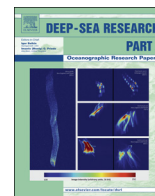




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Chemotaxonomic phytoplankton patterns on the eastern boundary of the Atlantic Ocean



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ABSTRACT

Surface pigment data from a transect along the eastern boundary of the Atlantic Ocean was analysed using CHEMTAX to yield more detailed information on the composition of phytoplankton communities. Total chlorophyll *a* concentrations varied from 0.03 mg m⁻³ in a northern oligotrophic region to 30.3 mg m⁻³ in the Benguela ecosystem. Diatoms dominated the Benguela, while both diatoms and haptophytes were the major groups in the Canary ecosystem and the temperate NE Atlantic. *Prochlorococcus* was the most prominent group in the southern oligotrophic region (15.5°S–15°N) although haptophytes were also a significant component of the population. In contrast, haptophytes dominated the northern oligotrophic region (21°–40°N). Photo-pigment indices indicated that chlorophyll *b* was mainly associated with prasinophytes and chlorophyll *c* with diatoms. Elevated photosynthetic carotenoids were due to increased proportions of haptophytes, but also linked with diatoms and dinoflagellates. Photoprotective carotenoids were more prominently associated with *Prochlorococcus* and to a lesser extent to *Synechococcus*.

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1. Introduction

The Atlantic Meridional Transect programme was initiated to investigate basin-scale variability in physical and biological processes in the Atlantic Ocean (Aiken et al., 2000; Robinson et al., 2006) and research cruises have been undertaken since 1995, mainly between the UK (50°N) and the Falkland Isles (50°S) (Aiken et al., 2009). Most of the cruise tracks have predominated across oligotrophic waters of the northern and southern gyres where TChl_a (total chlorophyll *a*) is < 0.25 mg m⁻³ and flow cytometric analysis demonstrated the dominance of picoprokaryotes (*Prochlorococcus* and *Synechococcus* spp.) and picoeukaryotes (Zubkov et al., 1998, 2000; Heywood et al., 2006; Tarran et al., 2006). Pigment data showed the dominance of divinyl chlorophyll *a* and zeaxanthin that were related to the prokaryotes in these regions (Gibb et al., 2000; Barlow et al., 2002). Pigment biomarkers for nanoeukaryotes were found to be dominant in mesotrophic zones of the Atlantic, while the pigments relating to diatoms and dinoflagellates were noted to be in higher concentrations in temperate

eutrophic waters (Gibb et al., 2000; Barlow et al., 2002; Poulton et al., 2006). Temporal changes in size classes for 2003–2010 indicated that there was an increase in nano- and picoplankton in the northern gyre in autumn despite no change in TChl_a, while there was an increase in TChl_a and picoplankton in the southern gyre in spring (Agirbas et al., 2015).

In 1998, the AMT-6 cruise was undertaken in May–June between Cape Town, South Africa, and the UK, with the purpose of investigating the eutrophic regions of the Benguela and Canary upwelling systems and the end of the spring bloom in the temperate NE Atlantic (Barlow et al., 2002). Barlow et al. (2002) compared phytoplankton pigment and absorption characteristics between the UK–Falklands transect (AMT-3) and the AMT-6 transect, with a focus on vertical patterns. In a companion study, AMT-6 data was used to elucidate pigment adaptations in surface phytoplankton in various regions along the eastern transect (Barlow et al., 2004). Diagnostic indices were derived according to Vidussi et al. (2001) and indicated that microplankton dominated the Benguela, nanoplankton dominated the temperate NE Atlantic, and mixed micro- and nanoplankton communities were present in the Canary region. Picoplankton was the major group in oligotrophic regions (Barlow et al., 2004). Photo-pigment indices indicated varying proportions of the chlorophylls and carotenoids, and whereas the chlorophyll *a* variation within the total pigment

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pool was small, the accessory pigments varied considerably (Barlow et al., 2004).

There has been a considerable increase in knowledge regarding phytoplankton pigments over the previous two decades (Jeffrey et al., 2011), and also in the evolution of statistical techniques such as CHEMTAX that allows more information to be gained regarding the diversity of groups contributing to the phytoplankton biomass (Higgins et al., 2011). The AMT-6 surface pigment data has therefore been reanalysed using CHEMTAX enabling greater detail to be elucidated concerning the phytoplankton groups than was reported by Barlow et al. (2004). This communication presents the results of this reanalysis and the following key questions are addressed: (1) Does a single group dominate in each of the different sectors of the Atlantic Ocean eastern boundary? (2) What was the dominant nano- and/or picoplankton group along the transect? (3) Are the prokaryotes *Prochlorococcus* and *Synechococcus* spp. the most important groups in the oligotrophic regions?

2. Methods

Surface temperature was recorded underway with an SBE thermosalinograph and by CTD on station. Surface seawater was collected from the non-contaminated seawater supply (4 m) every 2 h and from the daily CTD deployment on station, filtered through 25 mm GF/F filters, and filters were stored frozen in liquid nitrogen or in a $-60\text{ }^{\circ}\text{C}$ freezer. On board HPLC analysis of pigments followed the procedures of Barlow et al. (1997, 2004) and calibration was performed with chlorophyll and carotenoid standards (Barlow et al., 2004). Limits of detection were of the order of 0.001 mg m^{-3} .

Pigment data was analysed by CHEMTAX following Higgins et al. (2011), with chemotaxonomic groups being identified according to Jeffrey et al. (2011). Pigment starting ratios were obtained from Higgins et al. (2011) and functional groups included the following: diatoms-1, dinoflagellates-1, cryptophytes, pelagophytes, haptophytes-6, prasinophytes-1, cyanobacteria (*Synechococcus* spp.) and *Prochlorococcus* spp. Although *Prochlorococcus* is also a cyanobacterium, the distinct divinyl chlorophyll *a* signature allows *Prochlorococcus* to be distinguished from *Synechococcus* in the CHEMTAX analysis. An assumption made using CHEMTAX is that the pigment:chlorophyll *a* ratios are constant across all the samples within each analysis. Samples were therefore separated into the 5 regions identified by Barlow et al. (2004) and CHEMTAX was run on the data from each region separately.

CHEMTAX outputs are the fraction of chlorophyll *a* contained in each functional group specified in the matrix. The HPLC method separated monovinyl chlorophyll *a* allomer, monovinyl chlorophyll *a*, monovinyl chlorophyll *a* epimer and chlorophyllide *a*, and in CHEMTAX the sum of all 4 was used as the chlorophyll *a* concentration (Chla). Divinyl chlorophyll *a* was allocated entirely to *Prochlorococcus* spp. TChla was used as an index of phytoplankton biomass and is the sum of chlorophyll *a* plus divinyl chlorophyll *a*. The software may not discover the best global solution if it encounters local minima in the process. To circumvent this possibility, multiple starting points are used. Fifty-nine further pigment ratio tables were generated by multiplying each cell of the initial table by a randomly determined factor *F*, calculated as:

$$F = 1 + S \times (R - 0.5)$$

where *S* is a scaling factor of 0.7, and *R* is a random number between 0 and 1 generated using the Microsoft Excel RAND function. Each of the 60 ratio tables was used as the starting point for a CHEMTAX optimization. The solution with the smallest residual was used for the estimated taxonomic abundance. The optimized

ratios were generally not altered considerably from the starting ratios and compare well with the range of values published in Higgins et al. (2011).

Photo-pigment indices were derived to assess the changing contributions of the chlorophylls and carotenoids to the total pigment pool. The chlorophylls were distinguished as TChla, total chlorophyll *b* (TChlb) and total chlorophyll *c* (TChlc). The photo-synthetic carotenoids (PSC) comprised peridinin, fucoxanthin, 19'-hexanoyloxyfucoxanthin and 19'-butanoyloxyfucoxanthin. Photo-protective carotenoids (PPC) included alloxanthin, diadinoxanthin, diatoxanthin, violaxanthin, zeaxanthin, β,β carotene and β, ϵ carotene (Barlow et al., 2004).

3. Results and discussion

The cruise track in Fig. 1 shows the passage through eutrophic, mesotrophic and oligotrophic waters, while Fig. 2 illustrates the considerable variation in surface temperature, from cool waters in the Benguela and temperate NE Atlantic to warm water in the tropics. The changes in satellite chlorophyll *a* (Fig. 1) and temperature (Fig. 2), together with TChla and accessory pigments enabled 5 major regions to be identified along the transect, as originally identified by Barlow et al. (2004). The boundaries are shown in Fig. 2 and include the Benguela ecosystem (33° – 15.5°S), a southern oligotrophic region (15.5°S – 15°N), the Canary ecosystem (15° – 21°N), a northern oligotrophic region (21° – 40°N) and the temperate NE Atlantic (40° – 50°N).

A large variation in TChla was observed, with elevated TChla in the Benguela, Canary and temperate NE Atlantic, and much lower concentrations in the oligotrophic regions (Fig. 3). Diatoms were dominant in the 3 high biomass regions, except for 2 patches of particularly high TChla in the Benguela (18.8 and 30.6 mg m^{-3}) that was due to domination by dinoflagellates (Fig. 3). Haptophytes appeared to be the next most important group in these regions and it may be noted that cryptophytes and prasinophytes were also prominent in the Benguela, and at 49°N in the NE Atlantic (Fig. 3). The prokaryotes showed some interesting patterns, with *Synechococcus* being significant in the Benguela and Canary regions, while *Prochlorococcus* appeared to be the dominant prokaryote in the oligotrophic regions (Fig. 3).

To facilitate comparisons, the data was averaged for each region and Fig. 4a indicates that the mean TChla was greater for the Benguela compared to the Canary region and the temperate NE Atlantic. Mean TChla was also higher in the southern oligotrophic region than in the northern oligotrophic region (Fig. 4a). The data in Fig. 4a is similar to Fig. 6a in Barlow et al. (2004) and collectively it appears that the eastern boundary of the S Atlantic had higher phytoplankton biomass than the N Atlantic, as also noted by Barlow et al. (2004). The satellite image of chlorophyll *a* (Fig. 1) corroborates this observation.

Barlow et al. (2004) depicted the regional differences of collective micro-, nano- and picophytoplankton only, whereas Fig. 4b indicates more detail of 8 phytoplankton groups in each region. Diatoms were the dominant group in the Benguela and Canary regions (46%) and were co-dominant with haptophytes in the temperate NE Atlantic. Dinoflagellates were significant in the Benguela and the NE Atlantic, but less so in the Canary ecosystem. Haptophytes were the next most significant group after the diatoms in the Benguela, but were much more prominent in the Canary region and the temperate NE Atlantic. Other eukaryote groups were of lesser importance, although cryptophytes contributed 10–14% in the Benguela and temperate NE Atlantic. The southern oligotrophic region was dominated by *Prochlorococcus* (40%) and, unexpectedly, it was observed that the haptophyte proportion (24%) was greater than *Synechococcus* (16%). In

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