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Phytoplankton pigments and functional types in the Atlantic Ocean: A decadal assessment, 1995–2005

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ABSTRACT

The phytoplankton pigment composition (chlorophylls and carotenoids) from 17 Atlantic Meridional Transect (AMT) cruises over the period 1995–2005 was analysed to determine the distributions of pigments and plankton in the Atlantic Ocean between 50°N and 50°S. Data were quality assured by statistical methods, including regression of total chlorophyll *a* (TChla) versus accessory pigments (AP) and comparison of the AMT-TChla with contemporary SeaWiFS-TChla (cruises AMT-05 to -17). Comparisons of province-mean TChla (±SD) for *in situ* and satellite data showed good agreement for each cruise. 'Taxa-specific' pigments were used to define phytoplankton functional types (PFTs) for each of the biogeochemical provinces along the AMT. Pigment ratios (e.g. TChla/AP) were analysed for each cruise and for each province as indices (characteristic properties) of particular PFTs. Mostly robust positive correlations were observed between TChla and pigment ratios for different PFTs, for some provinces and most cruises. These were consistent with previous observations. Generally there were no significant trends of mean TChla or pigment ratios within provinces over the period 1995–2005, although the previously reported perturbation due to the 1997–1998 ENSO was evident.

1. Introduction

The Atlantic Meridional Transect (AMT) programme has completed a decade of observations (1995–2005) through the Atlantic Ocean from approximately 50°N (NW European shelf seas) to 50°S (Falkland Isles, FI) or 35°S (Republic of South Africa, RSA). In total 18 cruises were completed in two phases: AMT-01 to -11, 1995–2000 and AMT-12 to -17, 2003–2005. An overview of phase 1 has been given by Aiken et al. (2000) and phase 2 by Robinson et al. (2006). Fig. 1 shows the cruise tracks and the province boundaries using Longhurst (1998), who used physical and biological data from a range of sources to classify the global ocean into a number of biomes and partitioned these further into biogeochemical provinces, based on topography, patterns of stratification and seasonality. The biomes and provinces sampled on AMT cruises (listed in Fig. 1, using the nomenclature of Longhurst, 1998) were: Atlantic coastal biome (CNRY, BENG, BRAZ and FKLD); Atlantic west wind biome (NADR, NAST-E, -W); Atlantic trade wind biome (NATR, ETRA, WTRA and SATL). In the sub-polar southwest Atlantic, the SSTC, the Falkland Current and shelf were encountered on some cruises. We use SSTC for all provinces at the southern extremes of AMT. The partitioning of the cruise data into provinces was determined from an analysis of the surface water properties, temperature, salinity and density (Hooker et al., 2000) and analyses of the pigment and plankton distributions. Not all provinces were traversed on every cruise, depending on the cruise track and the ports of departure and destination.

The AMT cruise tracks were predominantly across oligotrophic waters between 35°N and 35°S, characterized by low surface nutrient and pigment concentrations (NO_3-N$<0.1\,mmol\,m^{-3}$, TChla$<0.25\,mg\,m^{-3}$) in which the phytoplankton were dominated by pico-prokaryotes (*Synechococcus* and *Prochlorococcus* spp.) and pico-eukaryotes (Zubkov et al., 1998, 2000; Heywood et al., 2006; Tarran et al., 2006). In the mesotrophic zones at mid-latitudes (>35°N/S) nano-eukaryotes, including prymnesiophytes and cryptophytes, were relatively abundant. In eutrophic waters, encountered sporadically in the upwelling boundary regions or convergent zones (CNRY, BENG, SSTC) and under conditions of

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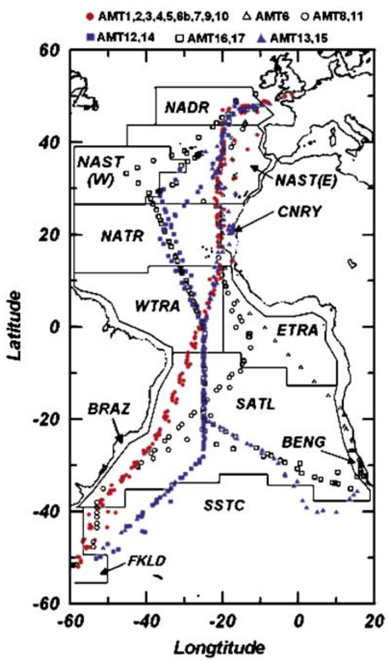

Fig. 1. Cruise tracks and station positions for AMT cruises 01–17 (inc 06b) with the nominal province boundaries as defined by Longhurst (1998): North Atlantic Drift (NADR); North Atlantic Subtropical Gyre (W, E), (NAST-W, -E); North Atlantic Tropical Gyre (NATR); Canary coastal upwelling (CNRY); Western Tropical Atlantic (WTRA); Eastern Tropical Atlantic (ETRA); South Atlantic Gyre (SATL); Brazil current (BRAZ); Benguela current upwelling (BENG); South Subtropical Convergence (SSTC) merged with the Falkland current convergence zone (FKLD).

seasonal stratification at the northern and southern extremes of AMT, the dominant phytoplankton were generally micro-eukaryotes, diatoms and dinoflagellates. TChla and phytoplankton pigment distributions (determined by HPLC) for AMT cruises have been reported previously by Aiken et al. (2000), Gibb et al. (2000), Barlow et al. (2002, 2004) and Poulton et al. (2006) for various sub-sets of the AMT pigment database. In this paper we examine the phytoplankton pigment distributions for 16 of the 17 data sets that passed quality assurance rules. The HPLC analyses were undertaken in several laboratories and differences in analytical techniques and sample storage methods have led to some uncertainty in the quantitative comparability of data between cruises. To minimise uncertainty and improve interpretations, diagnostic pigment ratios were used to derive the dominant phytoplankton functional types (PFTs, Vidussi et al., 2001; Uitz et al., 2006). Table 1 lists symbols and abbreviations for phytoplankton pigments, pigment formulae, taxa and species.

Previous studies have demonstrated direct correlations between bio-optical properties and particular pigment ratios (TChla/TP, TChla/AP, PPC/TC or PPC/PSC) by virtue of their specific absorption and bio-energetic (photosynthetic) properties (Aiken et al., 2004; Fishwick et al., 2006). Research from a seasonal study in the western English Channel (Aiken et al., 2004) and the Atlantic Ocean (Moore et al., 2005; Fishwick et al., 2006) has shown that the ratios TChla/AP or TChla/TP were not constant and increased with biomass, approximated by TChla or TP. Aiken et al. (2004) showed that TChla/TP was generally linearly correlated with photosynthetic quantum efficiency (PQE, measured by Fast Repetition Rate Fluorometry; Kolber et al., 1998), that TChla and TPig were both linearly correlated to phytoplankton carbon (C_{ph}) and the TChla:C_{ph} ratio (inverse of C:Chla) was significantly correlated with TChla/TP and PQE for the spring and summer periods. In the winter period (autumn to mid-winter to spring bloom) when the water column was mixed and nutrients replete, both TChla/TP and PQE were significantly correlated with the total integrated photon flux for the previous day or previous few days, indicating that the system was driven by light in the presence of N-luxury. It was concluded that phytoplankton synthesised TChla preferentially to other pigments or carbon compounds under conditions beneficial to enhanced growth (adequate light and sufficient nutrients, specifically N).

In a study of the Benguela ecosystem (Fishwick et al., 2006; Aiken et al., 2007) the pigments, bio-optical properties and photosynthetic parameters were used to characterise flagellate-dominated stations and microplankton-dominated stations. The discrete ranges of pigment concentrations (TChla or AP), pigment ratios (TChla/TPig or TChla/AP) or photosynthetic parameters (PQE and σ_{PSII}) for the dominant PFTs were used to partition MERIS data for the Benguela into the dominant phytoplankton types (Aiken et al., 2007).

Conventionally marine biologists have categorised phytoplankton types by size: picoplankton ($<2\,\mu$m in diameter), comprising pico-prokaryotes (cyanobacteria, prochlorophytes and other bacteria) and pico-eukaryotes; nanoplankton (2–20 μm), eukaryotic flagellates (cryptophytes, chrysophytes, prymnesiophytes and chlorophytes); microplankton (20–200 μm), diatoms and dinoflagellates; see Table 1. While this partitioning is not based on functional criteria, there is alignment of the functional roles of the phytoplankton with the size categories and the environmental niches (biogeochemical provinces) that they occupy. For their dynamic green ocean model (DGOM) Le Quéré et al. (2005) used 10 plankton functional types: 3 zooplankton, 6 phytoplankton and bacteria. The phytoplankton types were a combination of size and functional types: pico, (pico-autotrophs, prochlorophytes, cyanobacteria, N_2-fixers, pico-eukaryotes); nano, calcifiers (coccolithophores), DMS producers (*Phaeocystis* sp.) and other nano-flagellates; micro, silicifiers (diatoms) and other (dinoflagellates). Their classification focused on the involvement of phytoplankton in air–sea exchange of radiatively active gases and the biogeochemical cycling of C and S, with no inference that other flagellates (cryptophytes) or other microplankton (dinoflagellates) were functionally unimportant.

The conventional size categorisation conforms to a bio-energetic classification based on photosynthetic efficiency: microplankton prosper in high-nutrient environments and have high photosynthetic rates, C-biomass, TChla and TChla/AP; picoplankton survive in very low nutrient environments and have low photosynthetic rates, C-biomass, TChla and TChla/AP; nanoplankton grow in environments with some inorganic nutrients and additional re-cycled nutrients (organic) and have moderate photosynthetic rates, C-biomass, TChla and TChla/AP.

The objectives of this study are:

(1) To assess the quality and comparability of AMT pigment data over the decade 1995–2005.
(2) To examine systematically the distributions of phytoplankton pigments, pigment ratios (as indices of phytoplankton dynamics) and phytoplankton functional types (from diagnostic pigment analyses) within biogeochemical provinces.
(3) To examine temporal trends in pigment concentrations and pigment ratios.

2. Methods and analyses procedures

2.1. Pigment analysis

Phytoplankton pigments were determined by HPLC analysis, using methods reported by Barlow et al. (1997, 2004), largely consistent with the SCOR/UNESCO recommendations (Jeffrey et al., 1997). Water samples (2–4 L) were collected