

Pigment adaptations in surface phytoplankton along the eastern boundary of the Atlantic Ocean

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ABSTRACT: Pigment and ocean colour data were used to characterise the phytoplankton at the surface along an eastern boundary transect of the Atlantic Ocean in May and June 1998. Five major regions were delineated, including the Benguela and Canary upwelling systems off SW and NW Africa, the temperate NE Atlantic, the northern oligotrophic gyre and a southern oligotrophic zone. Diagnostic indices were derived to assess the chemotaxonomic composition of the phytoplankton community, while photo-pigment indices were derived to investigate pigment adaptations across the regions. A large range in chlorophyll *a* concentrations was observed along the transect, varying from 0.03 to 30.6 mg m⁻³. The levels were high in the high productivity regions, with mean concentrations being 3-fold greater in the Benguela region compared to the Canary and temperate NE Atlantic. Chlorophyll *a* levels were low in the oligotrophic regions, but concentrations in the southern oligotrophic region were double those in the northern. Diagnostic indices revealed that microplankton dominated the community in the Benguela region, nanoplankton dominated the temperate NE Atlantic and a mixed community of micro- and nanoplankton were present in the Canary region. Picoplankton comprised the majority of the communities in the 2 oligotrophic regions. Photo-pigment indices indicated that variation in the chlorophyll *a* proportion of total pigments was small, averaging 45% across the transect, but the accessory pigment pool varied considerably. Chlorophyll *c* and photosynthetic carotenoids were prominent in the high productivity regions, resulting in photosynthetic pigments (chlorophylls plus carotenoids) accounting for 87 to 93% of total pigments. In contrast, the level of photoprotective carotenoids was high in oligotrophic regions, resulting in a photosynthetic pigment content of only 68%.

KEY WORDS: Pigment indices · Ocean colour · Atlantic Ocean · Eastern transect

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INTRODUCTION

The oceans play a significant role in influencing global climate through such processes as heat transport and gas exchange with the atmosphere, while the cycling of carbon, in particular, is modulated by the phytoplankton via the mechanisms of photosynthesis and respiration (Aiken et al. 1992). A range of ecosystems of varying trophic status characterises the oceans, and one of the current objectives of marine research is to quantify the variation in phytoplankton biomass and production on basin-wide and global

scales (Maranon et al. 2000). Longhurst et al. (1995) evaluated the large scale patterns in productivity from remotely sensed ocean colour data and promoted the concept of biogeochemical provinces. To further the understanding of basin-scale variability, the Atlantic Meridional Transect (AMT) programme was initiated to investigate the physical and biological processes in the Atlantic Ocean (Aiken et al. 2000). One of the goals of the AMT programme is to improve the knowledge of marine biogeochemical processes, ecosystem dynamics and food webs through comparison of contrasting ecosystems.

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AMT cruises are usually conducted between the United Kingdom (UK) and the Falklands Islands (FI), but one other transect was run between South Africa (SA) and the UK. Previous investigations on the UK–FI transect showed that phytoplankton biomass was elevated in the temperate NE Atlantic, in the NW African (Canary) upwelling region, and in the Brazil–Falklands Current Confluence Zone (BFCCZ), compared to the low biomass in oligotrophic regions (Maranon & Holligan 1999, Maranon et al. 2000). Pigment chemotaxonomic studies revealed that eukaryotic diatoms and nanoflagellates were more abundant in surface waters in the high productivity regions, while cyanobacteria and prochlorophytes dominated the oligotrophic areas (Gibb et al. 2000). Barlow et al. (2002) compared the vertical distribution pattern of pigments between the UK–FI and the UK–SA transects and found that the chlorophyll *a* concentrations in the Benguela upwelling region were twice those in the BFCCZ, with diatoms dominating in the Benguela and nanoflagellates in the BFCCZ. Seasonal differences were observed in the Canary upwelling zone, where chlorophyll *a* levels were twice as high in the upper mixed layer in the spring relative to autumn, and the community was composed mainly of diatoms and nanoflagellates (Barlow et al. 2002).

The major role of chlorophyll *a* in phytoplankton is to absorb light for photosynthesis, but there are additional accessory pigments, the chlorophylls *b* and *c* and various carotenoids, which have a significant function in extending the light-harvesting spectrum in the phytoplankton, thus ensuring optimal absorption efficiencies (Kirk 1994). Other carotenoids, however, serve to protect microalgal cells against the effects of high irradiances that may damage the photosynthetic apparatus, and these pigments may be termed photoprotective carotenoids (Kirk 1994). The ratio of individual accessory pigments to chlorophyll *a* can vary with changes in community composition and physiological state, but the relationship between total accessory pigments and chlorophyll *a* is remarkably robust (Trees et al. 2000). Trees et al. (2000) demonstrated that the ratio of accessory pigments to chlorophyll *a* is constant at 0.934 for a global dataset of 5600 samples covering all trophic levels, with 95% of the variance explained.

Photosynthetic carotenoids are reported to be more prominent in high productivity ecosystems (Barlow et al. 2002), accounting for 80% of total carotenoids (Gibb et al. 2000). On the other hand, photoprotective carotenoids are dominant at the surface in low chlorophyll waters and can be >70% of the carotenoid pool (Gibb et al. 2000). These differences are associated with changes in phytoplankton community structure (Gibb et al. 2000, Trees et al. 2000, Barlow et al. 2002), but can also be due to physiological responses to

changing light and environmental conditions (Trees et al. 2000). In this investigation, the objective was to examine the variability within the total pigment pool, to gain an insight into pigment adaptations in surface phytoplankton between contrasting regions along the eastern boundary of the Atlantic Ocean. Five major regions were identified for comparison over 84° of latitude between South Africa and the UK.

MATERIALS AND METHODS

The AMT-6 cruise was conducted between South Africa and the UK during May and June 1998. Underway near-surface temperature and salinity were recorded with an SBE thermosalinograph, and by the CTD on station. High resolution SeaWiFS (Sea-viewing Wide Field-of-view Sensor) ocean colour images were sent to the ship from NASA Goddard Space Flight Centre each day and these were used to adjust the daily sampling strategy. Post cruise processing and compositing of SeaWiFS data was conducted at the Plymouth Marine Laboratory to produce regional images of pigment distribution using the NASA OC2V2 chlorophyll *a* algorithm (O'Reilly et al. 1998).

Seawater was collected in underway mode every 2 h from the non-contaminated seawater supply (intake at 4 m), and from the daily CTD deployment on station, filtered through 25 mm GF/F filters to harvest the phytoplankton, and filters were stored frozen in a –60°C freezer or in liquid nitrogen. Pigments were extracted in acetone with the aid of ultrasonication and clarified by centrifugation. On board analysis of pigments followed the reverse phase HPLC procedure outlined by Barlow et al. (1997) using a 3 µm Hypersil MOS2 C8 column (100 × 4.6 mm), a Shimadzu HPLC system, a Thermo Separations AS3000 autosampler, a Thermo Separations UV6000 diode array absorbance detector and PC1000 chromatography software. Pigments were detected at 440 and 665 nm, and identified by retention time and on-line diode array spectra. Chlorophyll *a* standard was obtained from Sigma-Aldrich, and divinyl chlorophylls *a* and *b* from R. Bidigare and M. Ondrusek, University of Hawaii. Other pigment standards were purchased from the DHI Institute for Water and Environment, Denmark. The method separates divinyl and monovinyl chlorophyll *a*, zeaxanthin and lutein, and achieves partial separation of divinyl and monovinyl chlorophyll *b*. Limits of detection were of the order of 0.001 mg m⁻³.

Diagnostic pigment indices were derived to assess the composition of phytoplankton communities, following the method of Vidussi et al. (2001). Diagnostic pigments (DP) were defined as the sum of 7 selected biomarker pigments, as given in Table 1. Total chloro-

Table 1. Symbols, names and formulae for chlorophylls, carotenoids, pigment sums and pigment indices

Symbol	Pigment	Formula
Chla	Chlorophyll <i>a</i> (plus allomers and epimers)	
Chlb	Chlorophyll <i>b</i>	
Chlc ₁	Chlorophyll <i>c</i> ₁	
Chlc ₂	Chlorophyll <i>c</i> ₂	
Chlc ₃	Chlorophyll <i>c</i> ₃	
Chlidea	Chlorophyllide <i>a</i>	
DVChla	Divinyl chlorophyll <i>a</i>	
All	Alloxanthin	
But	19'-Butanoyloxyfucoxanthin	
Caro	Carotenes	β,β -Carotene + β,ϵ -Carotene
Diad	Diadinoxanthin	
Diato	Diatoxanthin	
Fuc	Fucoxanthin	
Lut	Lutein	
Hex	19'-Hexanoyloxyfucoxanthin	
Per	Peridinin	
Viol	Violaxanthin	
Zea	Zeaxanthin	
TChla	Total chlorophyll <i>a</i>	Chla + DVChla + Chlidea
TChlc	Total chlorophyll <i>c</i>	Chlc ₁ + Chlc ₂ + Chlc ₃
Chlbc	Sum of chlorophyll <i>b</i> and <i>c</i>	Chlb + TChlc
PPC	Photoprotective carotenoids	All + Caro + Diad + Diato + Lut + Viol + Zea
PSC	Photosynthetic carotenoids	But + Fuc + Hex + Per
TPig	Total pigments	TChla + Chlbc + PPC + PSC
DP	Diagnostic pigments	All + But + Chlb + Fuc + Hex + Per + Zea
DVChla/TChla	Divinyl chlorophyll <i>a</i> to total chlorophyll <i>a</i>	DVChla/TChla
TChla _{TP}	Total chlorophyll <i>a</i> to total pigments	TChla/TPig
Chlb _{TP}	Sum of chlorophyll <i>b</i> and <i>c</i> to total pigments	Chlbc/TPig
TChlc _{TP}	Total chlorophyll <i>c</i> to total pigments	TChlc/TPig
PPC _{TP}	Photoprotective carotenoids to total pigments	PPC/TPig
PSC _{TP}	Photosynthetic carotenoids to total pigments	PSC/TPig
Micro _{DP}	Microplankton proportion of DP	(Fuc + Per)/DP
Nano _{DP}	Nanoplankton proportion of DP	(All + But + Hex)/DP
Pico _{DP}	Picoplankton proportion of DP	(Chlb + Zea)/DP

phyll *a* concentration (TChla) was estimated as the sum of monovinyl chlorophyll *a*, divinyl chlorophyll *a*, chlorophyllide *a*, and chlorophyll *a* allomers and epimers. A linear regression between DP and TChla showed a significant relationship ($r^2 = 0.97$, $n = 284$, $p < 0.01$), indicating that DP is also a valid estimate of phytoplankton biomass. Three major phytoplankton groups were characterised, namely microplankton, nanoplankton and picoplankton, following the criteria of Vidussi et al. (2001). The indices symbolising these groups were designated Micro_{DP}, Nano_{DP} and Pico_{DP} respectively, and the proportion of each group contributing to the biomass was defined as given in Table 1. The microplankton consisted of diatoms (Fuc) and dinoflagellates (Per), the nanoplankton of golden-brown flagellates (Hex, But) and cryptophytes (All), while the picoplankton comprised the cyanobacteria plus prochlorophytes (Zea) and green flagellates (Chlb).

The identified groups do not conform strictly to the actual size of the phytoplankton, based on size-

fractionated sampling, but oligotrophic samples contain a high level of zeaxanthin, where cyanobacteria and prochlorophytes are $< 2 \mu\text{m}$ (Moore et al. 1995, Jeffrey & Vesik 1997), with a smaller contribution from Chlb. Simon et al. (1994) demonstrated that a wide variety of picoflagellates isolated from the tropical NE Atlantic contain Chlb, and Jeffrey (1976) was the first to report the extensive occurrence of Chlb in oligotrophic Pacific waters. The grouping of cyanobacteria, prochlorophytes and green flagellates in the picoplankton group is therefore appropriate. Although the golden-brown flagellates (Hex, But) can comprise both pico- and nanoflagellates (Jeffrey & Vesik 1997), nanoflagellates were more abundant along the transect. This observation was based on the considerably greater concentration of Hex compared to But, and that Hex-containing flagellates are mostly in the nanoplankton range of 2 to 20 μm (Jeffrey & Vesik 1997). Alloxanthin was generally detected in high productivity waters, and since cryptophytes are 6 to 20 μm in size (Jeffrey & Vesik 1997), it is relevant to

include them in the nanoplankton group. Diatoms and dinoflagellates span a wide range in size from 5 to 200 μm (Jeffrey & Vesik 1997), and small cells can dominate in many regions of the world ocean. However, microscopic observations during the cruise revealed that although there were small diatoms and dinoflagellates present in seawater samples, large cells $>20 \mu\text{m}$ occurred in greater abundance, especially in the Benguela and Canary upwelling ecosystems, and the temperate NE Atlantic. No extensive microscopic analysis of phytoplankton was undertaken within the cruise programme and only selected qualitative observations were done on board. Since large cells occurred in greater abundance than small cells, fucoxanthin and peridinin were allocated to the microplankton group.

Photo-pigment indices were derived to assess the changing contribution of chlorophylls and carotenoids to the total pigment pool. The chlorophylls were proportioned into TChla and the sum of chlorophyll *b* plus chlorophyll *c*'s (Chlbc). The carotenoids were identified as the photosynthetic carotenoids (PSC) and the photoprotective carotenoids (PPC). The 4 photo-pigment indices were symbolised as TChla_{TP}, Chlbc_{TP}, PSC_{TP} and PPC_{TP}, and defined as given in Table 1. The carotenes were included in the photoprotective pool, but while β,β -carotene is a non-photosynthetic pigment in eukaryotes (Porra et al. 1997), β,β -carotene and β,ϵ -carotene are considered to be photosynthetic carotenoids in cyanobacteria (Kana et al. 1988, Moore et al. 1995). Photoprotective and photosynthetic carotenes were not distinguished in this study and, therefore, the PPC_{TP} index may be overestimated (and the PSC_{TP} index underestimated) when cyanobacteria are abundant in oligotrophic waters. Zeaxanthin is, however, the dominant photoprotective pigment in cyanobacteria (Moore et al. 1995) and the contribution of carotenes to the PPC was estimated to be 11.2% in oligotrophic regions and 15.1% in meso- and eutrophic regions. The diagnostic indices reveal that picoplankton accounted for an overall mean of 55% of DP in oligotrophic waters and, therefore, the PPC_{TP} index was overestimated by 6.2%.

RESULTS

Hydrography and satellite ocean colour

The cruise track from South Africa to the United Kingdom is shown in Fig. 1. Temperature and salinity (Fig. 2) varied considerably along the transect, with cool (13 to 16°C), low salinity waters (34.5 to 35.1) being monitored in the southern Benguela (34 to 25°S). In the northern Benguela (25 to 15.5°S) and

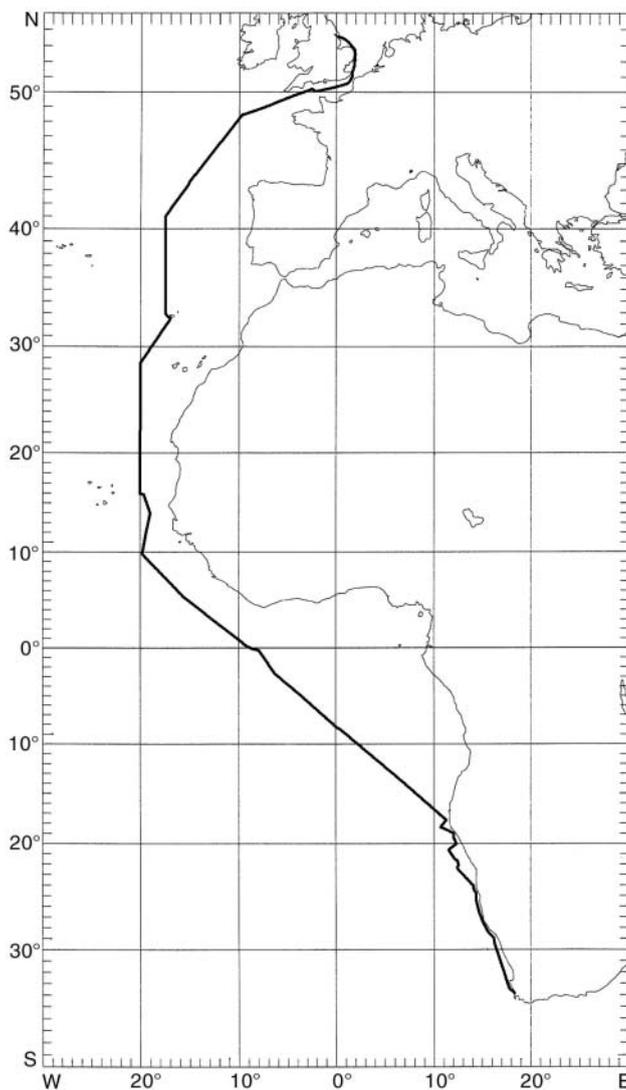


Fig. 1. Cruise track along the eastern boundary of the Atlantic Ocean in May–June 1998

through to 12°S, the temperature and salinity increased concomitantly to ca. 26°C and 36.7, respectively. In the equatorial zone (12°S to 20°N), excessive precipitation led to a significant fall in surface salinity to 2 minima at 8°S (34.7) and at 2 to 7°N (34.4, North Equatorial Counter Current), with a maximum on the equator (35.5) due to equatorial upwelling. Temperature increased steadily from 12°S latitude to reach a maximum of 29°C between 2 and 10°N, except for a minimum (25.6°C) corresponding to the equatorial upwelling. Northwards, temperature declined from 10°N latitude and salinity remained approximately constant to latitude 21°N. At 21°N, there was a marked increase in salinity and an increase in temperature, indicating the occurrence of a front at the inter-

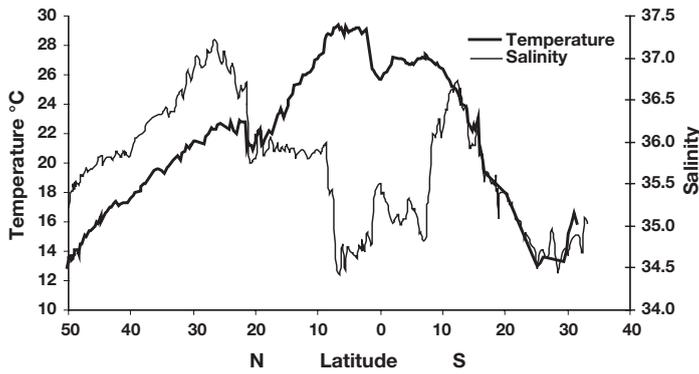


Fig. 2. Surface temperature and salinity along the eastern transect

face between upwelled and oligotrophic water masses. Thereafter (25 to 50°N), temperature and salinity declined concomitantly, consistent with a conservative evaporation-precipitation relationship typical of the sub-tropical and temperate zones.

Fig. 3 shows composite SeaWiFS images of chlorophyll *a* distribution for the NE Atlantic and the Benguela and Canary upwelling regions for May and June 1998. The end of the phytoplankton spring bloom in the temperate NE Atlantic in June 1998 is depicted in the chlorophyll *a* image in Fig. 3a. The image covers a large area and shows the extensive phytoplankton distribution from 44°N through to 51–52°N, and the patchy nature of the distribution pattern. The chlorophyll *a* image for NW Africa indicated the effects of upwelling in this region during spring, with elevated pigment levels extending for at least 7° of longitude (16 to 23°W), and the variations illustrate the patchy nature of the phytoplankton distribution (Fig. 3b). The sharp front at 21°N demarcated the boundary between the productive upwelling waters and the oligotrophic gyre in the tropical NE Atlantic. A wide band of high chlorophyll *a* was present along the SW African coast, extending for a considerable distance offshore (Fig. 3c), and the image reveals distinct, convoluted boundaries between eutrophic waters and the offshore oligotrophic water masses. The images highlight the contrast between the relatively high chlorophyll *a* concentrations (5.0 to 30.0 mg m⁻³) in upwelling and temperate regions, compared to the low levels in oligotrophic waters (0.06 to 0.2 mg m⁻³).

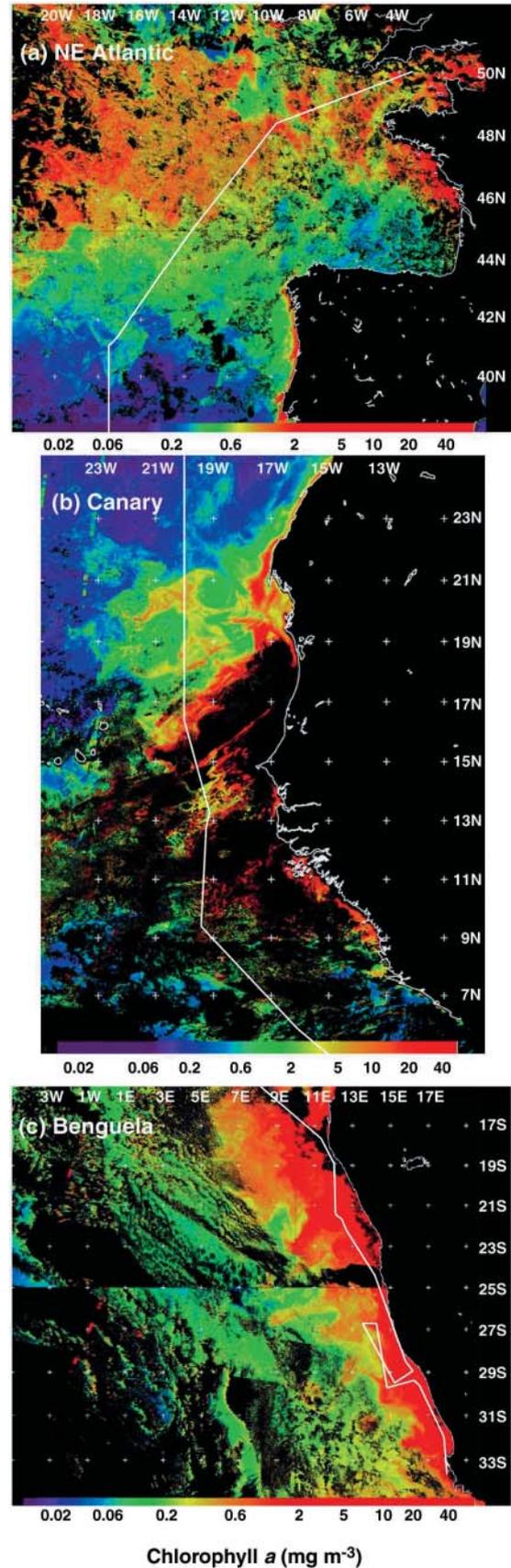


Fig. 3. Chlorophyll *a* concentration for (a) the NE Atlantic, (b) the Canary upwelling system, and (c) the Benguela ecosystem, as observed by SeaWiFS in May–June 1998. Note that the scaling is logarithmic and the scales are different in (a), (b) and (c)

Pigment indices

Five major regions were identified across the transect, with the purpose of evaluating inter-regional differences. Boundaries for each region were assessed from the changes in TChla and photo-pigment indices (Figs. 4 & 5). The Benguela upwelling region (34 to 15.5°S) was designated as a high TChla region ($>0.4 \text{ mg m}^{-3}$, Fig. 4a) where divinyl chlorophyll *a* (DVChla) levels were below the detection limit (Fig. 4b), while the southern oligotrophic region

(15.5°S to 15°N) was characterised by low TChla levels ($<0.4 \text{ mg m}^{-3}$, Fig. 4a) and elevated PSC_{TP} indices (Fig. 5b). The Canary upwelling region was bounded at 15°N, where TChla and PSC_{TP} increased, and at 21°N, where TChla and PSC_{TP} declined sharply across a front (Figs. 4a & 5b). The northern oligotrophic region (21 to 40°N) contained low TChla levels ($<0.4 \text{ mg m}^{-3}$, Fig. 4a) and elevated PSC_{TP} indices (Fig. 5b), and the temperate NE Atlantic region (40 to 50°N) was characterised by elevated TChla concentrations (Fig. 4a) and PSC_{TP} indices (Fig. 5b).

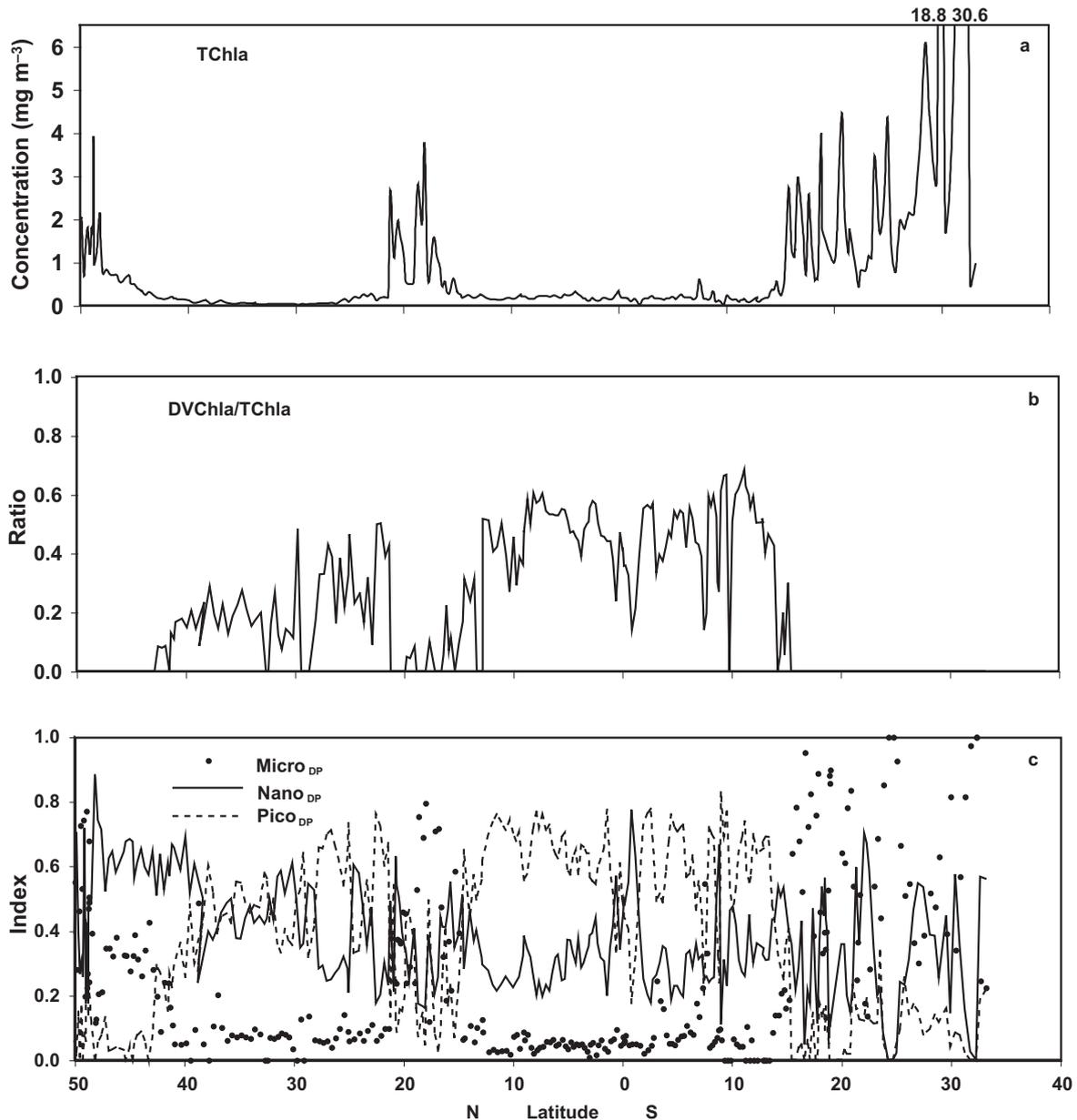


Fig. 4. (a) Surface TChla concentrations, (b) DVChla/TChla ratios, and (c) diagnostic indices, along the transect. Panel (a) has an expanded scale along the y-axis and the numbers indicate concentrations at the off-scale peak heights. See Table 1 for abbreviations

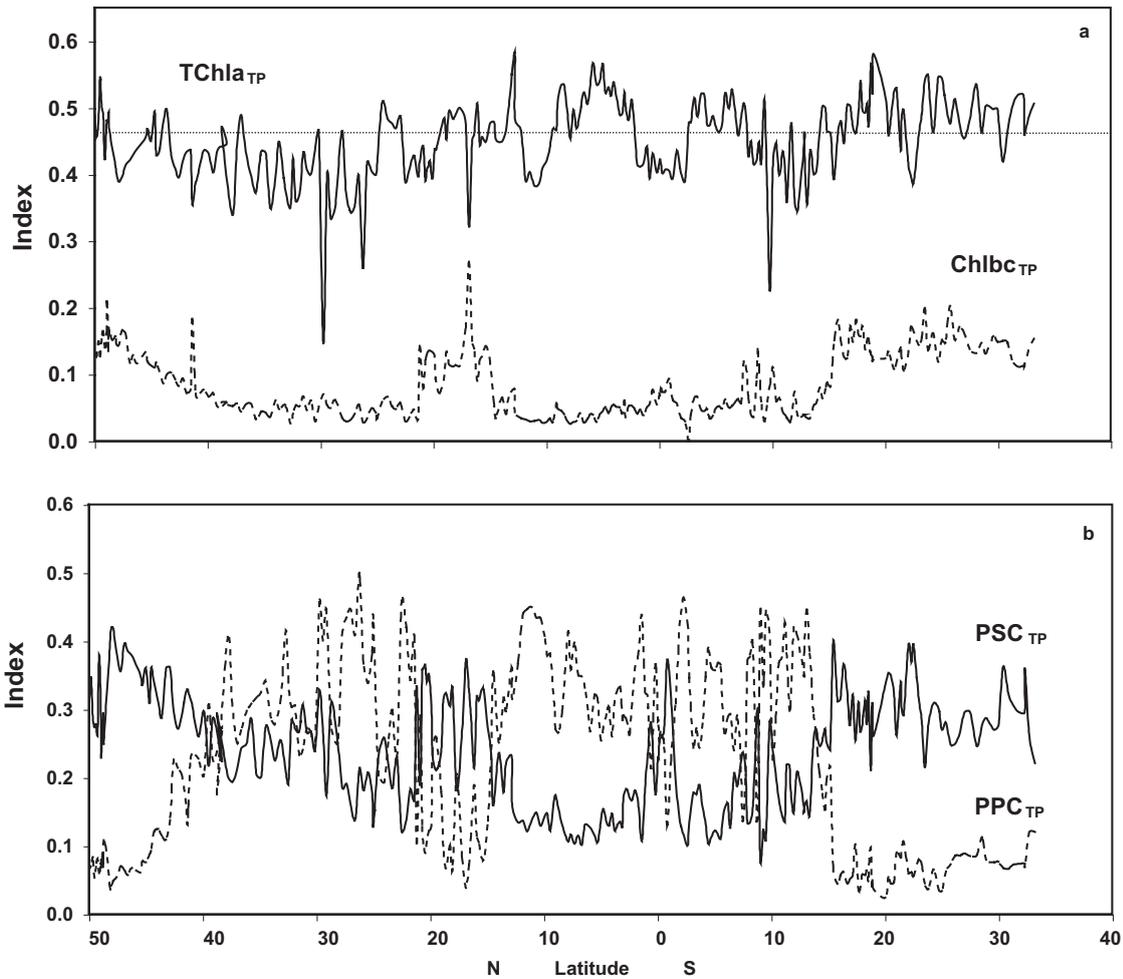


Fig. 5. Variations in photo-pigment indices along the transect in May–June 1998. (a) TChla_{TP} and Chlbc_{TP}, (b) PSC_{TP} and PPC_{TP}. Horizontal dotted line in (a) is the mean of all TChla values. See Table 1 for abbreviations

Fig. 4a shows the changing pattern of TChla along the transect in May and June 1998. Elevated TChla levels were observed in the 3 high productivity regions, but the considerable variation in concentration demonstrated the highly patchy nature of the phytoplankton distribution. Two very high chlorophyll patches were sampled in the southern Benguela with concentrations of 18.8 and 30.6 mg m⁻³ (Fig. 4a). Very low levels were recorded in the NE Atlantic gyre (21 to 40°N; <0.2 mg m⁻³), while TChla in the southern oligotrophic zone (15°S to 15°N) was greater at 0.2 to 0.4 mg m⁻³. An assessment of the divinyl chlorophyll *a* (DVChla) contribution to TChla is illustrated in Fig. 4b. DVChla was below the detection limit throughout the Benguela ecosystem and in the temperate NE Atlantic from 43 to 50°S. Low DVChla/TChla ratios were observed at 15 to 21°N, while the highest ratios were determined for the oligotrophic waters between 15.5°S and 15°N (up to 0.68). Ratios were lower in the NE

Atlantic gyre and declined towards the northern latitudes (Fig. 4b).

The variation in diagnostic indices revealed that microplankton (Micro_{DP}) dominated the phytoplankton in the Benguela ecosystem (Fig. 4c), where elevated fucoxanthin concentrations indicated that diatoms were generally the most important class. The 2 high chlorophyll patches in the southern Benguela at 29°S and 31°S were due to the presence of dinoflagellates, as indicated by high concentrations of peridinin. Microplankton were also significant off NW Africa (15 to 21°N) and in the temperate NE Atlantic (40 to 50°N), generally due to diatoms since peridinin concentrations were low. Nanoplankton (Nano_{DP}) were ubiquitous throughout the transect, being significant in all regions, and there was an increasing trend in the Nano_{DP} index from the southern to the northern latitudes, with nanoplankton dominating the community in the temperate NE Atlantic (40 to 48°N) (Fig. 4c). The

Pico_{DP} indices were low in the Benguela and temperate NE Atlantic, variable off NW Africa, but high in oligotrophic waters at latitudes 15.5° S to 15° N and 21 to 40° N (Fig. 4c). The picoplankton in the Benguela and the temperate NE Atlantic most probably consisted of the cyanobacterium *Synechococcus* sp., as only zeaxanthin was detected. The picoplankton most likely comprised both *Synechococcus* and *Prochlorococcus* between 15.5° S and 40° N, where both zeaxanthin and DVChla were detected.

There was a concomitant variability in photopigment indices with the change in community structure along the transect. The TChla_{TP} index (Fig. 5a) varied between 0.35 and 0.55, but no particular trend was associated with any region. Chlbc_{TP} indices were generally in the range 0.05 to 0.2, but were greater in the high productivity regions relative to the oligotrophic regions (Fig. 5a). Chlorophyll *b* levels were low

throughout the transect and the variability in Chlbc_{TP} indices was due to changes in chlorophyll *c* concentrations. The PSC_{TP} and PPC_{TP} indices showed distinctive regional differences. PSC_{TP} was elevated in the 3 high productivity regions, while PPC_{TP} indices were high in oligotrophic waters, except at the equator, where PPC_{TP} indices decreased as PSP_{TP} increased (Fig. 5b).

A comparison of regional differences across the transect was facilitated by averaging the data in each region (Fig. 6). The mean TChla for the Benguela region (3.59 mg m⁻³) was 3 times greater than the mean concentrations for the Canary (1.32 mg m⁻³) and temperate NE Atlantic (0.97 mg m⁻³) regions (Fig. 6a). Mean TChla was twice as high for the southern oligotrophic region (0.19 mg m⁻³) compared to the northern oligotrophic region (0.08 mg m⁻³). These comparisons suggest that the eastern boundary regions of the S Atlantic are more productive than the N Atlantic in

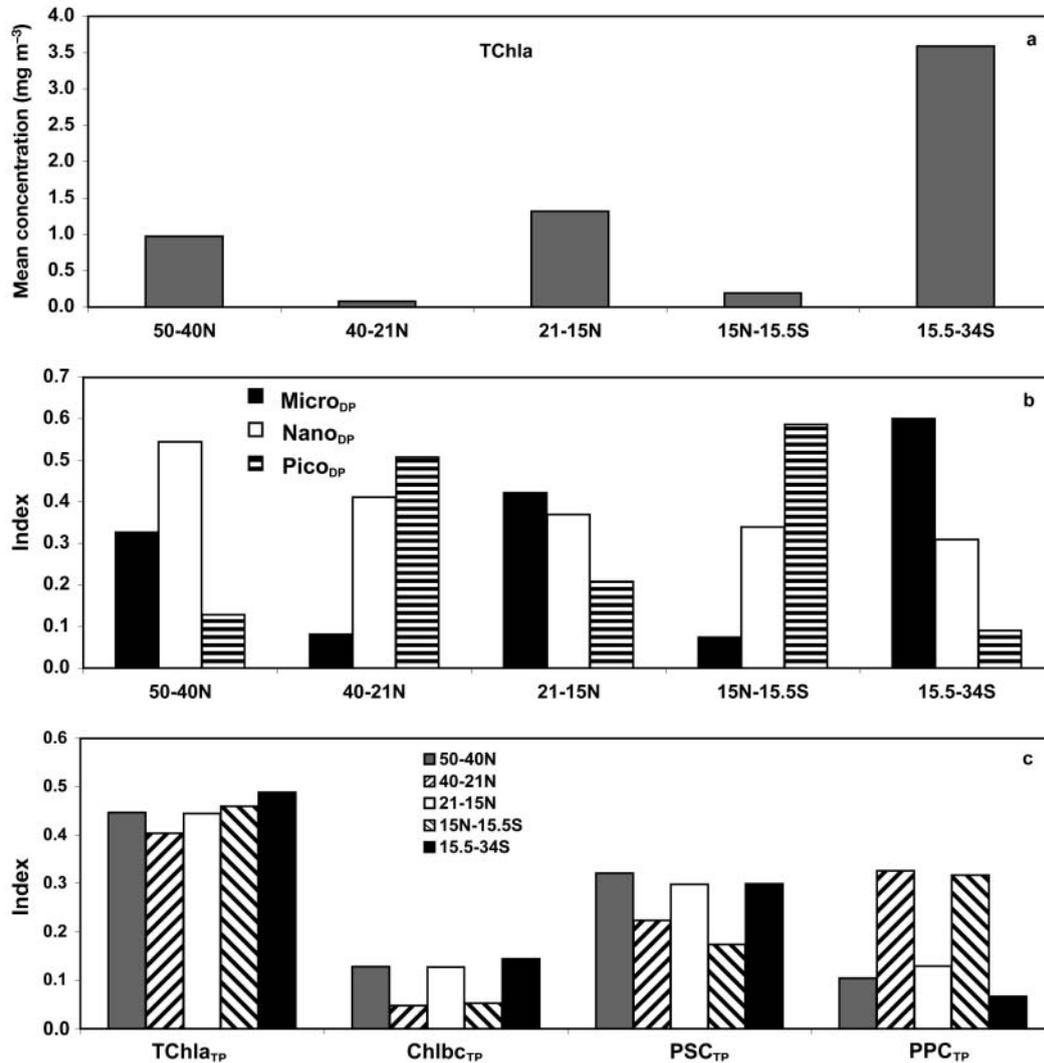


Fig. 6. (a) Mean TChla concentrations, (b) diagnostic indices, and (c) photo-pigment indices for 5 regions along the transect. See Table 1 for abbreviations

May and June, but a comprehensive analysis of mesoscale satellite data would be required to prove this hypothesis.

The mean diagnostic indices indicated the contrasting dominance of microplankton (Micro_{DP}) in the Benguela ecosystem and picoplankton (Pico_{DP}) in the southern oligotrophic region (Fig. 6b). The proportions of micro- and nanoplankton (Micro_{DP} , Nano_{DP}) were similar off NW Africa, although the picoplankton proportion was also significant. Picoplankton (Pico_{DP}) were the most abundant group between 21 and 40° N, together with the nanoplankton, while Nano_{DP} indices were the highest for the whole transect in the temperate NE Atlantic (Fig. 6b). The mean photo-pigment TChla_{TP} index showed only small differences between regions, with the index tending to be slightly greater in the 2 southern regions (Fig. 6c). A statistical test (t -test) comparing all 5 regions gave a transect average, and a 95 % confidence interval, of 0.449 ± 0.027 for TChla_{TP} . In contrast, the other photo-pigment indices varied considerably. Chlbc_{TP} and PSC_{TP} were elevated in the 3 high productivity regions, whereas PPC_{TP} was high in the oligotrophic regions compared to the productive regions (Fig. 6c). The transect averages, and 95 % con-

fidence intervals, for the Chlbc_{TP} , PSC_{TP} and PPC_{TP} indices were 0.100 ± 0.040 , 0.264 ± 0.054 and 0.189 ± 0.108 , respectively.

These differences in the composition of the total pigment pool were further explored by examining the relationships between photo-pigment indices and TChla . For this purpose, TChla was used as an indicator of biomass and trophic division between oligotrophic and meso- plus eutrophic regions, where oligotrophic regions were designated as water masses with TChla of $<0.4 \text{ mg m}^{-3}$. Although the variables in the plotted relationships (Fig. 7) are not strictly independent, the plots are useful for illustrating trends and no regression statistics have been determined. There was considerable scatter in the plot of TChla_{TP} as a function of TChla for concentrations up to 5 mg m^{-3} , but the variation in the index for oligotrophic regions was similar to that for meso- and eutrophic waters (Fig. 7a). In contrast, Chlbc_{TP} indices were very low in oligotrophic waters and 2 to 3 times greater in meso- and eutrophic waters (Fig. 7b). Similarly, the PSC_{TP} index tended to be higher in meso- and eutrophic waters compared to oligotrophic regions (Fig. 7c). PPC_{TP} indices, on the other hand, were very low in

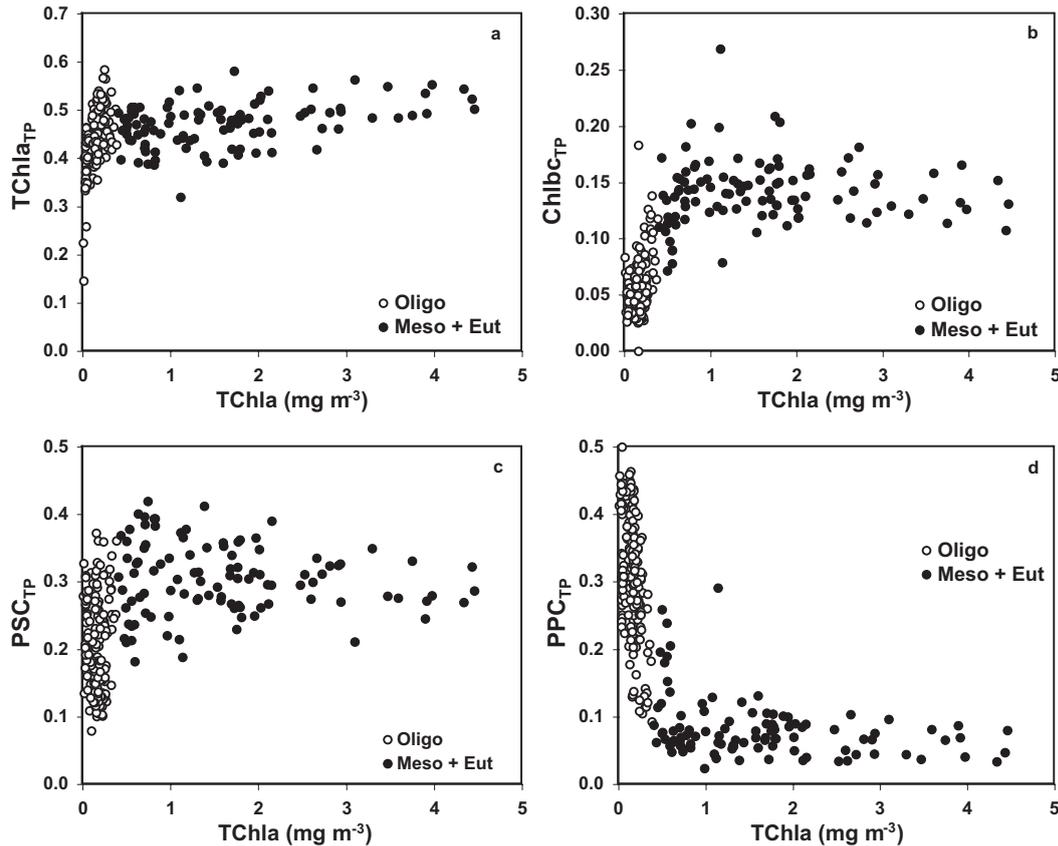


Fig. 7. Regression plots of (a) TChla_{TP} , (b) Chlbc_{TP} , (c) PSC_{TP} , and (d) PPC_{TP} , versus TChla concentration. Oligo and Meso + Eut indicate oligotrophic, and mesotrophic plus eutrophic water masses, respectively. See Table 1 for abbreviations

meso- and eutrophic waters and high in oligotrophic regions (Fig. 7d). The significance of these differences is discussed below.

DISCUSSION

Community structure

The data presented here highlight the variation in surface phytoplankton biomass and pigment composition in 5 major regions across 84° of latitude along the eastern boundary of the Atlantic Ocean. Phytoplankton biomass on the cruise track was much greater in the Benguela ecosystem than in the Canary system (Fig. 6a), and this may be attributed to the positioning of the track (Fig. 1). An inshore track, 30 to 100 km from the coast, was purposely chosen for the Benguela region so as to conduct measurements in high biomass waters (up to 30 mg m⁻³, Fig. 4a). Due to logistical constraints, however, the vessel had to sail offshore in the vicinity of 20° W longitude through the Canary region (300 to 400 km offshore, Fig. 1), where there was lower phytoplankton biomass. TChla concentrations of up to 4 mg m⁻³ (Fig. 4a) were similar to those observed by Babin et al. (1996) at 20.5° N, 18.6° W. If measurements had been conducted closer inshore to the west African coast, it is likely that high biomass waters, comparable to the Benguela, would have been encountered, as Morel (1982) and Howe (1982) have reported TChla values up to 18 mg m⁻³ off Mauritania.

There were notable differences in phytoplankton community structure between the Benguela and Canary upwelling ecosystems. The Benguela was dominated by microphytoplankton (60%), and nano- and picophytoplankton were of secondary and minor importance (Fig. 6b). In contrast, the Canary community consisted of 42% microplankton and 37% nanoplankton, with a significant 21% contribution by picoplankton. These differences may possibly be due to the nutrient status of the water masses. Barlow et al. (2002) reported nitrate levels of 10 to 20 µM in the upper 20 m in the Benguela during AMT-6 and this, together with the high TChla concentrations, indicated eutrophic conditions leading to the dominance by microplankton. Nitrate levels were considerably lower at 1.5 µM in the upper 20 m in the Canary region (Barlow et al. 2002), indicating that the water masses were tending towards mesotrophic conditions at the edge of the upwelling zone, conducive to a more diverse phytoplankton community. Similar observations of low nitrate levels and mixed micro-, nano- and picophytoplankton populations were made by Babin et al. (1996) and Lazzara et al. (1996) at a mesotrophic site in the Canary ecosystem.

Surface biomass levels in the southern oligotrophic region (15.5° S to 15° N) were greater than in the NE Atlantic gyre (21 to 40° N, Fig. 6a), and there were also some differences in community composition. Picoplankton were the dominant group in the southern oligotrophic region (59%), whereas a lower picoplankton proportion (51%), together with nanoplankton (41%), accounted for most of the biomass in the northern oligotrophic region (Fig. 6b). Varying environmental conditions may possibly account for these differences. Barlow et al. (2002) have shown that the euphotic zone, nitraclines and subsurface chlorophyll maxima tend to be shallower in the southern region (~40 m) than the northern region (~150 m). DVChla and zeaxanthin concentrations were about 0.1 mg m⁻³ in the shallow euphotic zones in the south, compared to levels of 0 to 0.05 mg m⁻³ in the deep euphotic zones in the north. It appears that the prokaryote cells exploit a more readily available supply of micronutrients in the shallower nitracline waters in the southern region, leading to an elevation in phytoplankton biomass relative to the north.

These observations for the eastern Atlantic are consistent with other investigations in various sectors of the world ocean. Latasa & Bidigare (1998) and Barlow et al. (1999) reported the presence of diatomnanoflagellate communities in upwelled waters in the Arabian Sea in response to monsoonal activity, and the dominance of the picophytoplankton in oligotrophic, low chlorophyll waters towards the equator. A transect study across the north Pacific by Ondrusek et al. (1991) revealed the dominance of diatoms (fucoxanthin) in nitrate-rich coastal waters, with cyanobacterial dominance (zeaxanthin) in nitrate-poor mid-ocean regions. The importance of the cyanobacteria and nanoflagellates in tropical and sub-tropical waters has been confirmed in a number of other investigations, as noted by Letelier et al. (1993), Claustre & Marty (1995), Bidigare & Ondrusek (1996), Mackey et al. (1998) and Goericke et al. (2000).

DVChla is an exclusive biomarker of prochlorophytes (Goericke & Repeta 1993), and the significance of DVChla in the Atlantic Ocean has been discussed extensively by Gibb et al. (2000, 2001). In this study, the contribution of prochlorophytes to TChla was generally <20% in the Canary region, while the average contribution was 30% at 20 to 30° N, and 20% between 30 and 43° N (Fig. 4b). The proportion in the southern oligotrophic region was much greater, however, averaging about 50%, but proportions >60% and up to 68% were observed between 11° S and 9° N (Fig. 4b). Thus, prochlorophytes appear to be the most important component of the phytoplankton community in surface waters of the southern oligotrophic region in May and June 1998. Gibb et al. (2000) reported similar high pro-

portions of prochlorophytes off Brazil, and collectively, these studies suggest that there is a consistency of high prochlorophyte biomass in surface oligotrophic waters along both the eastern and western boundaries of the South Atlantic.

Pigment adaptation

As discussed above, phytoplankton displays the unique ability of changing the structure of the community to adapt to changing environmental conditions (Gibb et al. 2000, Trees et al. 2000), and this influences the variation in pigment composition across the 5 regions. Chlorophyll *a* is the major pigment in phytoplankton, but the inter-regional differences in the TChl*a* proportion was small, ranging from 40 to 49% (Table 2), and overall TChl*a*_{TP} tended to be similar in oligo-, meso- and eutrophic waters (Fig. 7a), averaging 45%. The chlorophyll *a* proportion of the total pigments in surface phytoplankton appears to be highly conserved, as implied by Trees et al. (2000) through accessory pigment versus chlorophyll *a* relationships, and this means that the accessory pigments play an important role in adaptive strategies. The substantial elevation in the Chl*bc*_{TP} index in meso- and eutrophic waters (Fig. 7b), indicated that the accessory chlorophylls *b* and *c* were greater in the Benguela, Canary and temperate NE Atlantic regions, thereby increasing the total chlorophyll proportion to 57–63% in these ecosystems (Table 2). Chlorophylls *a*, *b* and *c* appear, therefore, to perform the major light-harvesting role in high productivity regions, and the Benguela region was particularly noteworthy as the total chlorophyll pool was significantly higher at 63% than in the other regions (Table 2). The total chlorophyll pool in the oligotrophic regions was lower at 45 to 51%, as a consequence of a very low contribution by the accessory chlorophylls (Table 2). This chlorophyll proportion was twice that of the photosynthetic carotenoids, however, indicating that the chlorophylls were also the key light-harvesting pigments in low productivity waters.

Table 2. Mean proportional contribution (%) of each photo-pigment group to the total pigment pool in each region. PSC: photosynthetic carotenoids; PPC: photoprotective carotenoids

Region	Total Chl <i>a</i>	Chl <i>b</i> and <i>c</i>	Total chlorophylls	PSC	PPC	Total carotenoids
50–40° N	44.7	12.8	57.5	32.1	10.4	42.5
40–21° N	40.4	4.7	45.1	22.4	32.5	54.9
21–15° N	44.5	12.7	57.2	29.9	12.9	42.8
15° N–15.5° S	46.0	5.2	51.2	17.3	31.5	48.8
15.5–34° S	48.9	14.4	63.3	30.0	6.7	36.7

The PSC_{TP} index was elevated in meso- and eutrophic waters (Fig. 7c), yielding photosynthetic carotenoid proportions of 30–32% in the high productivity regions, relative to 17–22% for oligotrophic waters (Table 2). In contrast, the PPC_{TP} index was very low in meso- and eutrophic waters and substantially greater in oligotrophic waters (Fig. 7d), resulting in photoprotective carotenoid proportions of 7–13% in the productive regions, but 32% in oligotrophic regions (Table 2). The total carotenoid pool was, therefore, significantly greater at 49–55% in the oligotrophic regions, as opposed to 37–43% in the Benguela, Canary and temperate NE Atlantic regions. These observations reveal that carotenoids tend to have a more important role in oligotrophic waters, mainly in a photoprotective capacity. This is well documented in other studies by Babin et al. (1996), Lazzara et al. (1996) and Gibb et al. (2000) for the tropical Atlantic, by Allali et al. (1997) for the subequatorial Pacific, and by Stuart et al. (1998) and Sathyendranath et al. (1999) for the Arabian Sea.

Accessory pigment change in relation to phytoplankton structure is explored further in the relationships in Fig. 8. Although the variables are not strictly independent, the plots are useful for indicating trends. The total chlorophyll *c* (TChl*c*_{TP}) and PSC_{TP} indices increased concomitantly with an increase in the Micro_{DP} index (Fig. 8a,b), indicating that diatoms and dinoflagellates increased the proportion of chlorophyll *c* and photosynthetic carotenoids to optimise their light-harvesting capability. This was corroborated by Stuart et al. (1998) and Barlow et al. (2002) who showed that absorption at 440 nm in diatom-dominated communities is due to chlorophylls *a* and *c*, and at 490 nm to photosynthetic carotenoids. The increase in PSC_{TP} with Nano_{DP} (Fig. 8c) suggests that photosynthetic carotenoids play an important light-harvesting role in nanoflagellate populations, while the concomitant increase in PPC_{TP} with Pico_{DP} (Fig. 8d) confirms the high photoprotective carotenoid content in picoplankton. This high PPC content reduced the photosynthetic chlorophyll and carotenoid pool to a mean of 68% in picoplankton-dominated communities

(40 to 21° N, 15° N to 15.5° S). Where microplankton and/or nanoplankton dominated, the photosynthetic pigment pool was 93%, 87% and 90% in the Benguela, Canary and temperate NE Atlantic regions, respectively. This high photosynthetic pigment content may partially explain the elevated productivity in these regions compared to the low productivity in oligotrophic waters. The suggestion by Sosik & Mitchell (1995) and Babin et al. (1996)

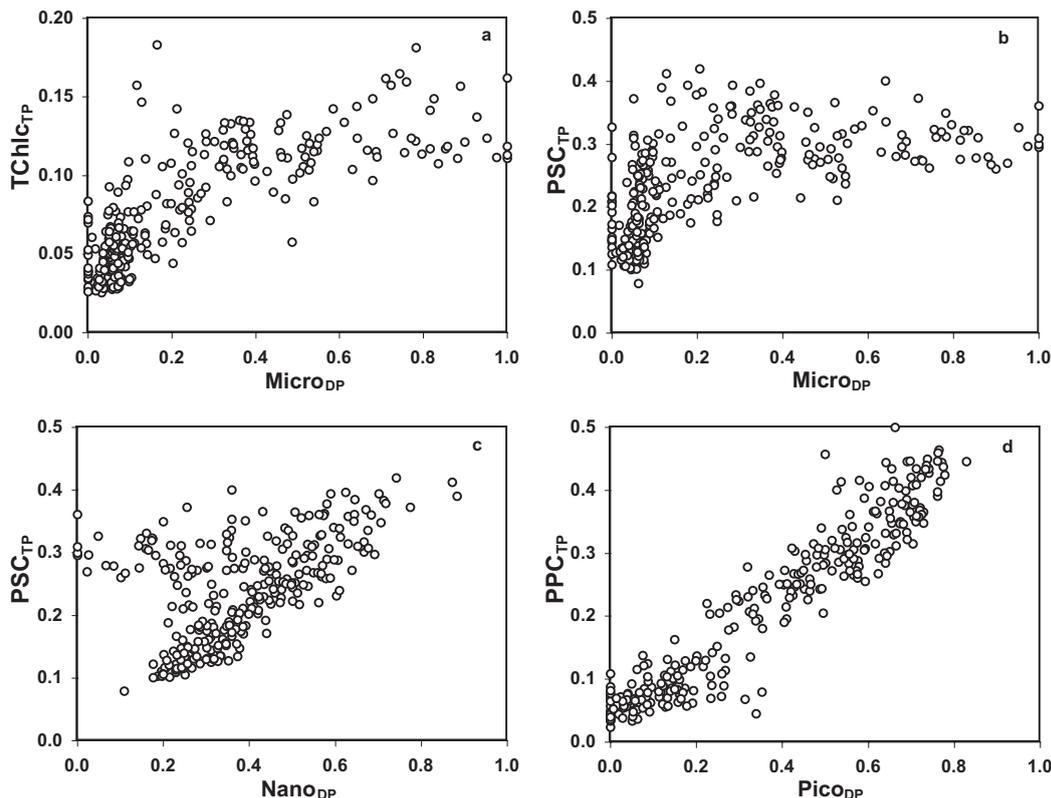


Fig. 8. Relationships between (a) TChlc_{TP} and Micro_{DP}, (b) PSC_{TP} and Micro_{DP}, (c) PSC_{TP} and Nano_{DP}, and (d) PPC_{TP} and Pico_{DP}. See Table 1 for abbreviations

that only photosynthetically active components be used in bio-optical models of primary production appears to be a sound one.

These surface pigment adaptations are likely to be related to, or controlled by, the nutrient regime in the different regions. During AMT-6, the Benguela region was characterised by elevated nitrates (10 to 20 μM , Barlow et al. 2002) and biomass, diatom domination, a high proportion of chlorophylls and a low PPC_{TP} index. Diatoms are opportunistic organisms that are able to respond rapidly to nitrate enrichment (Fogg 1991), and chlorophyll molecules contain nitrogen atoms, while carotenoids do not (Porra et al. 1997). This 'nitrogen' characteristic of diatoms and chlorophylls probably explains the dominance of diatoms and the elevated chlorophyll pool in the Benguela ecosystem. The Canary and temperate NE Atlantic regions had lower nitrate concentrations (0.5 to 1.5 μM , Barlow et al. 2002) and biomass, a greater contribution of nanoplankton in the community, a 6% lower chlorophyll pool compared to the Benguela, and an increased PPC_{TP} index. In the oligotrophic regions, nitrates were below detection limits (Barlow et al. 2002), biomass was very low, the communities were dominated by picoplankton, chlorophyll pools were 12 to 18% lower

than the Benguela, and the PPC_{TP} indices were the highest (Table 2). Thus, there appears to be a synchronicity between the decrease in nitrate concentrations, the change in community structure, and the decline in the proportion of the chlorophyll pool. Concomitantly, there was an inverse relationship between the decrease in nitrates and the increase in the PPC_{TP} index. Similar relationships for nitrate and photoprotective carotenoids have been observed by Babin et al. (1996), Johnson et al. (2002) and Lazzara et al. (1996) in the tropical NE Atlantic and Arabian Sea. It appears that nitrogen has a significant role in regulating the pattern of change within the pigment pool in surface phytoplankton, and these changes are related to shifts in community structure rather than acclimation by the same population. These observations also suggest that photoadaptation is greater in the Benguela, Canary and NE Atlantic regions where the photosynthetic chlorophylls and carotenoids accounted for 87 to 93% of total pigments, as opposed to 68% in the oligotrophic regions. The phytoplankton in the high productivity regions are therefore likely to have greater absorption and photosynthetic efficiencies, leading to elevated primary production and biomass, since phytoplankton in oligotrophic waters usually have reduced

photosynthetic efficiency when photoprotective pigments are high (Babin et al. 1996, Johnson et al. 2002).

This study has demonstrated the significant regional differences in surface phytoplankton and pigment characteristics along the eastern boundary of the Atlantic Ocean. The Benguela had a 3-fold greater phytoplankton biomass than the Canary and temperate NE Atlantic regions, comprising a microplankton community with a high content of photosynthetic chlorophylls and carotenoids. Although the biomass levels were considerably lower in the oligotrophic regions, the chlorophyll *a* concentration in the southern oligotrophic region was twice that in the northern oligotrophic region. Both oligotrophic regions were dominated by picoplankton, containing a high proportion of photoprotective carotenoids and a reduced pool of photosynthetic pigments. These differing proportions of photosynthetic and photoprotective pigments in phytoplankton across 84° of latitude may be useful in the development of bio-optical models for estimating primary production over basin scales in the Atlantic Ocean.

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