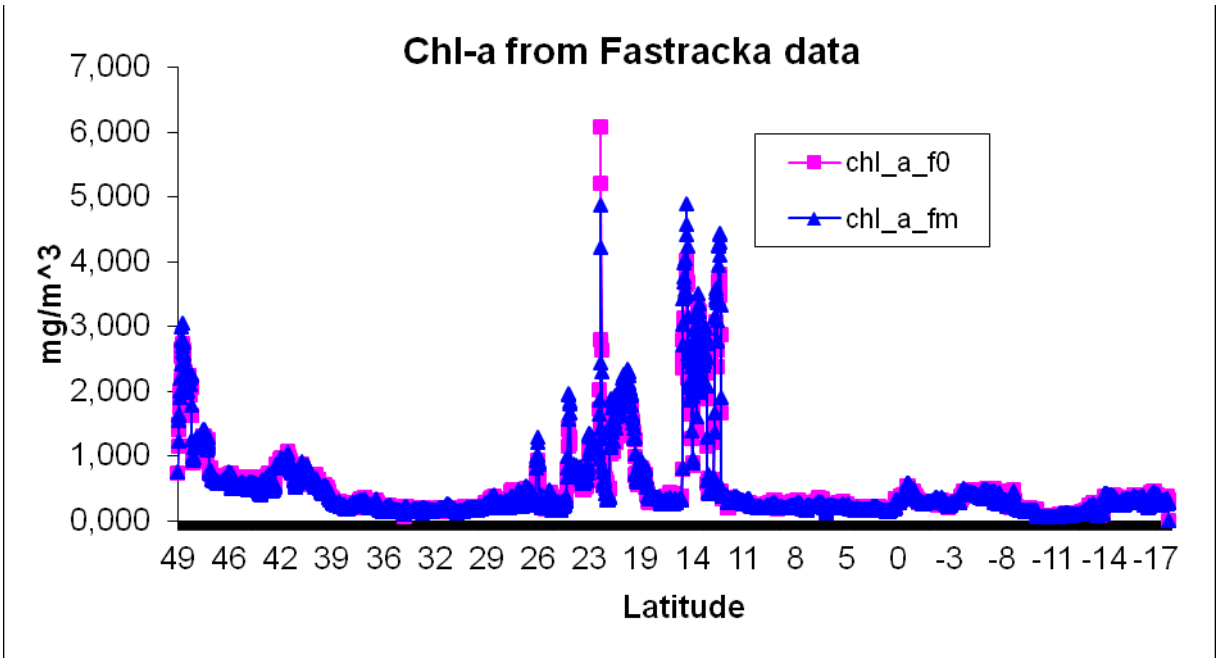

Fig. 1_rev1: Chl-a conc. derived from Fastracka F0 or Fm measurements by calibration with HPLC chl-a pigment data for the transect of ANTXXV-1 cruise in Nov 2008.

RC: *Can the authors give any indication on the estimated uncertainties for their TChl-a measurements?*

AC: Considering the F0 values the uncertainties in the different clusters were 53%, 18%, 20%, 28% and 4% with the number of collocations 4, 12, 3, 7, 8, and 4 for clusters III, IVa, IVb, V, VI, respectively. Considering the Fm values the uncertainties in the different clusters were 51%, 17%, 25%, 48% and 15% with the number of collocations 4, 12, 3, 7, 8, and 4 for clusters III, IVa, IVb, V, VI, respectively. The uncertainties for the F0 values have been added to section 2.1.4 of the revised manuscript.

RC: *Sections 2.2.3 and 2.2.4 - Flow cytometric analysis tends to discriminate against large cells and colonies. Was there any evidence from the microscopy to indicate whether this occurred to a significant extent during the cruise in question?*

AC: Only very few samples had a larger fraction of bigger cells (mainly the samples in the English Channel and in the Mauretanian Upwelling). The flow cytometric analysis did indeed not reveal these bigger cells, but we saw the cells in the microscopic analysis and could deduce some information from the pigment analysis. The discrimination against part of the sample was one of the reasons why we used the flow cytometry data only as supplement information and not as a main descriptor.

RC: *Section 3.3 - the choice of parameters (wavelength ranges for example) appears to have been adjusted freely to provide the best correspondence between clusters derived from pigments and those derived from optics. Surely it is necessary to test whether the correspondence exists in an independent data set in order to validate this procedure?*

AC: We recognize the importance of the reviewer's comment on the choice of parameters involved in the clusters derived from hyperspectral data. Among these parameters are the wavelength range used in the cluster analysis of absorption and reflectance data or the smoothing filter size and band separation also used in the derivative calculations of reflectance spectra. In that sense, in order to examine the sensitivity of our cluster results to the choice of these parameters, several tests were performed which were essential to optimize our performance. In particular, the degree of similarity between the pigment-based and the optical-based clusters was evaluated using the cophenetic index (described and successfully used for the same purpose and application in Torrecilla et al., 2011b) for calculations involving different combinations of spectral ranges and also derivative parameters when necessary.
Our results from this comprehensive analysis were discussed in a separate publication (see Torrecilla et al., 2011a), which was focused on this part of the analysis. Nevertheless, this information was just summarized in our discussion in section 3.3 and Table 5 of the manuscript by including the two references cited above. After the reviewer's comment and in order to better point out this issue, we have modified some sentences in section 3.3 in the revised paper as follows:
We changed "(see also Torrecilla et al., 2011a)" to "This issue is discussed and examined in greater detail in Torrecilla et al., 2011a" and added "As reported in past studies in which the aim was also the identification of phytoplankton pigment assemblages from $R_{rs}(\lambda)$-spectra (Torrecilla et al., 2011b), a good performance was only achieved when considering the second derivative of $R_{rs}(\lambda)$-spectra over the spectral range of 435 to 580 nm."

RC: *Section 4.2 - this section, comparing the cruise results with the Longhurst system, appears to be inconclusive. Might this be a reason for inserting the words 'Possible' or 'Tentative' at the beginning of the paper title?*

AC: The "bio-optical provinces" refer to the provinces we found with our method and which we relate to Longhurst's biogeographical provinces, hence the "biogeographical relevance". We are convinced that our method joins samples with specific bio-optical traits and as these samples are generally geographically clustered we called them "bio-optical provinces".

RC: *Section 5 - the conclusion seems to be that optical clusters derived from absorption or remote sensing measurements are congruous with those derived from pigment analyses, and therefore optical measurements could provide a short cut to identifying functional groups and bio-optical provinces. This argument depends critically on the degree to which the cluster relationships established for this data set are robust, and that surely depends on the acquisition and analysis of additional data which has not been used in the original clustering routines. Perhaps the authors could include this caution in their conclusions, or alternatively explain why it is irrelevant?*

AC: We agree with the reviewer and have added the following sentence to section 5:

"However, before this novel approach can be applied at a global scale, it will be necessary to validate it on larger databases consisting of simultaneous pigment and optical information from more diversified waters."

3 Anonymous Referee #2

General comments

RC: *Whereas the analysis and information (optical and biological) used for each sample was extensive, there was only 48 stations. It surprises me that there was not more comparison with AMT transect programme, considering it has transected the Atlantic over the past decade, including the Eastern Atlantic (e.g. see AMT 6 and 15). The pigment results shown in figure 3 are supported by a number of studies using AMT data (see especially Aiken et al. 2009), which is only briefly touched on (e.g. page 7179, line 14-16). More discussion on how the results presented in this paper compare with the AMT programme is likely to reinforce the conclusions of the manuscript.*

AC: The following paragraph comparing our data to the AMT cruises (specifically the Aiken et al., 2009 paper) has been added at the beginning of section 4.1.2.

"Generally, our results coincide with previously published works, especially with data from the Atlantic Meridional Transect (AMT) programme. The AMT cruises also crossed the Atlantic from North to South and specifically AMT cruise 6 had a very similar cruise track to ANT XXV-1. The phytoplankton pigment data of the AMT cruises between 1995 and 2005 has been summarized in Aiken et al. (2009). The trends are similar with overall low Tchl *a* concentrations and Tchl *a* peaks in the English Channel and at ~20°N in the Northwest-African Upwelling. A second bloom at ~14°N as was encountered on our cruise was not recorded by the AMT cruises. Aiken et al. (2009) found significant correlations between TChl *a* and accessory pigments (AP), which could be divided by trophic states and dominating phytoplankton size group. The slope of TChl *a* vs. AP in oligotrophic areas (TChla < 0.25µg/L, picoplankton dominating) was >1.00, indicating that on average the concentration of AP was greater than TChl *a*, which we could corroborate with our results (data not shown). For the meso- and eutrophic regimes the slope for our data was below 0.9 (i.e. on average more TChl *a* than AP), whereas Aiken et al. (2009) reported that results were inconclusive for these areas."

RC: *Furthermore, the relationships between phytoplankton functional groups, bio-optical traits and biogeochemical provinces has been explored recently by Aiken et al. (2008), albeit less quantitatively, and again the results presented in this paper are in support of the conclusions reached by Aiken et al. (2008), using a number of globally representative datasets. A discussion on this is likely to reinforce the manuscripts conclusions.*

AC: The following paragraph has been added at the beginning of section 4.1.2:

"Aiken et al. (2008) used the AMT data and other historical data to investigate links between bioenergetic scale and certain bio-optical traits (BOT) that are specific properties of phytoplankton types. They identified the change in the TChl *a*/AP ratio as "the biggest factors that alter the shape of ocean colour spectra" and showed that the three phytoplankton size classes can be identified and associated to three previously defined basic biomes on the basis of this ratio. The TChl *a*/AP ratio shows the relative change of blue (Chl a, centered at 443 nm) to green (carotenoids, centered at 490 nm) absorption, which lies within the wavelength range identified by our statistical approach as the optimal spectral range for clustering *a*ph(λ)- and *R*rs(λ)-data. With our approach we would like to develop a statistical method to investigate the detailed relationships between pigment distribution (and what it implies in terms of phytoplankton groups) and hyperspectral properties of the ocean surface in the biogeographical context of marine provinces."

RC: *Page 7174-7175, section 2.3.1 Interpretation of pigment data; and Page 7179-7180, section 3.2 Phytoplankton composition: I find it encouraging to observe similarities between the CHEMTAX and size-based pigment analysis, as highlighted in Figure 3. While the method of Vidussi et al. (2001), as refined by Uitz et al. (2006), has been used extensively in the literature, further refinements have been published recently such as fucoxanthin adjustments (see Devred et al. 2011 and Hirata et al. 2011), to account for the fact that Fuco is also a precursor for 19HF and 19BT and, therefore, partially attributed to the nanoplankton. Also a pico-eukaryote adjustment (see Brewin et al. 2010; Hirata et al. 2011), to account for the fact that 19HF is also attributed to pico-eukaryotes and therefore partially attributed to the picoplankton at low chl-a concentrations. Would these refinements help to further reconcile the CHEMTAX and size-based pigment analysis?*

AC: We thank the reviewer for pointing out this issue. We have recalculated the size classes fractions with both refined approaches published by Hirata et al (2011) and by Devred et al. (2011) and compared all results – including our old Uitz et al. (2006) calculations - with the CHEMTAX results (on the basis of sum of squared differences, see Fig. 1_rev)). As anticipated by the reviewer, the refined approaches generally compare better to the CHEMTAX results than the Uitz et al (2006) calculation. As the Hirata et al. (2011) approach performed best for pico- and nanoplankton, we used this calculation for our new figure. Figure 3, as well as sections 2.3.1. and 3.2 have been adapted.
The pico-eukaryote adjustment by Brewin et al. (2010) was not applied to our data as it refers to data with chl a concentrations below 0.08 mg m^{-3}, which we did not encounter on this cruise.

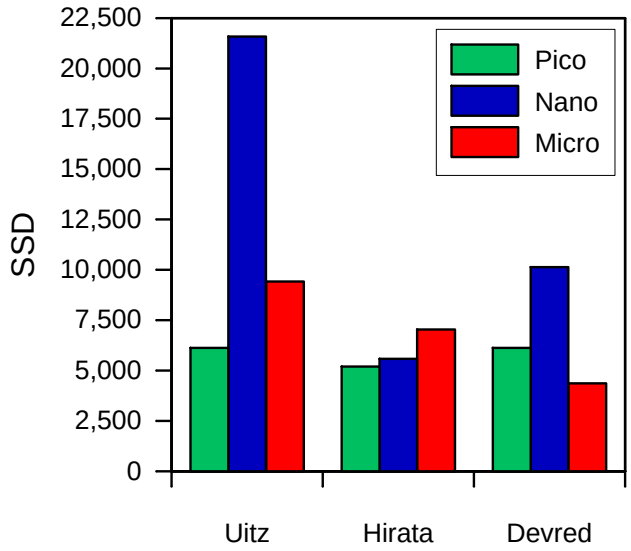

Fig 1_rev2: Sum of squared differences (SSD) between the calculations of phytoplankton size classes after Uitz et al. (2006), Hirata et al. (2011), Devred et al. (2011) and the calculation with CHEMTAX

RC: *In the abstract, it is stated that "This method has the potential to become an automated approach where satellite data could be used to identify shifting boundaries of established ecological provinces" yet there is very limited discussion on this. Can this be achieved using current satellite ocean-colour sensors, or, would this require further advancements in technology, e.g. better hyper-spectral sensors, in consideration of the results shown in Table 5? Could approaches that detect phytoplankton functional groups (PFTs) from satellite offer an additional route? Nothing is mentioned on the current approaches for detecting PFTs from satellite (to name a few, Ciotti and Bricaud 2006; Alvain et al. 2008; Raitsos et al. 2008; Bracher et al. 2009; Kostadinov et al. 2009; Mouw and Yoder 2010; Devred et al. 2011), or*

assessory pigments (e.g. Pan et al. 2011; Hirata et al. 2011), which is surprising given the statement in the abstract. Could this information be used to help map the bio-optical provinces using satellite data?

AC: We have now included this information in the conclusions:

5 Conclusions
Picophytoplankton, and among them specifically the genus Prochlorococcus, are responsible for most of the variability of PFTs in the eastern Atlantic Ocean. Our bio-optical clusters agree well with the established provinces established by Longhurst and thus can be used to classify areas of similar biogeography. However, in areas with high variability, such as along the Canary Current (cluster IV-N and most outliers) or at the NW African upwelling (cluster V) the Longhurst provinces do not harbour consistent phytoplankton assemblages. In such areas it would be advantageous to use a more flexible and dynamic approach, which could consist of a combination of physical and optical measurements, to describe the ecosystem. Since pigment composition corresponded well with the remotely observable aph(?)- and Rrs(?)-spectra at hyperspectral resolution, this method has potential to become an automated approach for the future. Hyperspectral sensors mounted on platforms such as buoys, gliders or satellites could provide the data to identify shifting boundaries of established provinces or to track exceptions from the rule in order to improve our understanding of the biogeochemical cycles in the ocean. Several approaches have already been proposed to detect PFTs from satellite sensors (e.g. Alvain et al., 2008), but only Bracher et al. (2009) used hyperspectral data. However, dominant PFT identification is a slightly different concept than clustering different spatially distributed phytoplankton assemblages. In this study, we used hyperspectral information to identify various phytoplankton groups co-existing at significant concentrations (i.e., non-bloom conditions). The method allowed us to define different bio-optical provinces on the basis of phytoplankton community structure and their bio-optical features, instead of a small set of functional groups. In terms of globally significant issues such as carbon export and primary production our hyperspectral and similarity-based approach represents a possibility for a fast and detailed assessment of the state of a temporally and spatially variable environment. However, before this novel approach can be applied at a global scale, it will be necessary to validate it on larger databases consisting of simultaneous pigment and optical information from more diversified waters.

RC: *The final comparison to the Longhurst's provinces is interesting, and there appears to be cases where the two approaches compliment each other, such as the SATL province, and in cases where there is no clear correlation the authors have explained well possible causes of such discrepancies, for example the static nature of Longhurst's classification and the dynamic nature of certain provinces. Have the authors not thought about comparing with a more bio-optical based province classification, such as a the static classification of Hardman-Mountford et al. (2008) based on Chl-a, or alternatively, the more dynamic fuzzy logic classification of optical water types by Moore et al. (2009).*

AC: We considered other comparisons and read both works and others, but resolved to stay with the comparison with the widely cited Longhurst provinces, which – in the revised version of 2007 – also include satellite chl a measurements and statistical tests. Due to the wide usage of the Longhurst provinces, the maps were easy to obtain, whereas the detailed comparison with small maps in other papers was more difficult. Each of the mentioned approaches used less parameters than we used to identify our provinces and does not work with hyperspectral information, which is a strong point in our work. Our basis is the clustering by pigments, not just bulk chl a, and we use physical parameters such as salinity, temperature and profile information to set our boundaries which brings us closer to the Longhurst approach. However, the referee's comment is valid and we hope can satisfy his requests with the following paragraph which we have added to the end of the discussion:

“It is clear, by the comparison of our clusters and the Longhurst provinces that in some areas a more dynamic approach is needed to do the ecosystem justice. Different approaches based on bio-optical data have been proposed, such as the classification by Hardman-Mountford (2008) based on satellite-derived chlorophyll data or the fuzzy c-means clustering algorithm by Moore et al. (2009) where optical water types are classified by the statistical properties of their associated Rrs(?). It becomes clear that the characterization of provinces in the dynamic marine realm cannot hold true for every season and every year, no matter if it is based on an averaged data set over several years or on the data of one specific year. To define marine provinces and their boundaries in space and time, a method has to be used which involves information of the spatial and temporal parameters in question. Thus, we suggest for the future the application of a cluster analysis to hyperspectral datasets from space once they are available with the simultaneous pigment as our validation tool. The proposed method would be similar to the clustering approach by Devred et al. (2007), who used a combination of optical and physical information to define provinces in the northwest Atlantic, but makes use of hyperspectral resolution data sets.”

Specific comments

RC: *Page 7167, line 1-3: There are in fact a number of satellite models that link the bulk Chl-a distribution to the size structure of the phytoplankton (see Uitz et al. 2006; Hirata et al. 2008; Brewin et al. 2010) and even to the taxonomic groups of phytoplankton (e.g. Hirata et al. 2011)?*

AC: The sentence was removed from the introduction.

RC: *Page 7167, line 7-9: I would suggest adding the Uitz et al. (2006) reference to this list.*

AC: Agreed.

RC: *Page 7168, line 8-9: I am not sure if I would refer to primary production and carbon cycling as measured parameters, I would consider that a parameter is a quantity that relates functions and variables using a common variable. Primary production is a variable, and the partitioning of ocean provinces can help constrain this variable through assigning province-specific parameters that relate to the mathematical function used to estimate primary production.*

AC: The sentence was reworded as follows:
“Partitioning the ocean into provinces can assist us in understanding complex patterns in the oceans and help us to extrapolate province-specific parameters over large spatial scales for a better estimation of global primary production and carbon budget”

RC: *Page 7172, line 12-21, Section 2.2.1 Pigment analysis: How were the pigment data used in the study quality controlled (QC)? Were specific QC methods used (e.g. Aiken et al. 2009)?*

AC: The pigment data was quality controlled according to the process in Aiken et al., 2009. The regression between Tchl a and AP had a slope of 0.928 and r^2=0.98. A sentence about the QC was added to section 2.2.1

RC: *Page 7177, line 7: The word "Spearman" is miss-spelt "Spearmen"*

AC: Corrected

RC: *Page 7179, line 8-9: The sentence needs re-wording (perhaps remove "of surface samples only are shown in" and replace with "for surface samples only".*

AC: Corrected

RC: *How does the analysis shown in figure 3 directly compare to that of Uitz et al. (2006), Brewin et al. (2010) or Hirata et al. (2011) (it would be interesting to use the November Globcolour Chl-a map as input to these satellite models (which are based on Chl-a) to derive a satellite map of the percentages, and map the in situ percentages for each station onto the satellite image, in a similar way to that to that of Figure 8 and 9?)*

AC: We agree with the referee that it would be very interesting to use the Globcolour Chl-a map as input to these satellite models for the space and time of our cruise and we will gladly pursue this for a future work. However, we feel that here, it would exceed the scope of this paper.

RC: *Page 7188, line 24-25: I would suggest adding the reference of Bouman et al. (2007) to this list.*

AC: Agreed.

RC: *Page 7189, line 23: the word "by" is repeated twice consecutively.*

RC: *Page 7198, line 14: The word "presence" is miss-spelt "presnce".*

AC: Both were corrected.