Coccolithophore ecology in the tropical and subtropical Atlantic Ocean: New perspectives from the Atlantic Meridional Transect (AMT) programme

Alex J. Poulton [a,*], Patrick M. Holligan [b], Anastasia Charalampopoulou [b], and Tim R. Adey [b]

[a] Ocean Biogeochemistry and Ecosystems, National Oceanography Centre, Waterfront Campus, Southampton, SO14 3ZH, UK.

[b] Ocean and Earth Sciences, National Oceanography Centre Southampton, University of Southampton, Southampton, SO14 3ZH, UK.

*Corresponding author.

Tel: +44 2380597086.

Email address: Alex.Poulton@noc.ac.uk

Highlights:

- Spatial and temporal species composition analysed in 199 samples from the Atlantic.
- Distinct floral groups identified vertically in the upper, lower and sub-euphotic zone.
- Vertical compositional differences statistically stronger than latitudinal changes.
- Thirty-one species represented 95% of cell numbers, with 140 species considered rare.
- Mixotrophy suggested as ecological strategy for deep-dwelling and upper-ocean species.

Abstract

Coccolithophore species composition was determined in 199 samples collected from the upper 300 m of the Atlantic Ocean, spanning temperate, tropical and subtropical waters in both hemispheres during four Atlantic Meridional Transect (AMT) cruises over the period 2003 to 2005. Of the 171 taxa observed, 140 consistently represented less than 5% of total cell numbers, and were classed as rare. Multivariate statistical techniques were used on the common taxa to assess variability in community composition vertically in the water column, horizontally across hydrographic provinces (subtropical gyres, equatorial waters, temperate waters), and temporally between cruises. Sharper gradients of statistical dissimilarity in species composition occurred vertically over a few tens of metres than horizontally over hundreds of kilometres. Three floral groups were identified from analysis of the depth of normalised abundance maxima in the subtropical gyres and equatorial waters: the upper euphotic zone (UEZ, >10% surface irradiance); the lower euphotic zone (LEZ, 10-1% surface irradiance); and the sub-euphotic zone (SEZ, <1% surface irradiance). The LEZ includes the deep chlorophyll maximum (DCM) and nutricline, and was characterised by species such as *Emiliania huxleyi* and *Gephyrocapsa ericsonii* which were also abundant at higher latitudes. It is suggested that this pattern reflects similarities in the light (and inorganic nutrient) conditions between the LEZ and temperate waters. The SEZ is below the depth where light is thought to be sufficient to support photosynthesis, suggesting that deep-dwelling species such as *Florisphaera profunda* and *Gladiolithus* spp. may be mixotrophic or phagotrophic, although conclusive proof will need to be gained experimentally. Mixotrophy could also be an important nutritional strategy for species abundant (*Umbellosphaera* spp., holococcolithophores) in the UEZ where inorganic nutrient concentrations are depleted and limiting to growth, although other nutritional strategies, such as the use of organic nutrients, are also possible. Statistical differences were also found in the species composition between the different cruises, with high levels of similarity for similar timed cruises (May or September-October). Few individual taxa showed significant variability in abundance over the time-span of sampling, except species such as *E. huxleyi* and *G. ericsonii* at higher latitudes. In subtropical and equatorial waters, high levels of species richness and low levels of species dominance remained throughout the sampling period indicating that seasonal fluctuations reflected differences in the whole coccolithophore community rather than in just one or a few species. Multivariate analyses of the taxa classified as rare also indicated some level of temporal, as well as vertical, zonation. Such insights into coccolithophore ecology and community composition provide important new perspectives that require innovative research to fully understand their impact on ocean biogeochemistry.

Keywords: Coccolithophores; euphotic zone; biogeography; physiology; mixotrophy.

Regional index terms: Atlantic Ocean; subtropical; tropics; equatorial waters; temperate waters.

1. Introduction

Coccolithophores are unicellular marine algae, belonging to the Class Prymnesiophyceae, that possess one or more external layers of calcite scales (coccoliths). Coccoliths are formed intracellularly via calcification and are then extruded onto the external surface of the cell to form a coccosphere. Around 200 species of coccolithophore are extant in the modern ocean (Young et al., 2003), with considerable diversity in the shape of the cell, the shape, construction and crystallography of the coccoliths, and their number, diversity and geometry around the cell (Monteiro et al., 2016). Variability in the crystallography of the coccoliths is based around two forms which represent linked species' life stages and reproductive strategies; in their diploid form many species produce heterococcoliths (HET), composed of complex radially arranged inter-grown calcite crystals; in contrast, in the haploid form many species produce holococcoliths (HOL) formed of small equidimensional calcite crystals (see Monteiro et al., 2016 and references therein). Transitions between HOL and HET life forms are now recognised as being a key component of how coccolithophore species can adapt to changing environmental conditions (Houdan et al., 2004, 2006), although the biogeography of many HOL (and HET) forms has still not been fully identified (e.g. Dimiza et al., 2008; Cros and Estrada, 2013).

Although global production of calcite by coccolithophores is still not well constrained (Berelson et al., 2007; Poulton et al., 2007), coccoliths make up the major fraction of carbonate in marine sediments (Broecker and Clark, 2009). Furthermore, extensive dissolution of coccoliths occurs both in the upper water column due to biological processes (Milliman et al., 1999; Poulton et al., 2006a) and in deep waters situated below the lysocline for calcite. Geochemical evidence suggests that low latitude calcite production is an important term in the global carbonate budget (Sarmiento et al., 2002; Berelson et al., 2007) and, in the context of climate change and ocean acidification, considerable attention is now being given to how the physiology and ecology of coccolithophores will respond to, and affect, air-sea exchanges of carbon dioxide (e.g. Bach et al., 2015; O'Brien et al., 2016). However, our knowledge of the distributions and nutritional strategies of coccolithophores across the extensive ocean gyres is still based on relatively few detailed studies (e.g. McIntyre and Bé, 1967; Winter et al., 1994; Hagino et al., 2000; Haidar and Thierstein, 2001). In this paper the coccolithophore communities in equatorial and subtropical waters of the Atlantic Ocean are examined through sampling on the Atlantic Meridional Transect (AMT) programme (Robinson et al., 2006).

The growth environment of coccolithophores, and other phytoplankton, living in equatorial and subtropical waters is strongly regulated by opposing gradients in light and nutrient availability. The upper water column above the semi-permanent thermocline is characterised by low (nano-molar; <100 nmol kg^{-1}) inorganic nutrient concentrations and high levels of irradiance, while

below the thermocline nutrient concentrations are relatively high (micro-molar; >1 µmol kg^{-1}) and light levels are low. Vertical profiles of chlorophyll fluorescence show a deep chlorophyll-*a* maximum (DCM) associated with the deep increase in nutrients (a nutricline), at depths ranging from ~60 m around the tropical Equator to as much as 150 m in the subtropical gyres. The DCM is generally regarded as neither a maximum in phytoplankton biomass or in primary production (Perez et al., 2005, 2006), but marks a depth where the relative availability of surface irradiance has decreased to 1% of its surface value and where photo-acclimation results in increased cellular chlorophyll levels. Phytoplankton associated with the DCM may be considered to be light-limited rather than nutrient-limited (Venrick, 1982; Poulton et al., 2006b), whereas the situation is reversed in the upper ocean.

The phytoplankton community in the warm, stratified waters of the Atlantic are dominated in terms of abundance, biomass and primary production by small (<2 µm) picoplankton, mainly prokaryotes such as *Prochlorococcus* and *Synechococcus*, as well as small eukaryotes (Tarran et al., 2006; Zubkov, 2014). The nanoplankton (2-20 µm), which includes most if not all species of coccolithophore as well non-calcifying haptophytes (Liu et al., 2009), generally contribute 10-20% of biomass (chlorophyll-*a*), with higher values in equatorial waters and higher latitude waters during spring (Marañón et al., 2001; Poulton et al., 2006b). Simple estimates of coccolithophore contributions to primary production, based on calcification rates and cellular ratios of inorganic to organic production, imply that coccolithophores account for only ~1-10% (maximum 20%) of total phytoplankton primary production in equatorial and subtropical waters (Poulton et al., 2006a, 2007). Such low coccolithophore contributions match with similar estimates made in temperate and sub-polar environments, with significant contributions (>30-40%) limited to coccolithophore blooms (Poulton et al., 2007, 2010, 2013, 2014).

Although coccolithophores are only a minor component of the phytoplankton community in the oligotrophic ocean they play an important role in the exchange of both carbon and sulphur between the atmosphere and surface waters and in the downward transport of biogenic material and its' accumulation in marine sediments (e.g. Holligan et al., 1993; Malin and Steinke, 2004; de Vargas et al., 2007; Ziveri et al., 2007). It is appropriate, therefore, to ask how the growth of coccolithophores in oligotrophic waters is regulated and how it might be affected by future changes in the oceanic environment (e.g. Bach et al., 2015). Despite numerous experimental studies of photosynthesis and calcification by coccolithophores (e.g. Bach et al., 2013), as well as examination of coccoliths in sediments across glacial-interglacial transitions (Beaufort et al., 2011; Meier et al., 2014), the effects on coccolithophore ecology of future changes in ocean carbonate chemistry due to rising CO_2 levels remain uncertain (Bach et al., 2015). This problem stems partly from the difficulties of growing most oceanic taxa in the laboratory and an incomplete understanding of their ecology and nutritional strategies in the open ocean.

Both latitudinal biogeographical and floral depth zones have been recognised on the basis of characteristic coccolithophore species assemblages (e.g. McIntyre and Bé, 1967; Okada and Intyre, 1977; Winter et al., 1994); with further work in the Atlantic (Kinkel et al., 2000; Haidar and Thierstein, 2001; Boeckel and Baumann, 2008) and Pacific (Hagino et al., 2000; Cortes et al., 2001) confirming the generality of earlier observations. Relative to the high cell density (>1000 cells mL^{-1}) blooms that may occur in sub-polar waters, the reported abundances for surface subtropical waters of the Atlantic are in the range of less than 1 to 300 coccospheres (cells) mL^{-1} (the higher values being generally dominated by *Emiliania huxleyi*), with ~25 coccospheres mL^{-1} being typical of low-latitude gyre waters (e.g. Boeckel and Baumann, 2008). Seasonal variations in abundance are most pronounced in higher latitude waters (>30°N/S) (e.g. Knappertsbusch and Brummer, 1995; Boeckel and Baumann, 2008; Baumann et al., 2008) and in equatorial upwelling regions (e.g. Kinkel et al. 2000), as a result of changes in water column stratification and nutrient distributions.

In this paper the results of SEM analyses of coccolithophore samples collected at depths of 5 m to 300 m between 47°N and 43°S on four AMT cruises during the period 2003 to 2005 are reported. The AMT programme provides an excellent platform to examine coccolithophore dynamics as it provides a wealth of ancillary environmental and ecological information to provide valuable contextual perspectives to view coccolithophore ecology in the wide expanses of the oligotrophic Atlantic Ocean. Our analysis of the coccolithophore database resulting from SEM analyses has four main aims: (1) to describe the general species composition of equatorial and subtropical communities in terms of species composition, relative abundance and diversity; (2) to examine the variability in vertical structure of the community in relation to light and nutrient availability; (3) to compare and contrast vertical biogeography with latitudinal variability in species composition; and (4) to investigate whether any temporal (inter-cruise) variability in species composition is evident across the short time period of sampling (2003-2005).

2. Materials and methods

2.1. Sampling

The cruise tracks and dates for the cruises on which samples were collected for analyses of the coccolithophore communities are shown in Figure 1. Coccolithophore data are analysed in relation to several hydrographic provinces across the Atlantic Ocean: Northern Gyre waters (NG, 35°N to 10°N), equatorial waters (EQ, 10°N to 10°S), and Southern Gyre waters (SG, 10°S to 30°S), with temperate (TMP) waters >35°N and >30°S (see Robinson et al., 2006; Poulton et al., 2006b; Fig. 1). Seawater samples were collected during daily pre-dawn (02:00-04:00 h, local time) and mid-morning (11:00-12:00 h) deployments of a rosette sampler fitted with 24 water bottles (20 L), a Sea-Bird 9/11 CTD, and a Chelsea MKIII Aquatracka fluorometer. Chlorophyll-

177 *a* and nitrate concentrations were measured at 10 to 15 depths from each CTD cast, while
178 samples for coccolithophore enumeration were collected from 5 to 13 water depths over the
179 upper 300 m. The standard sampling depths for the AMT programme during 2003 to 2005
180 (Poulton et al., 2006b; Robinson et al., 2006) were the depths of 55, 33, 14, 1 and 0.1% of
181 surface irradiance (with optical depths of 0.6, 1.1, 2.0, 4.6 and 6.9, respectively); additional
182 samples were collected at selected stations during AMT 14 to provide a more complete
183 description of properties across the DCM down to 300 m.
184
185 Light depths were determined from the previous days light measurements, or assuming that the
186 deep fluorescence maximum (DCM) approximates the depth (Z_{DCM}; m) of 1% surface irradiance
187 (optical depth = 4.6). The vertical attenuation coefficient of Photosynthetically Active Radiation
188 (PAR; m^{-1}) was determined for each station as $4.6/Z_{DCM}$ and subsequent light depths
189 determined as optical depth divided by the vertical attenuation coefficient. Optical depths for
190 samples not collected at the five standard light depths were calculated as depth (Z; m) × vertical
191 attenuation coefficient (m^{-1}). Sea-surface temperature was determined from the CTD sensors
192 during daily deployments. Chlorophyll-*a* measurements were made on 250 mL water samples
193 filtered onto Whatman GF/F filters, extracted in 90% acetone for 18-20 hours at 4^{o}C, and
194 measured on a TD700 Turner Designs fluorometer calibrated with a pure chlorophyll-*a* standard
195 (Sigma-Aldrich, UK) (see Poulton et al., 2006a,b for further details). Micromolar (μmol kg^{-1})
196 concentrations of nitrate were measured with a 5-channel Technicon, segmented flow
197 colourimetric auto-analyzer (Bran+Luebbe AAII) (see Poulton et al., 2006a, b for further details).
198
199 ***2.2. Coccolithophore enumeration and identification***
200 For coccolithophore enumeration, 1 to 2 L of seawater was taken from 20 L Niskin bottles
201 mounted on a CTD carousel, and filtered under gentle suction onto 25 mm 0.45 μm
202 polycarbonate filters which were then dried at room temperature and stored in sealed Perspex
203 boxes. The latitudes and depths for which samples were collected on the AMT 12 (May 2003)
204 and AMT 14 (May 2004) cruises are shown in Figure 2, together with data on the vertical
205 distributions of chlorophyll-*a* and nitrate for AMT 14, one of the AMT cruises with the highest
206 depth resolution of chlorophyll-*a* and nitrate sampling. For a comparison between AMT cruises
207 as to variability in the depth distribution of these properties see Robinson et al. (2006) (their
208 Figures 2 and 4). For the AMT 15 (September-October 2004) and AMT 17 (September-October
209 2005) cruises (see Fig. 1b), only surface samples (97% or 55% surface irradiance) were
210 analysed: AMT 15, 6 samples from between 0.1^{o}N (EQ) and 20.6^{o}S (SG); AMT 17, 21 samples
211 from between 44.3^{o}N and 35^{o}S.
212
213 Examination of filters by Scanning Electron Microscopy (SEM) generally followed the
214 methodology of Charalampopoulou et al. (2011). Filter segments were examined with a LEO

1450 SEM at 5000× magnification and coccospheres were counted from up to 700 fields-of-view (FOV), equivalent to a maximum sample volume of ~15 mL. The total number of coccospheres counted per sample were ~300 for cruises AMT 12 and AMT 14, and ~150 per sample for cruises AMT 15 and AMT 17; when coccospheres were rare (mainly samples from below the DCM), less than 150 coccospheres were often encountered.

Species identification followed the nomenclature of Young et al. (2003), as well as Bollmann et al. (2006) for *Solisphaera* spp. and Kleijne and Cros (2009) for *Syracosphaera* spp. A full list of the coccolithophore taxa identified in this study is given in Appendix 1. Counts of *Ophiaster formosus* and *O. hydroideus* were combined in order to remove uncertainty in distinguishing the two species when comparing coccosphere counts by different observers. No attempt was made to separate the different morphotypes of species such as *Emiliania huxleyi*, *Umbellosphaera tenuis* and *Calcidiscus leptoporus* (see Boeckel and Baumann, 2008), or *Florisphaera profunda* (see Quinn et al., 2005), although such information could be obtained from the digitally-stored SEM images. Counts of *Rhabdosphaera xiphos* are likely to have been underestimated due to the occurrence of aggregates of coccospheres on the SEM filters; also this species could not always be clearly separated from *Palusphaera vandelii*. The coccoliths of some species are readily detached on filters prepared for SEM analysis and in such cases aggregates of identical coccoliths were counted as a coccosphere. The full database of counts used in this study is available from the authors and via the British Oceanographic Data Centre (www.bodc.ac.uk). A total of 171 coccolithophore taxa (Appendix 1) were identified in the 199 samples examined from the four AMT cruises. These taxa include recognised alternate life history phases (HET and HOL), three unnamed species (Young et al., 2003) and a few life history combinations for which two species names are still used (see Cros and Fortuno, 2002).

The low cell numbers and high diversity characteristics of subtropical coccolithophore communities (i.e. <30 cells mL^{-1}) lead to concern over the accuracy of SEM analyses on an examination volume (15 mL) which is a relatively small fraction of the filtered volume (1-2 L) to fully quantify the cell abundance and species diversity. One method to address such issues is to investigate how similar repeat counts of a single sample or of replicated samples are of one another in terms of cell counts and species composition. In this study, four replicate counts were performed on representative samples from below (120 m, 1% surface irradiance; optical depth = 4.6) and above (31 m, 55% surface irradiance; optical depth = 0.6) the DCM (Table 1; Fig. 3).

In general, there was good reproducibility of total numbers of taxa (species richness) and of relatively abundant cells (i.e. >1 mL^{-1}). However, for both sampling depths, many taxa were recorded in only one or two of the replicates, although these made a relatively small contribution to total cell counts; for the deep sample 60% of such taxa comprised only 31% of the total cell

count, and for the surface the corresponding figures were 67% and 18%. The numbers of taxa recorded as a function of volume examined are shown in Figure 3. For both types of sub-sampling it appears that a complete description of the coccolithophore flora can only be achieved by examining relatively large (>100 mL) volumes of seawater. Thus SEM counts based on small seawater volumes (e.g. <15 mL as used for this study) give a measure of coccolithophore species richness while the abundance of rarer coccolithophore taxa can be described in relative terms only. To overcome such issues it is necessary to transform and pre-treat the resulting species counts before statistical analysis; including elimination of rare species which occur at low frequencies, consideration of standardised count data (i.e. percentage abundances), and a logarithmic transformation (log(X+1)), which will all remove the influence of low abundance species and focus the analysis on compositional changes rather than numerical changes (Clarke and Warwick, 2001).

2.3. Statistical analysis

Multivariate statistical techniques were used to assess the vertical and horizontal (dis)similarity in species composition of samples, as well as to examine whether any inter-cruise differences in species composition existed, using PRIMER-6 (v 6.1.6, PRIMER-E Ltd) (Clarke and Warwick, 2001). Bray-Curtis Similarity was calculated from standardised count data, with the exclusion of certain taxa considered to be in such low occurrences as to be rare (herein defined as consistently contributing <5% to total cell numbers), and with a Log(X+1) transformation. Cluster analysis and non-metric Multi-Dimensional Scaling (nMDS) ordinations were then performed, with related ANOSIM (Analysis of Similarity) and SIMPER (Similarity Percentages) performed on the resulting patterns, where appropriate (Clarke and Warwick, 2001). ANOSIM allows statistical comparison of the variation in species abundance and composition between groups of samples. SIMPER allows statistical identification of which species are primarily responsible for differences between groups of samples, with ANOSIM assessing the significance of the difference between groups. PRIMER was also used to calculate Pielou's Evenness (J') which is a measure of the spread of cell abundances between the species present (Clarke and Warwick, 2001). In this study, species richness was simply a measure of the number of taxa in each sample. Subsequent statistical analysis of the rare species was also performed on standardised data, with a Log(X+1) transformation.

The approach to the statistical examination of vertical, latitudinal and temporal patterns in species composition followed in this study follows a logical order of starting the analysis on a small set of samples (or species) and expanding our interpretation and analysis on this dataset by including other parts of the AMT database in steps. The main analysis focuses initially on the common (>95% total cell numbers) taxa, although an analysis of the rare species in the same manner to identify any potential patterns is also performed. The analysis follows the order: (a)

firstly an examination of three high-resolution profiles from AMT 14 to identify key floral groups and vertical patterns in species composition (section 3.1); (b) this vertical analysis is then widened to include the full cruise datasets from AMT 12 and AMT 14 (section 3.2); (c) then consideration of latitudinal patterns in species composition based on just AMT 14 surface samples to identify key floral groups and patterns in species composition (section 3.3); (d) this latitudinal analysis is then widened to include the full database (AMTs 12, 14, 15 and 17) to identify any inter-cruise differences or similarities in surface waters (section 3.4); and (e) finally, an analysis of the rare species distribution, in terms of both vertical and latitudinal patterns (section 3.5), using similar methods as used in the previous sections. The focus on AMT 14 is driven by this cruise representing the best sampled (vertically and latitudinally) AMT cruise, while only surface samples are included in the AMT database for AMT 15 and AMT 17.

3. Results

3.1. Vertical community structure: AMT 14 analysis

An in-depth analysis of vertical variability in coccolithophore species composition is firstly carried out using three high-resolution profiles from the AMT 14 cruise. These three stations represent the southern gyre (SG), equatorial waters (EQ) and northern gyre (NG) regions of the Atlantic (Figs. 1, 4 and 5). At each of these stations the numbers of taxa and cells were highest in the surface layer above the depth of the DCM (1% surface irradiance; optical depth = 4.6), and then declined to minimum values below the depth of 0.1% surface irradiance (optical depth = 6.9) (Fig. 4a). The relative abundance of cells and taxa within the DCM appears to vary between the two gyres, which may potentially be linked to seasonality, both being relatively low in the autumn (SG) when surface light is declining compared to the spring (NG) when surface light is increasing. In the EQ region, where the DCM and nutricline are shallow compared to the subtropical gyres (e.g. Fig. 2 for AMT 14), the decline in numbers of cells and taxa with depth are less marked. All three profiles show a relatively greater drop in cell number than in species richness below the DCM (Fig. 4a).

Each of the three profiles from AMT 14 (Fig. 4b) were characterised by a change in community structure of the coccolithophore population with depth as indicated by the fall in Bray-Curtis Similarity to less than 50% (with reference to the surface sample at each site) at or slightly above the depth of the DCM. In contrast, J' was relatively constant down to the DCM (Fig. 4b); since numbers of taxa for each profile were fairly uniform above the DCM it appears that changes in species composition with depth in the surface layer were not accompanied by changes in the relative abundance of the dominant species. In the two subtropical gyres the sharp drop in J' below the DCM suggests that the coccolithophore population below the depth of 1% surface irradiance (optical depth = 4.6) was distinct from that in surface waters in terms of both species composition and dominance by fewer species (Fig. 4a). However, J' increased

again below the depth of 0.1% surface irradiance (at optical depths greater than 8) and absolute depths deeper than 200 m, although these depths were characterised by very low cell numbers.

The depth distribution of the abundant coccolithophore taxa (i.e. >95% of total numbers) for the three stations in Figure 4 (AMT 14) was further examined by plotting depth profiles of each species' cell abundance normalised to its maximum cell abundance observed in that profile (plots not shown). In our study, normalised abundance is the abundance in each sample relative to the maximum observed in the dataset; so a value of 0 would represent zero abundance and 1 would represent that species' maximum abundance. A species' depth habitat was then classified as the uppermost depth horizon where the maximum value (i.e. 1) and consistent values >0.75 were observed between the main relative surface irradiance depths presented in Figure 4. Depth habitats were compared across the three stations and where, in a few cases, species had high normalised abundances in more than one depth zone, the overall depth habitat was defined as the one common across all stations. This analysis of the depth distribution of the more abundant coccolithophore taxa recorded at the three stations identified three floral groups in our study (Table 2) which are taken to characterize the Upper Euphotic Zone (UEZ, >10% surface irradiance), Lower Euphotic Zone (LEZ, 1-10% surface irradiance), and Sub-Euphotic Zone (SEZ, <1% surface irradiance). As the DCM is generally considered to mark the base of the euphotic zone (i.e. 1% of surface irradiance), the deepest coccolithophore zone is referred to as the 'sub-euphotic' rather than 'lower photic' as in other studies (e.g. Winter et al., 1994).

The vertical distributions of each of these floral groups at the three AMT 14 stations analysed, and of the rare species (consistently <5% of total cell number), are shown in Figure 5a. In general the UEZ and rare taxa were most numerous above the depth of 10% surface irradiance but extended down to the depth of 1% surface irradiance, whereas SEZ taxa were largely confined to below the depth of 1% surface irradiance. In contrast, the LEZ taxa reached a maximum relative abundance close to the depth of 1% surface irradiance but also made significant contributions to coccolithophore populations of the UEZ at all three stations and as well as the SEZ at the equatorial station. Total cell numbers below the depth of 1% surface irradiance (see Fig. 4a) were low in all three profiles from AMT 14 so that the apparent importance of LEZ species below this depth at the EQ and NG stations reflects relatively low numbers of coccospheres. As an example of the depth distribution of characteristic taxa in each of the floral groups identified, Figure 5b shows relative abundance profiles of two species from each of the UEZ, LEZ and SEZ groups (see Table 2) at the SG station. Figure 5b also shows how two zones exist in the upper section of the water column, with the depth distribution of certain species peaking at intermediate depths below the depth of 10% surface irradiance but above the depth of the DCM and euphotic zone (e.g. *Calciopappus* spp. and *G. ericsonii*; Fig

5b).The taxa within each floral group do not necessarily follow the same pattern; thus, for the UEZ, *Umbellosphaera tenuis* extended to a slightly greater depth than *U. irregularis* and, for the SEZ, the maximum abundance of *Gladiolithus flabellatus* was well below that of *Florisphaera profunda*.

Using a comparative pair-wise statistical analysis of the similarity between species composition (ANOSIM) for the three selected AMT 14 stations it is clear that there are strong statistical differences in species composition between UEZ and SEZ (R-statistic 0.97, $p<0.001$, average Bray-Curtis dissimilarity = 79.1%) and between LEZ and SEZ (R-statistic 0.74, $p<0.001$, average Bray-Curtis dissimilarity = 70.7%), whereas the differences between UEZ and LEZ are relatively weaker (R-statistic 0.19, $p<0.05$, dissimilarity = 55.2%; Table 3). The same pair-wise analysis for all the samples from AMT 14, where samples were assigned to floral group zones by their relative irradiance depths, gives further support for the three floral groups (Table 3), with high levels of dissimilarity (>60%) in terms of species composition and significant ($p<0.001$) R-statistics from the ANOSIM analyses. For both sets of analyses (selected AMT 14 stations and all AMT stations), the strongest statistical differences in terms of species composition were always seen between the UEZ and SEZ (R-Statistics >0.9, $p<0.001$) with average Bray-Curtis dissimilarity levels of almost 80%.

3.2. Vertical community structure: Comparison between AMT 12 and 14

Vertical segregation of coccolithophore taxa during AMT 14 is clearly supported by analysis of normalised abundance (Figs. 4 and 5, Table 2) and multivariate comparison of species composition between the different sample groupings (Table 3). To test how widely these patterns exist in the fuller AMT database a multivariate statistical analysis of species composition in all AMT 12 and AMT 14 samples was performed. Coccolithophore species structure for all AMT 12 and AMT 14 samples (total 150) was investigated through calculation of Bray-Curtis Similarity and then ordination by non-metric Multi-Dimensional Scaling (nMDS). nMDS ordinations showing sample distribution with respect to cruise number, hydrographic region and optical depth are shown in Figures 6 a-c, respectively.

The nMDS ordination (Fig. 6) shows several interesting patterns in species composition, with the relative distance between samples indicative of their relative (dis)similarity. Samples with statistically similar species composition are closely aligned, whereas samples with low statistical similarity in terms of species composition are more widely spaced. Hence, the overlap in the distribution of samples from the two cruises (AMT 12 and 14) suggests strong similarities in species composition, especially for the gyre and equatorial regions (Figs. 6a and 6b). In terms of hydrographic region, the temperate (TMP) samples, mainly from shallow water depths, appear as a variable but relatively distinct group (Fig. 6b). In terms of irradiance levels,

expressed as optical depth, the deep samples (from the depths of the 0.1% and, to a lesser extent, the 1% surface irradiance) appear as the most distinct groups (Fig. 6c), in contrast to the temperate samples (Fig. 6b) which show considerable overlap between optical depths (Fig. 6c).

Coccolithophores were found in all samples from AMT 12 and 14, with the highest cell concentrations in temperate waters (Figs. 6b-d) during both cruises. At gyre and equatorial stations (Figs. 6b and 6c), cell numbers below the DCM (1% surface irradiance; optical depth = 4.6) generally decreased with depth; for optical depths of 0.6 to 2, 4.6 and 6.9 (corresponding to the 55 to 14%, 1% and 0.1% surface irradiance levels, respectively) the mean cell counts were 24.4, 29.3 and 12.9 mL^{-1}, respectively.

The relative cell counts for the different floral groups identified in Table 2 are shown in Figures 6e-h (i.e. the relative abundance of taxa from each floral group in each sample to total numbers) for the two AMT cruises. The upper optical depths (0.6-2.0; 55 to 14% surface irradiance; Fig. 6c) of the gyre (NG, SG) and equatorial (EQ) regions (Fig. 6b) are characterised by abundant UEZ taxa (Fig. 6e), and the lowest optical depth (6.9; 1% surface irradiance; Fig. 6c) of the same regions by SEZ taxa (Fig. 6g). In contrast, LEZ taxa are relatively widely distributed (Fig. 6f), extending into the temperate region (Fig. 6b) and from the surface down to as deep as the 1% surface irradiance level (optical depth = 6.9; Fig. 6c). Rare taxa (Fig. 6h) are relatively evenly distributed in terms of latitude (Fig. 6b) and depth (Fig. 6c), with maximum cell numbers in the UEZ (Fig. 6e) and temperate waters (Fig. 6b); however, they are not a homogenous group, with different species occurring at different depths and latitudes (data not shown) as has been found for the common species (see Section 3.1).

3.3. Horizontal (meridional) community structure: AMT 14 analysis

Based on routine sampling from 5 depths per station it is not possible to analyse objectively latitudinal variations in the LEZ and SEZ coccolithophore flora as samples collected at the depths of 1% and 0.1% surface irradiance might, or might not, correspond to the maximum cell abundances of characteristic species for these depths (see Fig. 5b). On the other hand the surface samples (55% of surface irradiance) may be considered as representative of the UEZ flora (see Fig. 5) and hence our horizontal (meridional) analysis of species composition focuses on only surface samples. Again, AMT 14 is chosen as the first cruise to base the analysis on, with the next section (3.4) widening the analysis to include all four AMT cruises.

Results of a compositional statistical analysis of AMT 14 surface samples (55% relative surface irradiance only) are shown in Figure 7. Generally, coccolithophore cell numbers in surface waters between 30^{o}S and 35^{o}N ranged from 20 to 40 cells mL^{-1}, and the number of taxa (species richness) in each sample ranged from 25 to 45 (Fig. 7a). The highest coccosphere

numbers were recorded from temperate stations (>30^{o}S) and the lowest from equatorial stations. The number of taxa were relatively high (>30) within surface waters of the subtropical gyres (NG, SG), and decreased at the northern temperate station and at some equatorial and Northern Gyre stations; for example, the surface (13 m) sample from the AMT 14 14.8^{o}N station gave a coccosphere count of just 2.2 mL^{-1} for just 10 taxa (Fig. 7a).

Species composition in surface samples across the full AMT 14 cruise was examined by comparing statistically one station in the NG (22.3^{o}N) with all the other surface samples in terms of Bray-Curtis Similarity. This comparison showed that the coccolithophore communities were broadly comparable (i.e. ~50% similarity) in terms of species composition across a broad latitudinal range from 35^{o}N to 32^{o}S (Fig. 7b). A plot of Pielou's Evenness (Fig. 7b) for surface samples also suggests that the surface coccolithophore communities were comparable in terms of species diversity and dominance from 30^{o}N to 30^{o}S, except at higher latitudes where high cell densities (typically 10-100 cells mL^{-1}) of LEZ taxa such as *Emiliania huxleyi, Gephyrocapsa* spp.*,* and *Calcidiscus leptoporus* were found. However, as shown in Figure 7c, the relative abundance of individual taxa (e.g., *E. huxleyi*, *Umbellosphaera tenuis* and *U*. *irregularis*) between stations over 20 km apart was highly variable and latitudinal peaks in relative abundance were not always consecutive.

Using a similar approach for assessing the horizontal (latitudinal) distribution of coccolithophore species as used in Section 3.1 for vertical variability, the normalised species distribution for all species which represented over 5% of total numbers in surface samples was plotted again in order to determine whether each species' maximum relative abundance was consistently found (>0.75) within a specific hydrographic province (plots not shown). The results from this analysis are presented in Table 4, alongside the vertical floral group that each taxa (where appropriate) is aligned with. The nine UEZ taxa (see Table 2) are found mainly in the subtropical gyres (NG, SG), while LEZ taxa are found in both equatorial (EQ) and Temperate waters (Table 4). Of the SEZ taxa listed in Table 2, three species are found in surface temperate waters (*Algirosphaera robusta*, *Calciosolenia murrayi*, *Florisphaera profunda*), whereas the other four SEZ species were never observed in significant numbers in surface waters during AMT 14 (i.e., they were consistently <5% of total numbers and eliminated from the analysis). The relative abundances of these three biogeographic floras are plotted in Figure 7d, along with the distribution of the rare (<5% of total numbers) surface water taxa. As expected, the gyre, equatorial and temperate floras reach maximum relative abundances in each of these regions, while the rare flora are found throughout the transect, apart from in temperate waters at either end of the transect (Fig. 7d).

A comparison of the Bray-Curtis Similarity between successive vertical samples at each station representing the UEZ, LEZ and SEZ (i.e., the statistical similarity between the 55% and 14%, 55% and 1%, 55% and 0.1% relative surface irradiance depths, respectively) again shows clear vertical gradients in species composition (Fig. 7e; see also Fig. 4b). Temperate stations are characterised by weak vertical gradients in Bray-Curtis Similarity, while relatively stronger vertical declines in similarity can be seen in both subtropical gyre and equatorial waters. Also, there is a marked contrast between the SG and NG samples, with high similarity (>70%) between the 55% and 14% species composition in the north which declines to ~50% in the south. A comparison of Figures 7b and 7e shows that vertical gradients in species composition (in terms of Bray-Curtis Similarity) are much stronger than horizontal ones; similarity remains around 50% when comparing a sample from the NG with all samples from 30^{o}N to 32^{o}S (Fig. 7b), whereas similarity drops sharply below 50% when examining trends vertically over the upper 200 m (Fig. 7e). These trends highlight how there is sharper dissimilarity in coccolithophore species composition vertically over a few tens of metres than there is horizontally, over hundreds to thousands of kilometres.

3.4. Comparison between different cruises for surface communities

Analysis of meridional patterns of species composition in surface samples from AMT 14 shows several distinct features and trends in the level of statistical similarity between communities in different hydrographic provinces (Fig. 7). In this section this meridional analysis is widened to include UEZ samples (55% surface irradiance) from all four AMT cruises (AMTs 12, 14, 15 and 17), again using comparisons of Bray-Curtis Similarity in species composition in nMDS ordination (Fig. 8). In relation to cruise number, the northern spring / southern autumn (AMTs 12 and 14) and the northern autumn / southern spring (AMTs 15 and 17) samples appear to form distinct groups (Fig. 8a), a difference that may be attributable to seasonal changes in community composition rather than cellular abundances (due to the standardisation of the counts and pre-treatment of the data). When plotted in relation to hydrographic province the temperate samples form the most distinctive group and are the most scattered (Fig. 8b), again suggesting a potential seasonal signal. Variability between cruises is also evident in the equatorial and gyre waters of both hemispheres as samples from each temporal cruise pairing (i.e., AMT 12 and 14 versus AMT 15 and 17; Fig. 8a) are clearly distinct in the nMDS (Fig. 8b). Hence, the species composition of cruises sampled in the same season but different years appears to be more similar than between successive cruises in different years; i.e. implying that seasonal differences in coccolithophore species composition are stronger than inter-annual differences.

To further test the statistical significance of the sample segregation shown in Figure 8 an identical analysis used on spatial trends in species composition (Fig. 6) is applied to the dataset.

Table 5 shows the ANOSIM and SIMPER analyses on the data presented in Figure 8, while species level variability is further examined (Table 6) in the context of changes in sea-surface temperature and chlorophyll-*a* concentration. The ANOSIM analysis supports the trends identified, with statistically significant ($p<0.05$) differences in surface coccolithophore communities between AMT 12 and AMT 14 (May) versus AMT 15 and AMT 17 (September-October) for all four biogeographic provinces. Although the highest dissimilarity between seasonal samples was found for Temperate waters (69.1%), the other regions still had dissimilarity greater than 55% (57.5 - 62.6%) and statistically significant ($p<0.01$) R-statistics (Table 5). These results support the perspective that seasonal differences in coccolithophore species composition are stronger than inter-annual differences and the multivariate statistics are identifying seasonal variability (within the limited time-series of sampling).

Examining the raw count data further elucidates the compositional changes identified in Figure 8, although it should be noted that due to the data treatment (standardisation, log(X+1) transformation) actual cell numbers have limited impact on the nMDS. Average coccolithophore abundances were slightly higher during northern spring in the subtropical gyres and equatorial waters than during southern spring (Table 6), although the differences were not statistically significant. As expected, Temperate waters showed the highest absolute cell abundances and highest variability. The pattern for species richness is similar, with average species numbers being higher (>30) in Temperate, subtropical gyre and equatorial waters in northern spring than in southern spring (Table 6). Differences in J' between northern and southern spring cruises in gyre and equatorial waters were minor (Table 6). These trends imply that although the size and composition of the coccolithophore community may change seasonally, evenness (J') was consistently high (>0.8 in gyre and equatorial waters) indicating no overall dominance of the community by one or a few species.

Overall for the four cruises, values of J' were lowest in Temperate waters in both northern and southern spring (average 0.5-0.6, Table 6) which may be due to the high relative abundances of *E. huxleyi* (30-64%) and *G. ericsonii* (15-26%). In subtropical gyre and equatorial waters, *Umbellosphaera irregularis*, *U. tenuis*, *R. xiphos*, and *P. vandelii* (Table 6) had the highest relative abundances in the upper-ocean coccolithophore community. Although these four species contributed to the upper 15% of the dissimilarity between flora in the different hydrographic provinces in different seasons (according to a one-way SIMPER analysis), it is clear from their average relative abundances and high standard deviations in Table 6 that there is little consistent pattern in species level changes. Hence, the whole community (i.e. the species contributing to the other 85% of the dissimilarity) also varied and caused the seasonal differentiation seen in Figure 8 and Table 5. High values of J' further support this notion of whole community compositional variability rather than variability by a few species. A notable exception

to this was *P. vandelii*, which seems to have been completely absent in the subtropical gyre and equatorial waters during southern spring (Table 6) although, as already noted, distinguishing this species from *R. xiphos* can be difficult.

3.5. Distribution of rare taxa

Apart from the 31 taxa listed in Table 2, the other species in the AMT database consistently contributed less than 5% to total cell numbers and are regarded as rare in our analysis. Due to these low cell counts, intermittent occurrences will have a large influence on any statistical analysis of composition differences for this group and hence any trends should be viewed with caution. However, there is still value in examining the compositional changes of the rare species whilst being aware of the potential pitfalls. Examination of the distribution of the rare species shows that this group are widely distributed with respect to both depth and latitude (Figs. 5b and 7d).

A more detailed analysis of the distribution of this large group of species in the AMT samples by nMDS ordination (Fig. 9) shows strongly overlapping distributions, although subgroups of sample composition are identifiable and appear characteristic of temperate (Fig. 9b) and deep euphotic zone (1% and 0.1% surface irradiance; optical depths of 4.6 and 6.9) waters (Fig. 9c). ANOSIM pairwise tests further support statistically significant differences in rare species composition between samples in each of the hydrographic provinces, although differences between temperate and gyre/equatorial waters are statistically strongest ($p<0.001$) and between samples in the different floral zones, with the differences between UEZ and SEZ statistically strongest ($p<0.001$) (Table 7). This is indicative of the existence of biogeographic and euphotic zone floral groups within the rare species, although these species contribute little to the overall numerical abundances (i.e. consistently <5% of the total community).

4. Discussion

4.1. Coccolithophores in the equatorial and subtropical Atlantic Ocean

Total coccosphere (cell) counts of 150 to 300 per sample were sufficient to reliably quantify the abundance of species present at concentrations of greater than 0.5 cell mL^{-1} (see Table 1), who represented at least 95% of total cell numbers. The diversity (species richness) of coccolithophore communities is more difficult to determine due to the presence of a high number (140) of relatively rare species defined as consistently representing less than 5% of total numbers. The presence of a large number of rare coccolithophore species has also been described for other subtropical waters, such as the North Pacific gyre (Cortes et al., 2001; Thierstein et al., 2004). Species richness is dependent on the volume of sample examined which, for this study, was set by the number of coccospheres counted per sample and was generally in the range of 5 to 16 mL; consideration of Figure 3 indicates that 50 to 70% of total

species in any one sample were encountered depending on the volume examined. The high species richness, low evenness characteristics of phytoplankton communities, as discussed by Thierstein et al. (2004) for coccolithophores (see also O'Brien et al., 2016) and by Cermeno et al. (2014) for mixed phytoplankton populations, are likely to strongly influence ecological responses to both small and large scale variability in environmental conditions that affect cell growth and survival.

Setting the AMT dataset into the wider context of other open-ocean coccolithophore observations shows several interesting trends. The maximum observed counts for key coccolithophore taxa from the AMT dataset (199 samples) and from repeat sampling at the Bermuda Atlantic time-series (BATS) station (217 samples; Haidar and Thierstein, 2001) and the Hawaiian Oceanographic time-series (HOT) station (183 samples; Thierstein et al., 2004) in the subtropical Atlantic and Pacific oceans respectively are shown in Table 9. For the more numerous species, values are generally higher for BATS and lower for HOT compared to those from the AMT transect, reflecting relatively strong seasonality in surface stratification and nutrient levels at the subtropical gyre margin (BATS), which is poorly resolved within the AMT dataset, and persistent oligotrophic conditions throughout the year nearer to the gyre centre (HOT) compared to the more varied hydrography along the AMT transect (e.g. Fig. 2).

Another detailed taxonomic study of coccolithophores in the subtropical Atlantic is the work of Boeckel and Baumann (2008) who examined around 60 samples along a transect between 8^{o}S and 45^{o}S. Boeckel and Baumann (2008) did not provide coccosphere counts for individual taxa, preferring instead to express their results as ‘sphere units’ in order to take account of detached coccoliths. However, the most numerous taxa found by these authors north of 34^{o}S are all listed in Table 9. Similarly, analyses of coccolithophore assemblages in warm waters of the Pacific (Okada and Honjo, 1973; Honjo and Okada, 1974; Hagino et al., 2000; Hagino and Okada, 2004) and Indian Oceans (Takahashi and Okada, 2000) are also consistent with the AMT data (i.e. identical species lists to those in Tables 2 and 4). The main differences within the equatorial and subtropical Atlantic, and between the Atlantic and other oceanic regions, are in the regional abundances of taxa such as *E. huxleyi, G. oceanica* and *C. leptoporus*, which are all more abundant in areas of elevated nutrient levels, higher surface water temperatures and stronger water column stratification (Kinkel et al., 2000; Hagino et al., 2000; Franklin et al., 2009).

The species from each of the three floral depth groups and their ranges of maximum abundance listed in Table 9 can therefore be considered as representative of coccolithophore populations throughout the oligotrophic ocean. Regional increases in the strength of localized upwelling, both at the ocean margins and close to the Equator, and in seasonal mixing along the high latitude boundaries of the subtropical gyres are typically associated with a greater abundance of

LEZ taxa. Comparative quantitative information on the less common coccolithophore taxa has yet to be collated, but all open ocean samples examined by SEM have shown species richness comparable, though slightly lower, to that found for the AMT transect (171 taxa): 112 taxa were reported from the South Atlantic (Boeckel and Baumann, 2008); 100 to 125 taxa from the Pacific Ocean (Hagino et al., 2000; Cortes et al., 2001; Hagino and Okada, 2004); and 92 taxa from the Indian Ocean (Takahashi and Okada, 2000).

From an ecological perspective, in terms of the response of communities to environmental variability, it is important to consider the significance of the high diversity (species richness) of coccolithophore communities in oligotrophic waters (Fig. 3). Such diversity is characteristic of many types of microbes in the ocean, including the related non-calcifying haptophytes (Liu et al., 2009), generally taking the form of a few abundant species and a large number of rare ones (Logares et al., 2014), and is thought to be fundamental to the maintenance of ecosystem function and associated biogeochemical processes (Caron and Countway, 2009). The high species richness of each of the coccolithophore floral zones (UEZ, LEZ, SEZ) in the water column (see Tables 2 and 4) supports the conclusion of Logares et al. (2014), that assemblages have fairly regular proportions of abundant and rare taxa but contrasting structuring patterns across space and time. Within the context of environmental change, diversity represents a genetic reservoir of community adaptability. However, for coccolithophores or other types of microbes, it will not be possible to detect adaptation without initial detailed taxonomic or genomic descriptions of community structure, including the rare species.

Within the limits set by the AMT sampling programme (2 cruises per year, 2003-2005) inter-cruise differences in coccolithophore community composition were evident (Fig. 8a, Table 5). Such inter-cruise differences may relate to seasonal variability, though the timeframe of sampling is too limited to directly link these to seasonality. Clear and statistically significant (Table 5) inter-cruise differences were most obvious in Temperate waters (Fig. 8b), where large variations were observed in the abundance of common taxa such as *E. huxleyi*. Statistically significant differences in species composition were not limited to Temperate waters, with seasonal differences also detected in the subtropical gyres and equatorial waters (Table 5). Finally, it should be noted that, although large scale community distributional patterns can be generally related to large scale hydrographic and climatic factors, the causes for differences in the abundance of widespread taxa such as, for example, *Umbellosphaera* spp. over relatively small spatial scales (see Fig. 7c) remain unknown. High variability in rates of primary production in the oligotrophic Atlantic (e.g. Marañón et al., 2003) has been attributed to variations in rates of localized nutrient supply (see Johnson et al., 2010), and hence it appears that the structure, composition and dynamic properties of biological communities in the subtropical gyres is much less uniform than previously thought.

4.2. Coccolithophore biogeography: Vertical and horizontal distributions

The characteristic vertical distribution of coccolithophore taxa observed at stations representative of the subtropical gyres and equatorial waters (Fig. 5) follows closely the general pattern observed for subtropical waters from earlier studies (e.g. McIntyre and Bé, 1967; Winter et al., 1994). The terminology used in this study (UEZ, LEZ, SEZ) differs from that of other studies (e.g. Winter et al., 1994; Upper Photic Zone, Middle Photic Zone, Lower Photic Zone) due to a focus on the euphotic zone which supports upper ocean primary production. As the DCM is generally considered to mark the base of the euphotic zone (i.e. 1% of surface irradiance), the deepest coccolithophore zone is referred to as the 'Sub-euphotic Zone' rather than 'Lower Photic Zone', with two further zones in the upper euphotic zone (i.e. from the depth of 1% surface irradiance to the surface). The existence of the two upper euphotic zones (UEZ, LEZ) is supported by the species' normalised abundance profiles, with certain species having peaks not in the upper portion of the water column (UEZ) but deeper and above the depth of 1% surface irradiance (e.g. *Calciopappus* spp. and *G. ericsonii*; Fig 5b).

For stations where samples were taken from just the 5 standard light depths used for AMT primary production studies (e.g. Poulton et al., 2006a,b), it is difficult to describe or compare in detail the coccolithophore communities of the three vertical zones; the DCM (1% surface irradiance) is located at the transition between the LEZ and SEZ, with each of these two lower zones represented by just one sample (1% and 0.1% surface irradiances, respectively) that may or may not correspond to the maximum abundance of the key representative species (see Fig. 5). In contrast, the UEZ is better represented by three samples (55%, 33% and 14% surface irradiances).

Similarly, the horizontal (meridional) spacing of stations at which coccolithophores were sampled on AMT cruises 12 and 14 (Fig. 2a) is too coarse to show how oceanographic boundaries (see Aiken et al. 2000) or mesoscale eddy structure might relate to coccolithophore abundance or composition (e.g. Jin et al., 2016). In general, statistically similar communities in terms of species composition were found at closely spaced stations (<20 km apart, e.g. at the Equator on AMT 14; Fig. 7c), but there were wide differences in the relative abundance of common taxa (Fig. 7c). However, comparison of Figures 6b and 6c shows that, in general, coccolithophore communities differed to a much greater degree vertically in the water column (surface layer, DCM, sub-DCM) than horizontally across hydrographic provinces (gyres, equatorial waters). This is further supported through comparison of vertical profiles of (Bray-Curtis) similarity (Figs. 5a and 7e) to meridional changes in similarity with latitude (Fig. 7b).

The depth distribution of the main floral groups summarised in Table 2 is fully consistent with the conclusions of Winter et al. (1994) (see also McIntyre and Bé, 1967), who for subtropical waters, identified upper, middle and lower photic zones using similar reference light levels (>10%, 1-10%, and <1% of surface irradiance, with the DCM at the 1% level). Winter et al. (1994) stated that the middle photic zone was 'not easily distinguished by a characteristic flora', as also shown by the nMDS ordination analysis (Fig. 6c) for the AMT samples, with LEZ species (optical depth = 4.6) showing considerable overlap with both the UEZ group (optical depths 0.6, 1.1 and 2; irradiance levels 55, 33 and 14%) and SEZ group (optical depths 4.6 and 6.9; 1 and 0.1%). It is not surprising therefore that some species listed for the LEZ in Table 2 have been previously assigned to the layers above (e.g. *Ceratolithus* spp.) or below (e.g. *Syracosphaera anthos*). The conclusion of Winter et al. (1994) that *Umbellosphaera tenuis*, *Syracosphaera* spp., and placolith-bearing genera (such as *E. huxleyi* and *Gephyrocapsa* spp.) show no depth preference but tend to be most abundant in the middle photic zone is generally well supported by the AMT data, although some of the diverse *Syracosphaera* group (in particular *S. pulchra*) are found mainly in the UEZ (Table 2) and *U. tenuis* is classed as a UEZ taxon that extends to greater depths than *U. irregularis* (see Fig. 5a) in the AMT analysis.

Two general features of coccolithophore vertical distribution shown by the AMT data are firstly that the Bray-Curtis Similarity index declines with respect to the surface sample throughout the UEZ and LEZ (Fig. 4b; see also Fig. 7e), whereas the total numbers of both cells and species remain uniform between the surface and the depth of 1% surface irradiance (Fig. 4). Secondly, cell numbers for some characteristic SEZ taxa (in particular *Gladiolithus flabellatus*; see Fig. 5a) reach a maximum at or below the depth of 0.1% surface irradiance (Fig. 5b). The first observation implies that despite compositional changes in species composition with depth, the relative size of the community remains consistent, and that rare taxa as well as abundant ones (Table 2) change with depth; within the AMT dataset rare taxa that were largely confined to the LEZ include *Acanthoica quattrospina*, *Alisphaera pinnigera*, *Corisphaera gracilis*, *Gephyrocapsa oceanica*, *G. ornata*, *Helicosphaera* spp., *Picarola margalefi*, *Syracosphaera reniformis* and *Umbilicosphaera* spp. Peaks in species abundances well below the depth of 1% surface irradiance, where light can be assumed to be limiting to photosynthetic processes while nutrients are non-limiting (e.g. Poulton et al., 2006b), are likely indicative that most, if not all, SEZ species (e.g. *G. flabellatus*) have alternative nutritional strategies than autotrophy (i.e. mixotrophy or phagotrophy).

Regional anomalies in the vertical distribution of coccolithophores can be inferred from Figure 7e. Firstly, greater similarity between samples from the depths of 14% and 0.1% of surface irradiance in temperate waters compared to subtropical waters reflects greater vertical mixing of the upper water column at higher latitudes and a more uniform environment; in autumn (i.e. at

745 the southern stations on AMT 12 and 14), this trend can be attributed partly to populations of
746 SEZ species, including *Florisphaera profunda*, being mixed towards the surface, whereas in
747 spring (northern stations) UEZ and LEZ species occur throughout the water column before the
748 DCM and associated flora becomes well established. Secondly, greater statistical similarity of
749 species composition between samples from the 1% and 0.1% surface irradiance depths in
750 subtropical waters of the northern hemisphere (spring) compared to those of the southern
751 hemisphere (autumn) could be related to seasonal changes in the depth of the permanent DCM
752 (see Letelier et al., 2004); in spring, when the depth of 1% surface irradiance deepens such that
753 the DCM is displaced downwards into a layer where SEZ species, in particular, *F. profunda* are
754 relatively abundant.
755
756 The UEZ and SEZ coccolithophore taxa (Table 2) are largely confined to the well-stratified
757 upper waters (<100 m) of the equatorial and subtropical Atlantic (Figs. 7e), with their
758 distributions extending polewards in summer months with seasonal strengthening of
759 stratification (see Haidar and Thierstein, 2001). In contrast, LEZ taxa, and associated rare taxa
760 (e.g. as listed above, Fig. 10b), are widely distributed with respect to both latitude and depth
761 (Fig. 6f) and reach their maximum abundance in temperate waters (Figs. 6d and 7f) where high
762 concentrations (>50 coccospheres mL^{-1}) of species such as *E. huxleyi* and *G. ericsonii* are
763 observed. Hence, the LEZ taxa often represent the dominant species in temperate and high
764 latitude waters, a phenomenon potentially linked to light availability in that light levels
765 experienced in the LEZ (i.e. 10% of 2000 µmol photons m^{-2} s^{-1} on a 14 to 16 h day equates to
766 10.1 to 11.5 mol photons m^{-2} d^{-1}) are similar to average mixed layer irradiances experienced by
767 temperate coccolithophore communities (e.g. 10-15 mol photons m^{-2} d^{-1}; see for e.g. Poulton et
768 al., 2010, 2014).
769
770 ***4.3. Ecological and nutritional strategies of subtropical coccolithophores***
771 A notable feature of the AMT data is a strong difference in the mean vertical distribution
772 between HET and HOL forms of the same species (see Table 2 and 4), with the latter
773 consistently occurring at shallower depths as has been described for stratified waters of the
774 Mediterranean by Dimiza et al. (2008) and Cros and Estrada (2013). The best example in the
775 AMT dataset is provided by *Syracosphaera anthos* (Fig. 10a); with the distribution of the HET
776 form which belongs to the LEZ floral group often extending well below the DCM, whereas the
777 HOL form is characteristic of the UEZ group and typically confined to surface waters. Widening
778 this analysis to all species that have recognised HOL-HET stages in the AMT database (9
779 species; *Acanthoica quattrospina*, *Calcidicus leptoporus*, *Coccolithus pelagicus*, *Coronosphaera*
780 *mediterranea*, *Helicosphaera carteri*, *Syracospahera anthos*, *S. bannockii*, *S. nana*, and *S.*
781 *pulchra*) and plotting the ratio of HOL to HET cell counts (Fig. 10b) shows a clear decrease in
782 the relative abundance of HOL forms with depth. However, there are also clearly high numbers

783 of HET forms for some species (e.g. *Acanthoica quattrospina*) in surface waters as indicated by
784 the low HOL:HET ratios at light levels >10%.
785
786 A clear trend in the ecology of subtropical coccolithophores, in terms of floral groups, rare
787 species and HOL-HET species combinations is that a relatively large number of cells and
788 species are found deep in the water column (Tables 2 and 6; Figs. 4, 5, 6, 9 and 10). Such deep
789 waters experience low light levels in both relative (<1% of surface irradiance) and absolute
790 terms (<20 µmol photons m^{-2} s^{-1} based on a surface irradiance of 2000 µmol photons m^{-2} s^{-1} or
791 <2 mol photons m^{-2} d^{-1} on a 14 to 16 h day), which are likely to be limiting to autotrophic growth.
792 The oligotrophic waters of the equatorial and subtropical Atlantic Ocean are characterised by a
793 DCM which is situated on the nutricline (Fig. 2); autotrophs above the DCM are likely (inorganic)
794 nutrient-limited, while below they are likely light-limited (e.g. Poulton et al., 2006b). Hence, most
795 coccolithophore species face the problem of either insufficient inorganic (nitrate, phosphate)
796 nutrients (UEZ and LEZ taxa) in the upper water column or insufficient light (SEZ taxa) at depth
797 in order to compete with the dominant, small (<2 µm) photosynthetic picoplankton that have a
798 high efficiency for the assimilation of nutrients and light energy (Zubkov, 2014).
799
800 The DCM is generally considered to be a pigment rather than a biomass maximum (i.e.
801 composed of cells with a low carbon-to-chlorophyll ratio and hence high cellular pigmentation)
802 across the oligotrophic Atlantic Ocean. Picoeukaryotes, autotrophic cells <2 µm in diameter, are
803 relatively abundant in the DCM of the Atlantic subtropical gyres (<1000-5000 cells mL^{-1}; Tarran
804 et al., 2006) and, in the northern gyre, their distribution has been shown to be closely associated
805 with deep peaks in uptake rates for nitrate (Painter et al., 2014). Tarran et al. (2006) also
806 reported that the maximum biomass of autotrophic nanoeukaryotes (2-10 µm diameter)
807 occurred immediately above the DCM, where growth is likely to be enhanced close to the
808 nutricline by some upward diffusion of nutrients and by nutrient regeneration associated with
809 biological activity at the DCM.
810
811 For the coccolithophores, the DCM represents a transitional zone between the LEZ and SEZ
812 floral groups (Fig. 5a); the number of coccospheres in the DCM, although dominated by LEZ
813 taxa, is lower than in the UEZ except at equatorial stations (Fig. 4a), and important LEZ species
814 often show a clear maximum in abundance above, rather than at, the DCM (Fig. 5b). Thus,
815 there appears to be no clear relationship between the vertical distribution of coccolithophores
816 and the position of the nutricline, suggesting that irradiance at this depth is too low to support
817 nitrate assimilation by these relatively large (5-20 µm) cells. However, the LEZ group includes
818 taxa (*E. huxleyi, Gephyrocapsa* spp.) that increase in abundance in response to nutrient
819 enrichment as well as taxa (*Calciosolenia, Discosphaera, Michaelsarsia*) that do not (see Brand,
820 1994). The former probably have a similar nutritional status to the nano-eukaryotes mentioned

above whereas the latter, together with UEZ taxa, are considered more characteristic of nutrient-depleted oceanic waters and, almost without exception, have not been grown successfully in culture. Little is known about the biology of SEZ taxa, even to the extent as to whether or not they all have functional chloroplasts and are autotrophic. At light levels less than 1% of surface irradiance it seems very unlikely that they could reach observed abundances (Tables 8 and 9) by phototrophy (photosynthesis and reduction of inorganic nutrients) alone.

There are a number of references to possible mixotrophy by coccolithophores in connection with their survival in low-nutrient oceanic waters (Brand, 1994), the function of the haptonema (flagella) as a food gathering organelle (Kawachi and Inouye, 1995), the suggested function of modified coccoliths as 'particle collectors' (Aubry, 2009), and their phylogenetic linkages to heterotrophic flagellates (de Vargas et al., 2007). There is still little observational or experimental evidence for mixotrophy by coccolithophores. However, from a consideration of (i) the physiological ecology of species inhabiting oligotrophic oceanic waters (Brand, 1994), (ii) mixotrophy by non-calcifying haptophyes (Liu et al., 2009; Unrein et al., 2014), (iii) the quantitative importance of mixotrophy in oligotrophic oceanic ecosystems (Hartmann et al., 2012), (iv) the existence of heterotrophic coccolithophores in polar waters (Thomsen et al., 1991), and (v) the recognition of the significance of mixotrophy for the oceanic biological carbon pump (Mitra et al*.,* 2014) it is highly likely that many coccolithophores are actually mixotrophic, with possible exceptions being placolith-bearing species belonging to the LEZ group which form blooms in nutrient-enriched waters (e.g. *E. huxleyi, Gephyrocapsa* spp., *Calcidiscus* spp*., Umbilicosphaera* spp.).

The distinct vertical profiles for the HOL and HET forms of the same species (Dimiza et al., 2008; Cros and Estrada, 2013), may therefore reflect differences in the degree or type of mixotrophy across the group; HOLs in shallower, more oligotrophic water could supplement phototrophy with heterotrophy whereas HETs, in the absence of evidence for an ability to utilise nitrate under low light at depth, could be largely or entirely heterotrophic. A shift from one life-cycle stage to another may also represent an ecological strategy (Houdan et al., 2004, 2006) in response to changes in environmental conditions. In the case of the HET form of *Syracosphaera anthos* (Fig. 10), nano-eukaryotes in the DCM (Painter et al., 2014) are potentially an important food source. Alternative nutritional strategies for coccolithophores in low (inorganic) nutrient conditions may also include the use of dissolved organic carbon and nutrient sources to supplement or replace photosynthetic growth, though the composition, lability and bioavailability of this material is unclear. Clearly, innovative future research on the nutritional strategies of (subtropical) coccolithophores is key to fully understanding the ecology and biogeography of such species, as well as gaining a better perspective on coccolithophore impacts on the biological carbon pump in the oligotrophic ocean.

A better understanding of the nutrition of coccolithophores will also open the way to improved interpretation of data on the distribution of coccoliths in marine sediments in relation to environmental conditions. In particular for the important palaeo-indicator species *Florisphaera profunda*, SEZ taxa are mainly or entirely found below the DCM and if they are partly or wholly heterotrophic then their abundance is more likely to reflect the availability of living and non-living particulate material rather than of irradiance or inorganic nutrients (e.g. Molfino and McIntyre, 1990) or of a well-developed DCM (e.g. Grelaud et al., 2012). Furthermore, the depths of the nutricline and the SEZ are probably not independent variables as envisaged by Molfino and McIntyre (1990), in the sense that the depth of the nutricline approximates the 1% surface irradiance level, whether it is deep or shallow, and varies with the degree of biological attenuation of light in the overlying water (and the uptake of nitrate as light becomes available; Letelier et al., 2007). Hence, a shallowing of the depth of the 1% surface irradiance will be accompanied by a shallower nutricline as nitrate uptake follows light availability.

Furthermore, oceanic ecosystems associated with a shallow thermocline are more productive, and also generally show a greater abundance of *F. profunda* in the water column; for example, Figure 2 shows how the nutricline (and DCM) shallows in the equatorial region and northern gyre in spring during AMT 14 (see also Figs. 2 and 4 in Robinson et al., 2006), also at gyre margins (BATS) compared to gyre centres (HOT) (see Table 9). Therefore, it appears that changes in the relative abundance of *F. profunda* coccoliths in ocean sediments may reflect changes in the production and/or dissolution of coccoliths of UEZ and LEZ taxa. In the oligotrophic subtropical ocean with a deep nutricline, phytoplankton are relatively scarce and will be efficiently consumed by herbivores within surface waters (e.g. Poulton et al., 2006a), leading to high losses of coccoliths due to dissolution (Milliman et al., 1999), whereas at gyre boundaries and around upwelling regions, increases in coccolithophore abundance in the euphotic layer will lead to sudden downward fluxes of UEZ and LEZ coccoliths, a proportion of which may escape dissolution. However, at ocean boundaries and within enclosed seas, other factors may control the relative abundance of different types of coccoliths in the sediments (Ahagon et al., 1993); organic matter derived from continental shelf and terrestrial sources may be a significant source of food for heterotrophic coccolithophores, while freshwater inputs can affect the growth conditions for autotrophic taxa either positively or negatively through effects on nutrient levels, on light penetration (turbidity), and on depth of the thermocline. For example, in the western subtropical Atlantic, sediments in which *G. flabellatus* is more abundant than *F. profunda* are found in offshore regions affected by the outflow of the Amazon River, close to the continental slope affected by the Brazil Current and over the mid-Atlantic ridge (Boeckel et al., 2006); it would be of great interest to know why this happens in such contrasting situations.

4.4. Future recommendations

Though sample collection was limited to a depth resolution of only five standard light depths across much of the AMT transect, these light depths still reflected the general pattern of the vertical distribution of species composition in the equatorial and subtropical Atlantic Ocean. Ideally, higher resolution sampling (e.g. 15-20 sampling levels) would lend further support to the vertical patterns identified in this study, and if combined with increased meridional sampling frequency would also greatly expand the species level insights gained. The difficulty in reaching an examination volume which fully accounts for the incredible level of species diversity represents a limitation to gaining further insights into the biogeography and ecology of the rare species. Furthermore, the point where the cumulative species richness plateaus against examination volume (i.e. where the rarefaction curve plateaus) will likely be sample specific, also providing a limitation. However, examination of 150 to 300 coccospheres per sample did account for the dominant species in terms of cell numbers: with 31 out of the 171 taxa representing 95% of total cell numbers, and hence though it is not possible to fully describe the full species richness of the community it is possible to reliably analyse the vertical and meridional distribution of the numerically dominant species. In order to confidently identify seasonal and interannual variability in species composition in the subtropical ocean, a longer time-frame is required to be able to differentiate random variability from temporal trends. Such an expanded dataset, if geographically aliased in a suitable way, would also provide further insights into the biogeography of rare coccolithophore species.

The new perspectives gained from statistical exploration of coccolithophore distribution in the equatorial and subtropical Atlantic Ocean warrant further examination and confirmation. Such research will require innovative methodology and experimentation to confirm the nutritional strategies of upper-ocean and deep-dwelling coccolithophore species. For example, tracing particulate uptake through the use of fluorescently labelled prey items, high-resolution microscopy to examine the presence / absence of chloroplasts, and tracing the cellular uptake of labelled compounds. Heterotrophic or mixotrophic nutrition of coccolithophores has significant implications for their biogeochemical roles; for example, the impact on dissolved inorganic carbon and alkalinity through calcification, photosynthesis, respiration and dissolution will be very different to a cell which lacks photosynthesis and has high ratios of calcification to respiration. Indeed, the cellular coupling of photosynthesis and calcification, in terms of internal (carbon) substrate competition, will be very different in a cell which attains its energetic needs through respiration rather than autotrophy. How this impacts on cellular rates of calcification and growth, and hence the fitness and competition between autotrophic and heterotrophic (partly or fully) coccolithophores is completely unknown, but a key issue to be addressed when considering the species composition of oceanic communities. Moreover, communities dominated by autotrophic, heterotrophic or mixotrophic coccolithophores will have different

influences on air-sea CO_2 fluxes through variable roles in organic and inorganic production, and the biological carbon pump and carbonate-counter pump.

5. Conclusions

Across 199 samples collected in the equatorial and subtropical Atlantic Ocean, 171 coccolithophore taxa were identified (Appendix 1); of which 140 were classified as rare, consistently representing less than 5% of total cell numbers in all samples, while 31 were observed in enough abundance to allow us to analyse their vertical and meridional distribution. From multivariate statistical analysis, strong vertical gradients in species composition were identified in equatorial and subtropical waters, which lessened in Temperate waters. Three vertical zones in terms of floral composition were identified: an upper euphotic zone (UEZ), a lower euphotic zone (LEZ), and a sub-euphotic zone (SEZ). This vertical zonation is closely tied to the light availability through the water column, and the species involved in each zone are broadly similar to those identified by Winter et al. (1994) (see also McIntyre and Bé, 1967). Light levels in the SEZ are likely to be well below those required to support photosynthesis and hence it is suggested that ingestion of other plankton (mixotrophy or full phagotrophy) or dissolved organic compounds may support the growth (and hence calcification) of species at these depths.

Coccolithophore cell numbers were highest in temperate waters, while species richness was highest in the subtropical gyres and equatorial waters; comparison of gyre samples with other surface samples highlights relatively high similarity (>50%) across large horizontal distances, which contrasts with the sharp declines in similarity with depth seen in the gyres and equatorial waters. UEZ taxa were largely restricted to the subtropical gyres, while the LEZ taxa were found in both equatorial (EQ) and Temperate regions and some SEZ species were found in surface Temperate waters. LEZ species often represent the dominant species in Temperate and high latitude waters, which is potentially linked to similar light (and inorganic nutrient) climes between the LEZ in the subtropics and mixed layers in Temperate waters. Seasonal differences in coccolithophore species composition were stronger than inter-annual differences. The strongest seasonal variability seen was in Temperate waters, with elevated abundances of species such as *E. huxleyi* and *G. ericsonii* (both LEZ). Clearly the coccolithophore communities in low-latitude, low (inorganic) nutrient waters respond to temporal changes in environmental conditions and these environments are not quiescent regions of the global ocean.

Acknowledgements

The authors would like to acknowledge Dr Jeremy Young (University College London) for his constructive comments and discussions, as well as reviews and comments from the guest editor

and two reviewers of previous versions of the manuscript. We also acknowledge the support of the captains, officers and crews associated with AMT cruises 12, 14, 15 and 17, as well as the principal scientific officers for these cruises. This study is a contribution to the international IMBER project and was supported by the UK Natural Environment Research Council National Capability funding to Plymouth Marine Laboratory and the National Oceanography Centre, Southampton. This is contribution number 293 of the AMT programme. This work was also supported by a consortium grant (NER/O/S/2001/00680) and a NERC Fellowship to AJ Poulton (NE/F015054/1).

References

Ahagon, N., Tanaka, Y., Ujiie, H., 1993. *Florisphaera profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the north-western margin of the Pacific. Marine Micropaleontology 22, 255-273.

Aiken, J., Rees, N., Hooker, S., Holligan, P., Bale, A., Robins, D., Moore, G., Harris, R., Pilgrim, D., 2000. The Atlantic Meridional Transect: Overview and synthesis of data. Progress in Oceanography 45, 257-312.

Aiken, J., Pradhan, Y., Barlow, R., Lavender, S., Poulton, A.J., Holligan, P., Hardman-Mountford, N., 2009. Phytoplankton pigments and functional types in the Atlantic Ocean: A decadal assessment, 1995-2005. Deep-Sea Research II 56, 899-917.

Archer, D., 1996. An atlas of the distribution of calcium carbonate in sediments of the deep sea. Global Biogeochemical Cycles 10, 159-174.

Aubry, M.-P., 2009. A sea of Lilliputians. Palaeogeography Palaeoclimate Palaeoecology 284, 88-113.

Bach, L.T., MacKinder, L.C.M., Schulz, K.G., Wheeler, G., Schroeder, D.C., Brownlee, C., Riebesell, U., 2013. Dissecting the impact of CO_2 and pH on the mechanisms of photosynthesis and calcification in the coccolithophore *Emiliania huxleyi*. New Phytologist 199, 121-134.

Bach, L.T., Riebesell, U., Gutowska, M.A., Federwisch, L., Schulz, K.G., 2015. A unifying concept of coccolithophore sensitivity to changing carbonate chemistry embedded in an ecological framework. Progress in Oceanography 135, 125-138.

Balch, W.M., Gordon, H.R., Bowler, B.C., Drapeau, D.T., Booth, E.S., 2005. Calcium carbonate measurements in the surface global ocean based on Moderate-Resolution Imaging Spectroradiometer data. Journal of Geophysical Research 114, C07020.

Barlow, R.G., Aiken, J., Holligan, P.M., Cummings, D.G., Maritorena, S., Hooker, S., 2002. Phytoplankton pigment and absorption characteristics along meridional transects in the Atlantic Ocean. Deep-Sea Research I 47, 637-660.

1009 Baumann, K.-H., Boeckel, B., Čepek, M., 2008. Spatial distribution of living coccolithophores
1010 along an east-west transec in the subtropical South Atlantic. Journal of Nannoplankton
1011 Research 30, 9-21.
1012 Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E.M., Ruiz-Pino, D., Metzl, N, Goyet, C.,
1013 Buchet, N., Coupel, P., Grelaud, M., Rost, B., Rickaby, R.E.M., de Vargas, C., 2011.
1014 Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. Nature
1015 476, 80-83.
1016 Berelson, W.M., Balch, W.M., Najjar, R., Feely, R.A., Sabine, C., Lee, K., 2007. Relating
1017 estimates of $CaCO_3$ production, export and dissolution in the water column to
1018 measurements of $CaCO_3$ rain into sediment traps and dissolution on the sea floor: A
1019 revised global carbonate budget. Global Biogeochemical Cycles 21, GB1024.
1020 Boeckel, B., Baumann, K.H., Henrich, R., Kinkel, H., 2006. Coccolith distribution patterns in
1021 South Atlantic and Southern Ocean surface sediments in relation to environmental
1022 gradients. Deep-Sea Research I 53, 1073-1099.
1023 Boeckel, B., Baumann, K.-H., 2008. Vertical and lateral variations in coccolithophore community
1024 structure across the subtropical front in the South Atlantic Ocean. Marine
1025 Micropalaeontology 67, 255-273.
1026 Bollmann, J., Cortes, M.Y., Kleijne, A., Ostergaard, J.B., Young, J.R., 2006. *Solisphaera* gen.
1027 nov. (Prymnesiophyceae), a new coccolithophore genus from the lower photic zone.
1028 Phycologia 45, 465-477.
1029 Brand, L.E., 1994. Physiological ecology of marine coccolithophores. In *Coccolithophores (*eds
1030 Winter, A., Siesser W.G.), Cambridge University Press, Cambridge pp 39-49.
1031 Broecker, W., Clark, E., 2009. Ratio of coccolith $CaCO_3$ to foraminifera $CaCO_3$ in late Holocene
1032 deep sea sediments. Paleoceanography 24, PA3205.
1033 Caron, D.A., Countway, P.D., 2009. Hypotheses on the role of protistan rare biosphere in a
1034 changing world. Aquatic Microbial Ecology 57, 227-238.
1035 Cermeno, P., Teixeira, I.G., Branco, M., Figueiras, F.G., Marañón, E., 2014. Sampling the limits
1036 of species richness in marine phytoplankton communities. Journal Plankton Research 36,
1037 1135-1139.
1038 Charalampopoulou, A., Poulton, A.J., Tyrrell, T., Lucas, M.I., 2011. Irradiance and pH affect
1039 coccolithophore community composition on a transect between the North Sea and the
1040 Arctic Ocean. Marine Ecology Progress Series 431, 25-43.
1041 Clark, K.R., Warwick, R.M., 2001. Change in marine communities: An approach to statistical
1042 analysis and interpretation, 2nd ed. PRIMER-E, Plymouth.
1043 Cortes, M.Y., Bollmann, J., Thierstein, H.R., 2001. Coccolithophore ecology at the HOT station
1044 ALOHA, Hawaii. Deep-Sea Research II 48, 1957-1981.
1045 Cros, L., Fortuno, J.-M., 2002. Atlas of North-western Mediterranean coccolithophores.
1046 Scientifica Marina 66, 186.

1047 Cros, L., Estrada, M., 2013. Holo-heterococcolithophore life cycles: ecological implications.
1048 Marine Ecology Progress Series 492, 57-68.
1049 de Vargas, C., Aubry, M.-P., Probert, I., Young, J., 2007. Origin and evolution of
1050 coccolithophores: From coastal hunters to oceanic farmers. In *Evolution of Primary*
1051 *Producers in the Sea* (eds Falkowski, P.G., Knoll, A.H.), Elsevier Academic Press, pp
1052 251-285.
1053 Dimiza M.D., Triantaphyllou, M.V., Dermitzakis, M.D., 2008. Vertical distribution and ecology of
1054 living coccolithophores in the marine ecosystems of Andros Island (Middle Aegean Sea)
1055 during late summer 2001. Hellenic Journal of Geoscience 43, 7-20.
1056 Franklin, D.J., Poulton, A.J., Steinke, M., Young, J., Peeken, I., Malin, G., 2009.
1057 Dimethylsulphide, DMSP-lyase activity and microplankton community structure inside and
1058 outside of the Mauritanian upwelling. Progress in Oceanography 83, 134-142.
1059 Grelaud M., Marino, G., Ziveri, P., Rohling, E.J., 2012. Abrupt shoaling of the nutricline in
1060 response to massive freshwater flooding at the onset of the last interglacial sapropel
1061 event. Paleoceanography 27, PA3208.
1062 Hagino, K., Okada, H., 2004. Floral response of coccolithophores to progressive
1063 oligotrophication in the South Equatorial Current, Pacific Ocean. In *Global Environmental*
1064 *Change in the Ocean and on Land*, (eds Shiyomi, M. *et al.*), pp 121-132.
1065 Hagino, K., Okada, H., Matsuoka, H., 2000. Spatial dynamics of coccolithophore assemblages
1066 in the equatorial West-Central Pacific Ocean. Marine Micropaleontology 39, 53-72.
1067 Haidar, A.T., Thierstein, H.R., Deuser, W.G., 2000. Calcareous phytoplankton standing stocks,
1068 fluxes and accumulation in Holocene sediments off Bermuda (North Atlantic). Deep-Sea
1069 Research II 47, 1907-1938.
1070 Haidar, A.T., Thierstein, H.R., 2001. Coccolithophore dynamics off Bermuda (North Atlantic).
1071 Deep-Sea Research II 48, 1925-1956.
1072 Hartmann, M., Grob, C., Tarran, G.A., Martin, A.P., Burkill, P.H., Scanlan, D.J., Zubkov, M.V.,
1073 2012. Mixotrophic basis of Atlantic oligotrophic ecosystems. Proceedings of the National
1074 Academy Science 109, 5756-5760.
1075 Henriksson, A.S., 2000. Coccolithophore response to oceanographic changes in the equatorial
1076 Atlantic during the last 200,000 years. Palaeogeography Palaeoclimate Palaeoecology
1077 156, 161-173.
1078 Holligan, P.M., Fernández, E., Aiken, J., Balch, W.M., Boyd, P., Burkill, P.H., Finch, M., Groom,
1079 S.B., Malin, G., Muller, K., Purdie, D.A., Robinson, C., Trees, C.C., Turner, S.M., van der
1080 Wal, P., 1993. A biogeochemical study of the coccolithophore, *Emiliania huxleyi*, in the
1081 North Atlantic. Global Biogeochemical Cycles 7, 879-900.
1082 Honjo, S., Okada, H., 1974. Community structure of coccolithophores in the photic layer of the
1083 mid-Pacific. Micropalaeontology 20, 209-230.

1084 Houdan, A., Billard, C., Marie, D., Not, F., Saez, A.G., Young, J.R., Probert, I., 2004.
1085 Holococcolithophore-heterococcolithophore (Haptophyta) life cycles: Flow cytometric
1086 analysis of relative ploidy levels. Systematics and Biodiversity 1, 453-465.
1087 Houdan, A., Probert, I., Zatylny, C., Veron, B. and Billard, C., 2006. Ecology of oceanic
1088 coccolithophores. I. Nutritional preferences of the two stages in the life cycle of
1089 *Cocccolithus braarudii* and *Calcidiscus leptoporus*. Aquatic Microbial Ecology 44, 291-
1090 301.
1091 Jin, X., Liu, C., Poulton, A.J., Dai, M., Guo, X., 2016. Coccolithophore responses to
1092 environmental variability in the South China Sea: species composition and calcite content.
1093 Biogeosciences 13, 4843-4861.
1094 Johnson, K.S., Riser, S.C., Karl, D.M., 2010. Nitrate supply from deep to near-surface waters of
1095 the North Pacific subtropical gyre. Nature 465, 1062-1065.
1096 Kawachi, M., Inouye, I., 1995. Functional roles of the haptonema and the spine scales in the
1097 feeding process of *Chrysochromulina spinifera* (Fournier) Pienaar et Norris (Haptophyta =
1098 Prymnesiophyta). Phycologia 34, 193-200.
1099 Kinkel, H., Baumann, K.-H., Cepek, M., 2000. Coccolithophores in the equatorial Atlantic
1100 Ocean: Response to seasonal and Late Quaternary surface water variability. Marine
1101 Micropalaeontology 39, 87-112.
1102 Kleijne, A., Cros, L., 2009. Ten new extant species of the coccolithophore *Syracosphaera* and a
1103 revised classification scheme for the genus. Micropalaeontology 55, 425-462.
1104 Knappertsbusch, M., Brummer, G.-J.A., 1995. A sediment trap investigation of sinking
1105 coccolithophorids in the North Atlantic. Deep-Sea Research I 42, 1083-1109.
1106 Letelier, R.M., Karl, D.M., Abbott, M.R., Bidigare, R.R., 2004. Light driven seasonal patterns of
1107 chlorophyll and nitrate in the lower euphotic zone of the North Pacific subtropical gyre.
1108 Limnology and Oceanography 49, 508-519.
1109 Liu, H., Probert, I., Claustre H., Aris-Brossou, S., Frada, M., Not, F., de Vargas, C., 2009.
1110 Extreme diversity in non-calcifying haptophytes explains a major pigment paradox in open
1111 oceans. Proceedings of the National Academy of Sciences 106, 12803-12808.
1112 Logares, R., Audic, S., Bass, D., Bittner, L., Boutte, C., Christen, R., Claverie, J.-M., Decalle, J.,
1113 Dolan, J.R., Dunthom, M., Edvardsen, B., Gobet, A., Kooistra, W.H.C.F., Mahe, F., Not,
1114 F., Ogata, H., Pawlowski, J., Pernice, M.C., Romac, S., Shalchian-Tabrizi, K., Simon, N.,
1115 Stoeck, T., Santini, S., Siano, R., Wincker, P., Zingone, A., Richards, T.A., de Vargas, C.,
1116 Massana, R., 2014. Patterns of rare and abundant marine microbial eukaryotes. Current
1117 Biology 24, 813-821.
1118 Malin, G., Steinke, M., 2004. Dimthyl sulphide production: What is the contribution of the
1119 coccolithophores? In *Coccolithophores: From Molecular Processes to Global Impact* (eds
1120 Thierstein, H.R., Young, J.R.), Springer-Verlag, pp 455-479.

Marañón, E., Holligan, P.M., Varela, M., Mourino, B., Bale, A.J., 2000. Basin-scale variability of phytoplankton biomass, production and growth in the Atlantic Ocean. Deep-Sea Research I 47, 825-857.

Marañón, E., Holligan, P.M., Barciela, R., Gonzalez, N., Mourino, B., Pazo, M.J., Varela, M., 2001. Patterns of phytoplankton size structure and productivity in contrasting open-ocean environments. Marine Ecology Progress Series 216, 43-56.

Marañón, E., Behrenfeld, M.J., Gonzalez, N., Mourino, B., Zubkov, M.V., 2003. High variability of primary production in oligotrophic waters of the Atlantic Ocean: Uncoupling from phytoplankton biomass and size structure. Marine Ecology Progress Series 257, 1-11.

McIntyre, A., Be, A.W.H., 1967. Modern coccolithophores of the Atlantic Ocean I. Placoliths and cyrtoliths. Deep-Sea Research 14, 561-597.

Meier, K.J.S., Berger, C., Kinkel, H., 2014. Increasing coccolith calcification during CO_2 rise of the penultimate deglaciation (Termination II). Marine Micropaleontology 112, 1-12.

Memery, L., Arhan, M., Alvarez-Salgado, X.A., Messias, M.-J., Mercier, H., Castro, C.G., Rios, A.F., 2000. The water masses along the western boundary of the south and equatorial Atlantic. Progress in Oceanography 47, 69-98.

Menden-Deuer, S., Lessard E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protest plankton. Limnology and Oceanography 45, 569-579.

Milliman J.D., Troy, P.J., Balch, W.M., Adams, A.K., Li, Y.-H., Mackenzie, F.T., 1999. Biologically mediated dissolution of calcium carbonate above the chemical lysocline? Deep-Sea Research I 46, 1653-1669.

Mitra, A., Flynn, K.J, Burkholder, J.M., Berge, T., Calbet, A., Raven, J.A., Graneli, E., Glibert, P.M., Hansen, P.J., Stoecker, D.K., Thingstad, F., Tillmann, U., Våge, S., Zubkov, M.V., 2014. The role of mixotrophic protists in the biological carbon pump. Biogeosciences 11, 995-1005.

Molfino, B., McIntyre, A., 1990. Precessional forcing of nutricline dynamics in the equatorial Atlantic. Science 249, 766-769.

Monteiro, F.M., Bach, L.T., Brownlee, C., Bown, P., Rickaby, R.E.M., Poulton, A.J., Tyrrell, T., Beaufort, L., Dutkiewicz, S., Gibbs, S., Gutowska, M.A., Lee, R., Riebesell, U., Young, J., Ridgwell, A., 2016. Why marine phytoplankton calcify. Scientific Advances 2, e1501822.

O'Brien, C.J., Peloquin, J.A., Vogt, M., Heinle, M., Gruber, N., Ajani, P., Andruleit, H., Aristegui, J., Beaufort, L., Estrada, M., Karentz, D., Kopczyńska, E., Lee, R., Poulton A.J., Pritchard, T., Widdicombe, C., 2013. Global marine plankton functional type biomass distributions: Coccolithophores. Earth System Science Data 5, 259-276.

O'Brien, C.J., Vogt, M., Gruber, N., 2016. Global coccolithophore diversity: Drivers and future change. Progress in Oceanography 140, 27-42.

Okada, H., Honjo, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. Deep-Sea Research 20, 355-374.

1159 Okada, H., McIntyre, A., 1977. Modern coccolithophores of the Pacific and North Atlantic
1160 Oceans. Micropaleontology 23, 1-55.
1161 Painter, S.C., Patey, M.D., Tarran, G.A., Torres-Valdes, S., 2014. Pico-eukaryote distribution in
1162 relation to nitrate uptake in the oceanic nitracline. Aquatic Microbial Ecology 72, 195-213.
1163 Perez, V., Fernandez, E., Marañón, E., Serret, P., Garcia-Soto, C., 2005. Seasonal and
1164 interannual variability of chlorophyll *a* and primary production in the equatorial Atlantic: *In*
1165 *situ* and remote sensing observations. Journal of Plankton Research 27, 189-197.
1166 Perez, V., Fernandez, E., Marañón, E., Moran, X.A.G., Zubkov, M.V., 2006. Vertical distribution
1167 of phytoplankton biomass, production and growth in the Atlantic subtropical gyres. Deep-
1168 Sea Research I 53, 1616-1634.
1169 Poulton, A.J., Sanders, R., Holligan, P.M., Stinchcombe, M.C., Adey, T.R., Brown, L.,
1170 Chamberlain, K., 2006a. Phytoplankton mineralization in the tropical and subtropical
1171 Atlantic Ocean. Global Biogeochemical Cycles 20, GB4002.
1172 Poulton, A.J., Holligan, P.M., Hickman, A., Kim, Y.-N., Adey, T.R., Stinchcombe, M.C., Holeton,
1173 C., Root, S., Woodward, E.M.S., 2006b. Phytoplankton carbon fixation, chlorophyll-
1174 biomass and diagnostic pigments in the Atlantic Ocean. Deep-Sea Research II 53, 1593-
1175 1610.
1176 Poulton, A.J., Adey, T.R., Balch, W.M., Holligan, P.M., 2007. Relating coccolithophore
1177 calcification rates to phytoplankton community dynamics: Regional differences and
1178 implications for carbon export. Deep-Sea Research II 54, 538-557.
1179 Poulton, A.J., Charalampopoulou, A., Young, J.R., Tarran, G.A., Lucas, M.I., Quartly, G.D.,
1180 2010. Coccolithophore dynamics in non-bloom conditions during late summer in the
1181 central Iceland Basin (July-August 2007). Limnology and Oceanography 55, 1601-1613.
1182 Poulton, A.J., Painter, S.C., Young, J.R., Bates, N.R., Bowler, B., Drapeau, D., Lyczsckowski,
1183 E., Balch, W.M., 2013. The 2008 *Emiliania huxleyi* bloom along the Patagonian Shelf:
1184 Ecology, biogeochemistry, and cellular calcification. Global Biogeochemical Cycles 27, 1-
1185 11.
1186 Poulton, A.J., Stinchcombe, M.C., Achterberg, E.P., Bakker, D.C.E., Dumousseaud, C.,
1187 Lawson, H.E., Lee, G.A., Richier, S., Suggett, D.J., Young, J.R., 2014. Coccolithophores
1188 on the north-west European shelf: Calcification rates and environmental controls.
1189 Biogeosciences 11, 3919-3940.
1190 Quinn, P.S., Cortes, M.Y., Bollmann, J., 2005. Morphological variation in the deep ocean-
1191 dwelling coccolithophore *Florisphaera profunda* (Haptophyta). European Journal of
1192 Phycology 40, 123-133.
1193 Robinson, C., Poulton, A.J., Holligan, P.M., Baker, A.R., Forster, G., Gist, N., Jickells, T.D.,
1194 Malin, G., Upstill-Goddard, R., Williams, R.G., Woodward, E.M.S., Zubkov, M.V., 2006.
1195 The Atlantic Meridional Transect (AMT) programme: A contextual view, 1995-2005. Deep-
1196 Sea Research II 53, 1593-1610.

1197 Sarmiento, J.L., Dunno, J., Gnanadesikan, A., Key, R.M., Matsumoto, K., Slater, R., 2002. A
1198 new estimate of the $CaCO_3$ to organic carbon export ratio. Global Biogeochemical Cycles 16,
1199 1107.
1200 Schwab, C., Kinkel, H., Weinelt, M., Repschläger, J., 2012. Coccolithophore paleo-productivity
1201 and ecology response to de-glacial and Holocene changes in the Azores Current System.
1202 Palaeoceanography 27, PA3210.
1203 Takahashi, K., Okada, H., 2000. Environmental control on the biogeography of modern
1204 coccolithophores in the south-eastern Indian Ocean offshore of Western Australia. Marine
1205 Micropaleontology 39, 73-86.
1206 Tarran, G.A., Heywood, J.L., Zubkov, M.V., 2006. Latitudinal changes in the standing stocks of
1207 nano- and picoeukaryotic phytoplankton in the Atlantic Ocean. Deep-Sea Research II 53,
1208 1516-1529.
1209 Thierstein, H.R., Cortes, M.Y., Haidar, A.T., 2004. Plankton community behaviour on ecological
1210 and evolutionary timescales: When models confront evidence. In *Coccolithophores: From*
1211 *Molecular Processes to Global Impact* (eds Thierstein, H.R., Young, J.R.), Springer-
1212 Verlag, pp 455-479.
1213 Thomsen, H.A., Ostergaard, J.B., Hansen, L.E., 1991. Heteromorphic life histories in Arctic
1214 coccolithophorids (Prymnesiophyceae). Journal of Phycology 27, 634-642.
1215 Unrein, F., Gasol, J.M., Not, F., Forn, I., Massana, R., 2013. Mixotrophic haptophytes are key
1216 bacterial grazers in oligotrophic coastal waters. ISME Journal 8, 174-176.
1217 Young, J.R., Geisen, M., Cros, L., Kleijne, A., Probert, I., Ostergaard, J.B., 2003. A guide to
1218 extant coccolithophore taxonomy. Journal of Nannoplankton Research, Special Issue 1, 1-
1219 132.
1220 Venrick, E., 1982. Phytoplankton in an oligotrophic ocean: Observations and questions.
1221 Ecological Monographs 52, 129-154.
1222 Winter, A., Jordan, R.W., Roth, P.H., 1994. Biogeography of living coccolithophores in ocean
1223 waters. In *Coccolithophores* (eds. A. Winter, A., Siesser, W.G.), Cambridge University
1224 Press, pp 161-177.
1225 Ziveri, P., Baumann, K.-H., Boeckel, B., Bollmann, J., Young, J.R., 2004. Biogeography of
1226 selected Holocene coccoliths in the Atlantic Ocean. In *Coccolithophores: From Molecular*
1227 *Processes to Global Impact* (eds Thierstein, H.R., Young, J.R.), Springer-Verlag, pp 403-
1228 428.
1229 Ziveri, P., de Bernardi, B., Baumann, K.-H., Stoll, H.M., Mortyn, P.G., 2007. Sinking of coccolith
1230 carbonate and potential contribution to organic carbon ballasting in the deep ocean. Deep-
1231 Sea Research II 54, 659-675.
1232 Zubkov, M.V., Tarran, G.A., 2008. High bacterivory by the smallest phytoplankton in the North
1233 Atlantic Ocean. Nature 455, 224-226.

1234 Zubkov, M.V., 2014. Faster growth of the major prokaryotic versus eukaryotic CO_2 fixers in the
1235 oligotrophic ocean. Nature Communications 5, 3776.
1236

FIGURE LEGENDS

Figure 1. Station positions (symbols) and cruise tracks (solid black lines) for the four AMT cruises sampled for coccolithophores in this study. (a) AMT 12 (12 May - 15 June, 2003) and AMT 14 (26 April - 2 June, 2004) superimposed on a spring 2014 (March 21st to June 20th) composite of MODIS-Aqua derived chlorophyll. (b) AMT 15 (19 September - 29 October, 2004) and AMT 17 (15 October - 28 November, 2005) superimposed on an autumn 2014 (September 21st to December 20th) composite of MODIS-Aqua derived chlorophyll. Yellow filled squares indicate the relative positions of the three high-resolution profiles presented in Figures 4 and 5 (see Section 3.1). Horizontal dashed lines indicate the major hydrographic provinces used in the meridional analysis (see Sections 3.3 and 3.4) of coccolithophore taxa distribution (TMP, temperate waters; NG, Northern Gyre waters; EQ, equatorial waters; SG, Southern Gyre waters).

Figure 2. Latitudinal sections showing (a) the depths at which coccolithophore samples were collected on the AMT 12 and AMT 14 cruises in relation to the depth of 1% surface irradiance (euphotic zone, Z_{eup}) for AMT 14, (b) the distribution of fluorometrically-determined chlorophyll *a* (mg m^{-3}) in relation to the depth of 1% surface irradiance (solid black line) for AMT 14, and (c) the distribution of nitrate (µmol kg^{-1}) in relation to the depth of 1% surface irradiance (solid black line) for AMT 14. Vertical dashed lines in (a) indicate the major hydrographic provinces used in the meridional analysis (see Sections 3.3 and 3.4) of coccolithophore taxa distribution (TMP, temperate waters; NG, Northern Gyre waters; EQ, equatorial waters; SG, Southern Gyre waters).

Figure 3. Histograms of cumulative species richness in selected samples from AMT 14 (CTD 71, 31m; a, b) and AMT 12 (CTD 26, 120m; c). Replicate counts from the same Scanning Electron Microscopy stub (a) and repeat counts from the same sample but different stubs (b, c) are shown. The cumulative volume (mL) counted for each sample is given as a value above each histogram. Horizontal bars on (b) and (c) indicate the number of species identified in each sample.

Figure 4. Vertical profiles of coccolithophore community characteristics against optical and percentage surface irradiance depths for three AMT 14 stations taken to be representative of the Southern Gyre, equatorial waters, and the Northern Gyre. (a) Normalised chlorophyll *a* (Chl), coccosphere abundance (cells mL^{-1}), and the number of coccolithophore taxa (species richness) (S). (b) Normalised chlorophyll *a* (Chl), Pielou's Evenness (J'), and Bray-Curtis Similarity (*Sim*) referenced to the near-surface sample. The depth (m) of indicative levels of percentage surface irradiance are given against the horizontal dashed lines indicating the 10%, 1% and 0.1% surface irradiance depths.

Figure 5. Vertical profiles of abundance of the different coccolithophore floral groups (see Table 2; Section 3.1) and selected taxa from each group against optical and percentage surface irradiance depth for three AMT 14 stations taken to be representative of the Southern Gyre, equatorial waters, and the Northern Gyre. (a) Relative abundance of Upper Euphotic Zone (UEZ), Lower Euphotic Zone (LEZ), Sub-Euphotic Zone (SEZ) and rare (consistently <5% of total cell numbers) coccolithophore groups at the three stations. (b) Normalised abundance of taxa representative of the UEZ (*Umbellosphaera irregularis* and *U. tenuis*), LEZ (*Gephyrocapsa ericsonii* and *Calciopappus spp.*), and SEZ (*Florisphaera profunda* and *Gladiolithus flabellatus*) groups at the Southern Gyre station.

Figure 6. Normalised Multi-Dimensional Scaling (nMDS) ordination and bubble plots showing latitudinal and depth variability in coccolithophore community structure for AMT 12 and AMT 14: (a) by cruise; (b) by latitudinal (TMP, Temperate waters; EQ, equatorial waters; NG, Northern Gyre waters; SG, Southern Gyre waters); (c) by optical depth; (d) by coccosphere abundance (log); (e) for UEZ taxa (relative abundance to other floral groups); (f) for LEZ taxa (relative abundance to other floral groups); (g) for SEZ taxa (relative abundance to other floral groups); and (h) for rare taxa (relative abundance to other floral groups). The samples from the three high-resolution depth profiles presented in Figures 4 and 5 are identified in panel (a) as filled square symbols. Stress on the two-dimensional plot (see (a)) was 0.17 which indicates a 'good representation of the data in two-dimensional space' (Clarke and Warwick, 2001).

Figure 7. Latitudinal trends of coccolithophore composition in samples from the near-surface (optical depth = 0.6 (55% surface irradiance)) during AMT 14. (a) Chlorophyll *a* (Chl, mg m^{-3}), cell abundance (cells, mL^{-1}) and the number of coccolithophore taxa (species richness) (S). (b) Pielou's Evenness (J') and Bray-Curtis Similarity (*Sim*) referenced to a Northern Gyre station at 22.3^{o}N. (c) Normalised abundance of *Umbellosphaera tenuis*, *U. irregularis* and *E. huxleyi.* (d) Relative abundance of coccolithophore flora (see Table 4) representative of Temperate waters, Gyre waters (northern and southern), and equatorial waters, as well as the rare group (consistently <5% of total cell numbers). (e) The degree of similarity of species composition from the 14%, 1% and 0.1% surface irradiance depths compared to the 55% sample (see a) expressed as percentage Bray-Curtis Similarity (*Sim*). Vertical dashed lines in panel (a) indicate the positions of the major hydrographic provinces (TMP, temperate waters; NG, Northern Gyre waters; EQ, equatorial waters; SG, Southern Gyre waters).

Figure 8. Normalised Multi-Dimensional Scaling (nMDS) ordination showing inter-cruise and latitudinal differences in the UEZ coccolithophore community composition for AMTs 12, 14, 15 and 17: (a) by cruise; and (b) by hydrographic provinces (TMP, temperate waters; NG, Northern

Gyre waters; EQ, equatorial waters; SG, Southern Gyre waters). Stress on the two-dimensional plot (see (a)) was 0.20 which indicates a 'good representation of the data in two-dimensional space' (Clarke and Warwick, 2001).

Figure 9. Normalised Multi-Dimensional Scaling (nMDS) ordination showing relative distributions of rare coccolithophore taxa recorded for all AMT 12 and AMT 14 samples: (a) by cruise; (b) by hydrographic province (TMP, temperate waters; NG, Northern Gyre waters; EQ, equatorial waters; SG, Southern Gyre waters); and (c) by optical depth. Stress on the two-dimensional plot (see (a)) was 0.23 which indicates a 'good representation of the data in two-dimensional space' (Clarke and Warwick, 2001).

Figure 10. Depth distribution of hetero- (HET) and holo-coccosphere (HOL) taxa against optical and percentage surface irradiance depth for all AMT 12 and AMT 14 samples from Southern Gyre waters, equatorial waters and Northern Gyre waters. (a) Depth distribution of *Syracosphaera anthos* cells in both HET and HOL form. (b) All coccolithophore taxa present as both HOL and HET forms (i.e. *Acanthoica quattrospina*, *Calcidicus leptoporus*, *Coccolithus pelagicus*, *Coronosphaera mediterranea*, *Helicosphaera carteri*, *Syracosphaera anthos*, *S. bannockii*, *S. nana*, and *S. pulchra*). Vertical dashed lines indicate the percentage surface irradiance depths used to differentiate between floral depth zones (UEZ, >10%; LEZ, 10% to 1%; SEZ, <0.1%).

Table 1. Replicate counts of coccospheres for samples collected on AMT 12 (Deep Chlorophyll Maximum, chlorophyll *a* = 0.19 mg m^{-3}) and AMT 14 (surface layer, chlorophyll *a* = 0.05 mg m^{-3}). AMT 12 sample: 15 taxa were recorded from all 4 Scanning Electron Microscopy (SEM) stubs, with the 3 most abundant (>1 mL^{-1}) taxa (*F. profunda,* (average ± standard deviation) 4.4 ± 0.1 cells mL^{-1}; *Ophiaster* spp., 1.3 ± 0.1 cells mL^{-1}; *Palusphaera vandelii*, 1.2 ± 0.2 cells mL^{-1}) making up 57% of the total cell numbers; mean Relative Standard Deviation (RSD) for the other 12 taxa present was 11%; a further 4 taxa were recorded in 3 out of the 4 stubs. AMT 14 sample: 16 taxa were recorded from all 4 stubs, with the 4 most abundant (>1mL^{-1}) taxa (*E. huxleyi*, 1.1 ± 0.3 cells mL^{-1}; *G. ericsonii*, 2.4 ± 0.2 cells mL^{-1}; *Syracosphaera delicata,* 1.4 ± 0.4 cells mL^{-1}; *U. tenuis,* 4.9 ± 0.7 cells mL^{-1}) making up 48% of the total number of coccospheres; mean RSD for the other 11 taxa was 7%; a further 6 taxa were recorded in 3 out of the 4 stubs.

	AMT 12, CTD-26, 120 m			AMT 14, CTD-71, 31 m		
	Count volume (mL)	No. of taxa	Cells (mL^{-1})	Count volume (mL)	No. of taxa	Cells (mL^{-1})
Stub 1	15.1	27	12.9	6.6	40	22.6
Stub 2	15.1	29	12.3	7.3	32	19.2
Stub 3	15.0	28	10.7	7.2	36	20.2
Stub 4	15.0	32	12.6	7.2	37	19.7
Cumulative	60.2	49		28.3	66	
Mean (± S.D)			12.1 (± 1.0)			20.4 (± 1.5)

Table 2. Coccolithophore floral groups based on analysis of each species' cell abundance normalised to its maximum cell abundance observed in three stations taken as representative of Southern Gyre waters, equatorial waters, and Northern Gyre waters (see Fig. 1) during AMT 14. A species' depth habitat was classified as the uppermost depth horizon where the maximum value (i.e. 1) and consistent values >0.75 were observed between the 100%, 10%, 1% and 0.1% percentage surface irradiance depths (see Fig. 4). Each of the listed taxa consistently made up more than 5% of total cell numbers, and was assigned to the photic zone of overall maximum abundance. The number (n) of samples in each depth zone (across the three stations) in which species were analysed is given in parenthesis.

Upper Euphotic Zone (UEZ), >10% surface irradiance (n = 7)	Lower Euphotic Zone (LEZ), 10-1% surface irradiance (n = 8)	Sub-euphotic Zone (SEZ), <1% surface irradiance (n = 13)
Corisphaera gracilis	*Calciopappus sp.*	*Algirosphaera robusta*
Palusphaera vandelii	*Calciosolenia brasiliensis*	*Calciosolenia murrayi*
Rhabdosphaera xiphos	*Ceratolithus* spp.	*Florisphaera profunda*
Syracosphaera bannockii	*Discosphaera tubifera*	*Gladiolithus flabellatus*
S. bannockii HOL	*Emiliania huxleyi*	*Hayaster perplexus*
Syracosphaera delicata	*Gephyrocapsa ericsonii*	*Reticulofenestra sessilis*
Syracosphaera pulchra HOL	*Michaelsarsia elegans*	*Tetralithoides quadrilaminata*
Umbellosphaera irregularis	*Oolithus antillarum*	
Umbellosphaera tenuis	*Ophiaster spp.*	
	Rhabdosphaera clavigera	
	Solisphaera spp.	
	Syracosphaera anthos	
	Syracosphaera nana	
	Syracosphaera reniformis	
	Syracosphaera sp.	

Table 3. Multivariate statistical analyses of differences in coccolithophore species composition for the three photic zones identified (UEZ, Upper Euphotic Zone; LEZ, Lower Euphotic Zone; SEZ, Sub-euphotic Zone). ANOSIM is a one way analysis of similarities; SIMPER is a one way analysis of (dis)similarity percentages species contributions to the differences between euphotic zone groups.

Groups	ANOSIM		SIMPER
	R-Statistic	*p* level	Average dissimilarity (%)
Comparison for selected stations in Figure 4 (n = 28 samples)			
UEZ (n = 7) v LEZ (n = 8)	0.19	p<0.05	55.2
UEZ (n = 7) v SEZ (n = 13)	0.97	*p*<0.001	79.1
LEZ (n = 8) v SEZ (n = 13)	0.74	*p*<0.001	70.7
Comparison for all AMT-14 stations (n = 85 samples)			
UEZ (n = 41) v LEZ (n = 19)	0.49	p<0.001	64.3
UEZ (n = 41) v SEZ (n = 25)	0.94	*p*<0.001	79.2
LEZ (n = 19) v SEZ (n = 25)	0.54	*p*<0.001	67.8

Table 4. Coccolithophore floral groups based on the latitudinal range of their maximum abundance relative to hydrographic provinces (see Fig. 1; TMP, Temperate waters; EQ, equatorial waters; Northern and Southern Gyre waters, NG and SG). The list is based on taxa found in 16 surface (55% surface irradiance) samples from AMT 14 and which represented more than 5% of total cell numbers in at least one surface sample. The affiliation of taxa in terms of the vertical floral zones (see Table 2) are also indicated (UEZ, Upper Euphotic Zone; LEZ, Lower Euphotic Zone; SEZ, Sub-euphotic Zone).

Temperate (TMP), >35°N or >30°S	Gyres (SG, NG), 30°S to 10°S or 10°N to 35°N	Equator (EQ), <10°S to <10°N
Algirosphaera robusta (SEZ)	*Acanthoica quattrospina*	*Calciosolenia brasiliensis* (LEZ)
Alisphaera ordinata	*Anthosphaera fragaria*	*Corisphaera tyrrheniensis*
Alisphaera pinnigera	*Anthosphaera periperforata*	*Gephyrocapsa oceanica*
Alisphaera quadrilatera	*Calcidiscus leptoporus*	*Homozygosphaera spinosa*
Calciopappus sp. (LEZ)	*Calyptrolithina multipora*	*Michaelsarsia elegans* (LEZ)
Calciosolenia murrayi (SEZ)	*Calyptrolithophora papillifera*	*Palusphaera vandelii* (UEZ)
Calyptrolithina divergens	*Ceratolithus* spp. (LEZ)	*Papposphaera lepida*
Emiliania huxleyi (LEZ)	*Corisphaera gracilis* (UEZ)	*Poricalyptra magnaghii*
Florisphaera profunda (SEZ)	*Coronosphaera mediterranea* HOL *hellenica*	*Syracosphaera ampliora*
Gephyrocapsa ericsonii (LEZ)	*Cyrtosphaera* sp.	*Syracosphaera marginaporata*
Gephyrocapsa muellerae	*Discosphaera tubifera* (LEZ)	*Syracosphaera pirus*
Gephyrocapsa ornata	*Helicosphaera carteri*	*Syracosphaera rotula*
Helicosphaera pavimentum	*Helicosphaera carteri* HOL	
Oolithotus antillarum (LEZ)	*Helladosphaera cornifera*	
Oolithotus fragilis	*Homozygosphaera arethusae*	
Ophiaster spp. (LEZ)	*Pappomonas* sp. Type 4	
Reticulofenestra parvula	*Pappomonas* sp.	
Syracosphaera anthos (LEZ)	*Polycrater galapagensis*	
Syracosphaera corolla	*Poricalyptra aurisinae*	
Syracosphaera delicate (UEZ)	*Rhabdosphaera clavigera* (LEZ)	
Syracosphaera halldalii	*Rhabdosphaera xiphos* (UEZ)	
Syracosphaera histrica	*Solisphaera* spp. (LEZ)	
Syracosphaera molischii	*Sphaerocalyptra* sp.1	
Syracosphaera nana HOL	*Syracosphaera anthos* HOL	
Syracosphaera nodosa	*Syracosphaera bannockii* (UEZ)	
Syracosphaera ossa	*S. bannockii* HOL (UEZ)	
Syracosphaera protrudens	*Syracosphaera lamina*	
Syracosphaera squamosa	*Syracosphaera nana* (LEZ)	
Syracosphaera sp. (LEZ)	*Syracosphaera noroitica*	
Umbilicosphaera sibogae	*Syracosphaera prolongata*	
	Syracosphaera pulchra	
	Syracosphaera pulchra HOL (UEZ)	
	Syracosphaera hastata	
	Syaracosphaera reniformis (LEZ)	
	Umbellosphaera irregularis (UEZ)	
	Umbellosphaera tenuis (UEZ)	
	Umbilicosphaera hulburtiana	
	Unknown holococcolith	

Table 5. Analysis of inter-cruise differences between surface coccolithophore communities during cruises in May (M) (AMT 12, n = 15; AMT 14, n = 17) and September (S) (AMT 15, n = 6; AMT 17, n = 21) for the four hydrographic provinces (see Fig. 1; TMP, Temperate waters; EQ, equatorial waters; NG, Northern Gyre waters; SG, Southern Gyre waters). ANOSIM is a one way analysis of similarities; SIMPER is a one way analysis on (dis)similarity percentages species contributions to the statistical differences between communities. The number of samples (n) in each province in each season is given in parenthesis.

Groups	ANOSIM		SIMPER
	R-Statistic	*p* level	Average Dissimilarity (%)
M-TMP (n = 9) v S-TMP (n = 8)	0.44	$p<0.001$	69.1
M-SG (n = 7) v S-SG (n = 11)	0.54	$p<0.001$	57.5
M-EQ (n = 8) v S-EQ (n = 5)	0.41	$p<0.01$	57.6
M-NG (n = 10) v S-NG (n = 4)	0.53	$p<0.01$	62.6

Table 6. Comparison of mean values (± Standard Deviation) of surface coccolithophore community composition, sea-surface temperature (SST) and chlorophyll *a* concentrations. Hydrographic provinces (see Fig. 1) are: TMP, Temperate waters; NG, Northern Gyre waters; SG, Southern Gyre waters; EQ, equatorial waters. Species were selected from one-way SIMPER analysis of species contributing to the upper 15% of dissimilarity between flora in different hydrographic provinces grouped by season. The number of samples (n) included in the analysis in each season and each province are also indicated.

Characteristic	Northern spring (AMT 12 and 14, n = 35)				Southern spring (AMT 15 and 17, (n = 27)			
	TMP (n = 9)	NG (n = 10)	SG (n = 7)	EQ (n = 8)	TMP (n = 8)	NG (n = 4)	SG (n = 5)	EQ (n = 10)
Total cells (cells mL^{-1})	51.2 (52.4)	24.6 (11.5)	23.7 (4.3)	19.5 (10.0)	166.3 (103.3)	18.2 (4.8)	13.8 (3.5)	16.6 (6.9)
Species richness	30.6 (14.4)	38.9 (11.1)	36.7 (4.2)	32.4 (5.4)	18.7 (6.7)	30.5 (4.1)	29.8 (3.3)	25.6 (4.8)
Pielou's Evenness (J')	0.6 (0.2)	0.8 (0.1)	0.8 (0.1)	0.8 (0.0)	0.5 (0.2)	0.8 (0.1)	0.8 (0.0)	0.8 (0.0)
Shannon-Weiner diversity (H')	2.1 (0.7)	3.0 (0.4)	2.8 (0.2)	2.8 (0.1)	1.6 (0.4)	2.6 (0.3)	2.6 (2.1)	2.6 (0.2)
Emiliania huxleyi	0.30 (0.74)	0.10 (0.06)	0.07 (0.05)	0.08 (0.06)	0.64 (0.55)	0.18 (0.13)	0.12 (0.06)	0.24 (0.11)
Gephyrocapsa ericsonii	0.26 (0.44)	0.05 (0.06)	0.02 (0.03)	-	0.15 (0.19)	0.22 (0.16)	0.27 (0.06)	0.03 (-)
Umbellosphaera irregularis	-	0.03 (0.04)	0.18 (0.17)	0.14 (0.14)	-	0.06 (0.04)	0.08 (0.03)	0.11 (0.05)
Umbellosphaera tenuis	0.05 (0.07)	0.10 (0.10)	0.09 (0.09)	0.06 (0.03)	0.02 (0.01)	0.14 (0.07)	0.21 (0.13)	0.09 (0.06)
Rhabdosphaera xiphos	0.01 (0.01)	0.03 (0.03)	0.08 (0.11)	0.01 (0.01)	0.01 (0.01)	0.08 (0.05)	0.07 (0.03)	0.06 (0.04)
Palusphaera vandelii	0.06 (0.03)	0.11 (0.05)	0.12 (0.05)	0.13 (0.11)	0.01 (0.00)	0.01 (-)	-	0.01 (-)
SST (^{o}C)	17.8 (3.9)	22.9 (1.5)	25.3 (2.2)	27.5 (0.8)	17.9 (0.8)	24.0 (1.4)	24.3 (0.9)	26.9 (0.9)
Chlorophyll *a* (mg m^{-3})	0.18 (0.15)	0.04 (0.01)	0.05 (0.02)	0.16 (0.07)	0.26 (0.14)	0.05 (0.02)	0.04 (0.02)	0.16 (0.06)

1398 **Table 7.** Multivariate statistical analyses of rare coccolithophore distributions (i.e. species
1399 consistently contributing less than 5% of total numbers in all samples) for all stations on the AMT
1400 12 and AMT 14 cruises. The species composition for each sample is examined in relation to: (a)
1401 cruise number (AMT 12 or AMT 14); (b) hydrographic province; and (c) photic zone floral group.
1402 Hydrographic provinces (see Fig. 1) are: Temperate waters (TMP), equatorial waters (EQ),
1403 Northern Gyre waters (NG), and Southern Gyre waters (SG). Photic zone floral groups are: Upper
1404 Euphotic Zone (UEZ), Lower Euphotic Zone (LEZ), and Sub-euphotic Zone (SEZ). ANOSIM is a
1405 one way analysis of similarities; SIMPER is a one way analysis of (dis)similarity percentages
1406 species contributions to the differences between euphotic zone groups. The number of samples (n)
1407 in each province in each season is given in parenthesis.
1408

Groups	ANOSIM R-Statistic	*p* level	SIMPER Average dissimilarity (%)
Comparison by Hydrographic province (n = 150)			
TMP (n = 35) v SG (n = 38)	0.21	p<0.001	80.7
TMP (n = 35) v EQ (n = 34)	0.18	p<0.001	80.1
TMP (n = 35) v NG (n = 43)	0.15	p<0.001	81.6
SG (n = 38) v EQ (n = 34)	0.14	p<0.001	80.8
SG (n = 38) v NG (n = 43)	0.07	p<0.005	81.0
EQ (n = 34) v NG (n = 43)	0.10	p<0.01	81.8
Comparison by Euphotic Zone Floral Groups (n = 85)			
UEZ (n = 41) v LEZ (n = 19)	0.29	p<0.001	79.3
UEZ (n = 41) v SEZ (n = 25)	0.58	p<0.001	90.4
LEZ (n = 19) v SEZ (n = 25)	0.12	p<0.01	86.8

Table 8. Estimates of the maximum particulate organic carbon (POC) biomass for major coccolithophore species from the equatorial and subtropical Atlantic Ocean (Northern Gyre waters, Southern Gyre waters, equatorial waters) in samples from AMT cruises 12, 14, 15 and 17. Table includes the vertical floral group affiliation (UEZ, Upper Euphotic Zone; LEZ, Lower Euphotic Zone; SEZ, Sub-euphotic Zone; R indicates species classified as rare in the vertical floral analysis, see Section 3.1), the maximum cell count in the AMT database (see Table 9), estimated cell POC (following O'Brien et al., 2013), the maximum POC biomass, and the sample ID (cruise number, depth and latitude).

Species	Floral Group	Maximum cell count (cells mL^{-1})	Cell POC (pmol C $cell^{-1}$)	Maximum POC (nmol C L^{-1})	AMT Cruise	Sample Depth (m)	Latitude
Umbellosphaera irregularis	UEZ	11.2	2.4	27	12	16	10.6°S
Umbellosphaera tenuis	UEZ	9.8	2.5	25	14	13	33.0°S
Syracosphaera pulchra	UEZ	1.8	10.8	19	12	20	26.5°S
Umbilicosphaera hulburtiana	R	2.6	5.5	14	14	15	22.3°S
Emiliania huxleyi	LEZ	35.4	1.1	39	14	60	0.1°S
Umbilicosphaera sibogae	R	1.2	17.1	21	17	21	23.8°S
Oolithotus antillarum	LEZ	9.4	1.9	18	14	60	7.3°N
Rhabdosphaera clavigera	LEZ	6.2	1.3	8	12	10	6.5°S
Calcidiscus leptoporus	R	1.5	5.2	8	17	8	30.7°S
Hayaster perplexus	SEZ	0.8	53.1	42	14	160	28.7°N
Florisphaera profunda	SEZ	42.7	0.8	34	12	100	14.4°N
Calciosolenia murrayi	SEZ	4.9	3.6	18	14	130	29.3°N
Gladiolithus flabellatus	SEZ	9.6	1.3	12	12	150	18.0°N
Algirosphaera robusta	SEZ	4.8	1.8	9	12	135	29.4°N

Table 9. A comparison of maximum coccosphere counts (cells mL^{-1}) from equatorial and subtropical samples from AMT (cruises 12, 14, 15 and 17; this study) with those from the Bermuda Atlantic Time-Series (BATS; Haidar and Thierstein, 2001) and Hawaii Ocean Time-series (HOT; Cortes et al., 2001, Thierstein et al., 2004). LM indicates light microscope counts; SEM indicates Scanning Electron Microscope counts. The vertical floral group affiliations are also indicated (UEZ, Upper Euphotic Zone; LEZ, Lower Euphotic Zone; SEZ, Sub-euphotic Zone; R indicates species classified as rare in the vertical floral analysis, see Section 3.1). Values in parentheses are maximum counts from AMT temperate water samples.

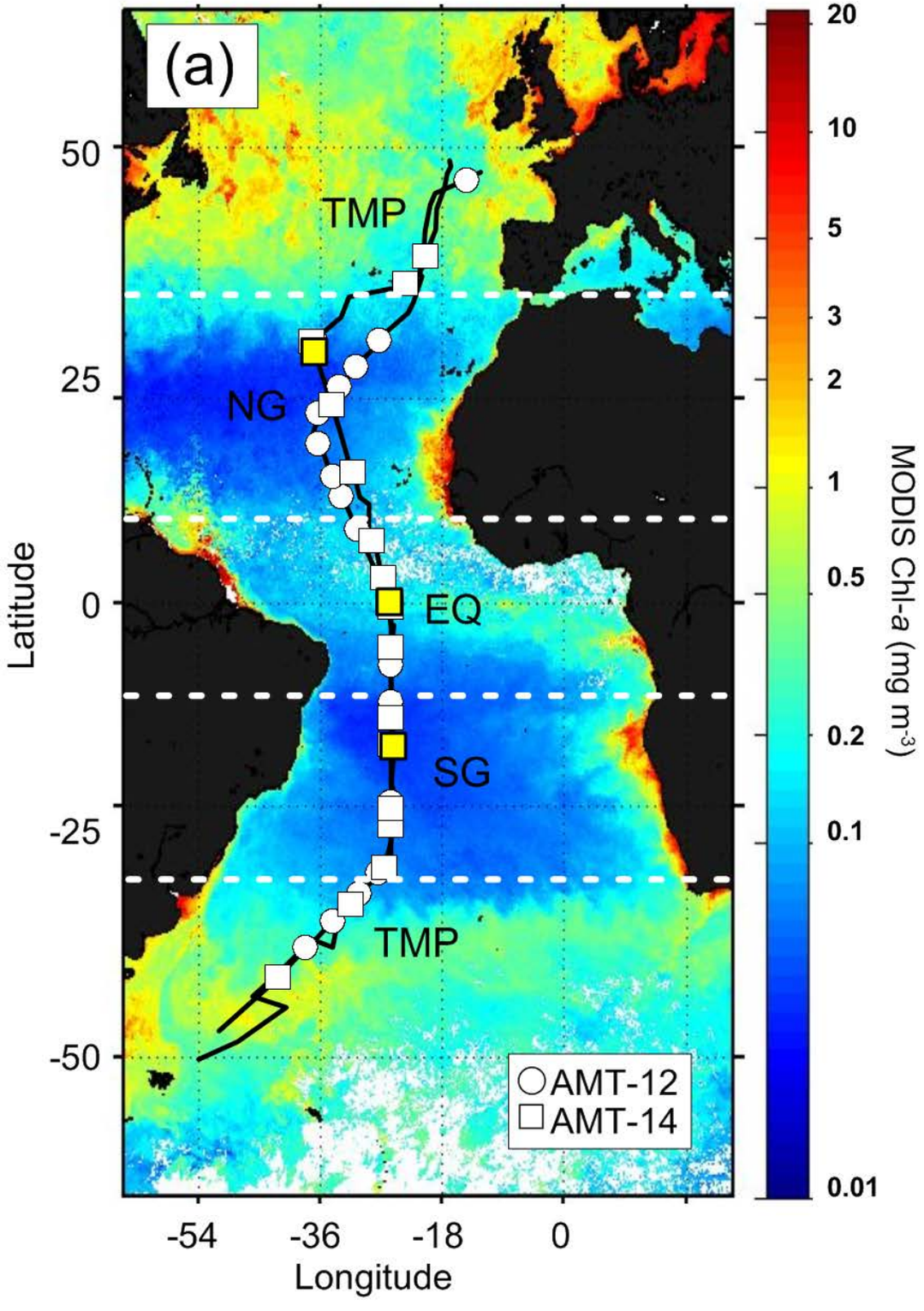
Species	Floral Group	AMT 32°S-30°N SEM	BATS 32.2°N LM	HOT 22.7°N SEM
Calcidiscus leptoporus	R	1.5 (37.0)	2.3	0.2
Discosphaera tubifera	UEZ	3.7 (8.2)	2.3	na
Emiliania huxleyi	LEZ	35.4 (265.8)	92.7	19.9
Florisphaera profunda	SEZ	42.7	67.5	15.0
Gephyrocapsa ericsonii	LEZ	12.0 (224.1)	26.2 [a]	7.9
G. oceanica	R	4.0	1.4	3.1
Gladiolithus flabellatus	SEZ	9.6	5.2	na
Helicosphaera spp	R	1.2	1.4	0.2
Rhabdosphaera clavigera	LEZ	6.2	4.7	na
Syracosphaera pulchra	UEZ	1.8	0.9	0.8
Umbellosphaera irregularis	UEZ	11.2	16.2	19.9
U. tenuis	UEZ	9.8	34.1	16.4
Umbilicosphaera hulburtiana	R	2.6 (8.8)	0.5	na
U. sibogae	R	1.2 (1.4)	1.6	0.2

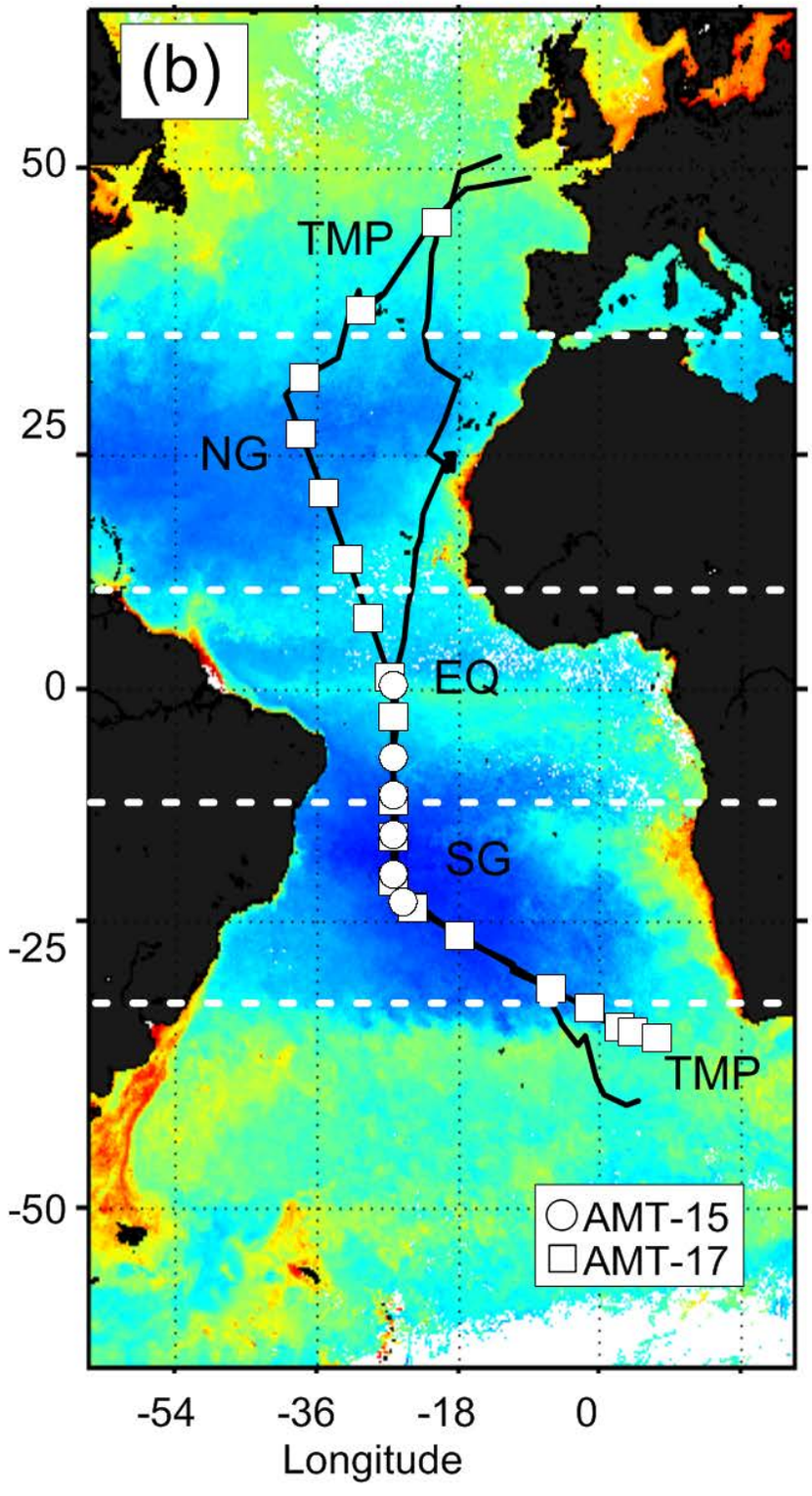
[a] counted as small coccospheres; na = not available.

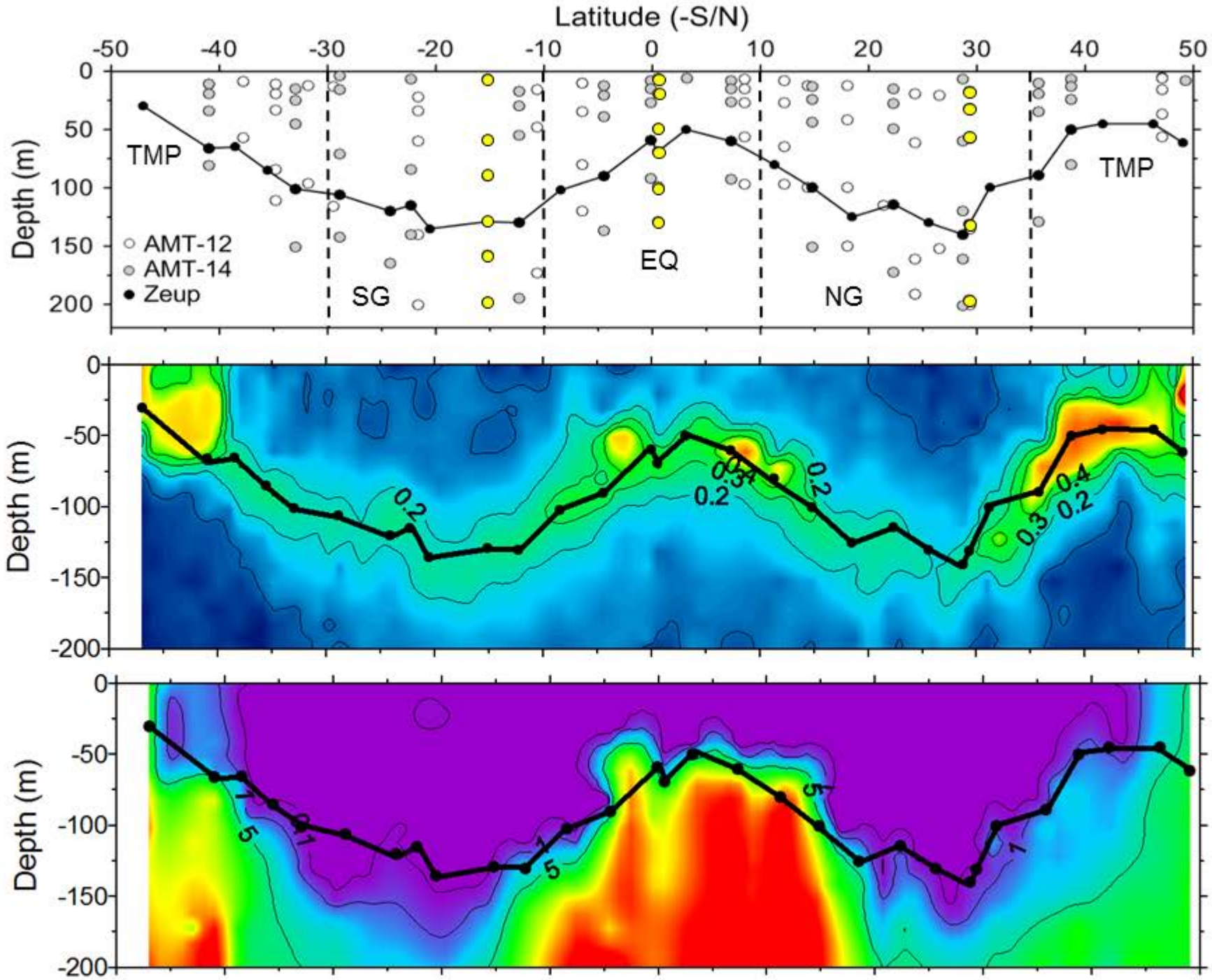
Appendix 1: List of taxa identified by Scanning Electron Microscopy. Holococcolithophores (HOL) indicated in bold italics.

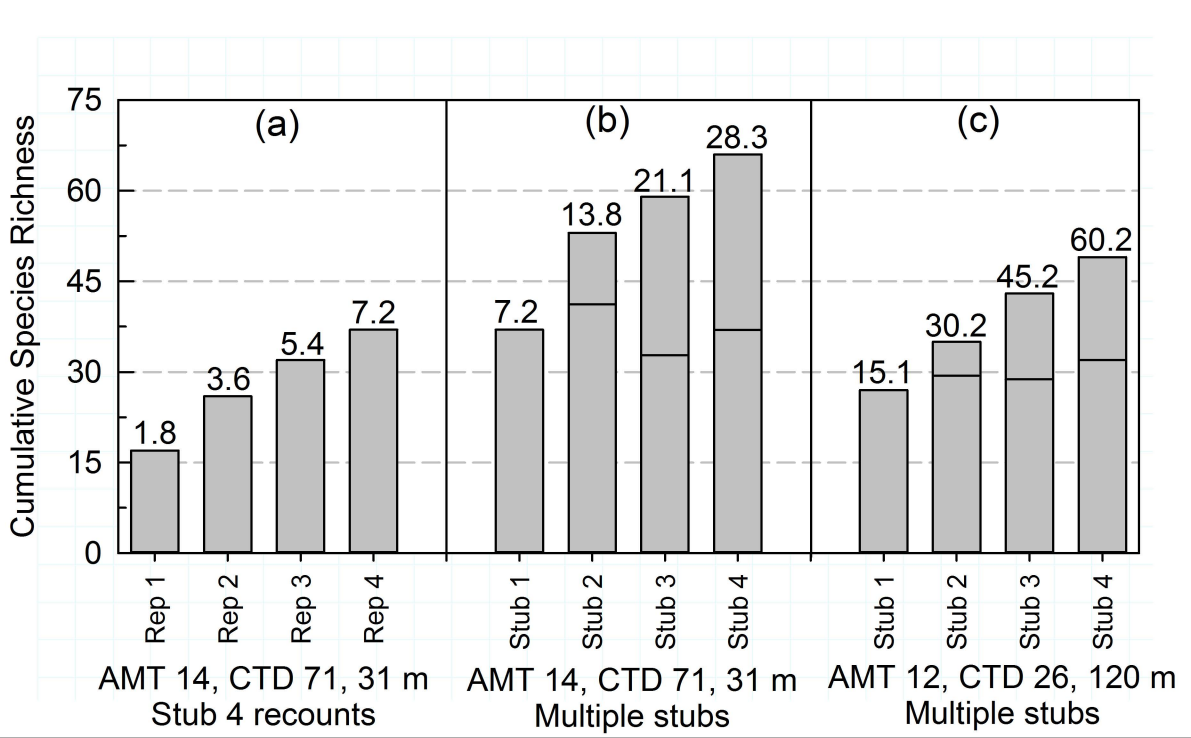
Species name	**Species name**
Acanthoica maxima	*Cyrtosphaera lecaliae*
Acanthoica quattrospina	*Cyrtosphaera sp.*
***Acanthoica quattrospina* HOL**	*Discosphaera tubifera*
Acanthoica sp.	*Emiliania huxleyi*
Algirosphaera cucullata	*Ericiolus*? sp.
Algirosphaera robusta	*Florisphaera profunda*
Alisphaera capulata	***Flosculosphaera calceolariopsis***
Alisphaera extenta	*Gephyrocapsa ericsonii*
Alisphaera gaudii	*Gephyrocapsa muellerae*
Alisphaera ordinata	*Gephyrocapsa oceanica*
Alisphaera pinnigera	*Gephyrocapsa ornata*
Alisphaera quadrilatera	*Gephyrocapsa* sp.
Alisphaera unicornis	*Gladiolithus flabellatus*
Alisphaera sp.	***Gliscolithus amitakareniae***
Alveosphaera bimurata	*Hayaster perplexus*
Anacanthoica acanthos	*Helicosphaera carteri*
Anacanthoica cidaris	***Helicosphaera carteri* HOL**
Anthosphaera fragaria	*Helicosphaera hyalina*
Anthosphaera lafourcadii	*Helicosphaera pavimentum*
Anthosphaera periperforata	*Helicosphaera wallichii*
Calcidiscus leptoporus	*Helicosphaera* sp.
***Calcidiscus leptoporus* HOL**	***Helladosphaera cornifera***
Calciopappus sp.	***Helladosphaera pienaarii***
Calciosolenia brasiliensis	***Helladosphaera vavilovii***
Calciosolenia murrayi	***Homozygosphaera arethusae***
Calicasphaera diconstrictra	***Homozygosphaera spinosa***
Calyptrolithina divergens	***Homozygosphaera triarcha***
Calyptrolithina multipora	***Homozygosphaera vercellii***
Calyptrolithophora papillifera	*Hymenomonas lacunae*
Calyptrosphaera dentata	*Jomonlithus* sp.
Calyptrosphaera heimdaliae	*Michaelsarsia adriaticus*
Calyptrosphaera sphaeroidea	*Michaelsarsia elegans*
Canistrolithus sp.1	*Ochrosphaera neapolitana*
Ceratolithus spp	*Oolithotus antillarum*
Coccolithus pelagicus	*Oolithotus fragilis*
***Coccolithus pelagicus* HOL**	*Ophiaster* spp.
Corisphaera gracilis	*Palusphaera vandelii*
Corisphaera strigilis	*Palusphaera* sp.1
Corisphaera tyrrheniensis	*Pappomonas* sp. Type 2
Coronosphaera binodata	*Pappomonas* sp. Type 3
Coronosphaera maxima	*Pappomonas* sp. Type 4
Coronosphaera mediterranea	*Pappomonas* sp.
Coronosphaera mediterranea* HOL *hellenica	*Papposhaera arctica*
Coronosphaera mediterranea* HOL *wettsteinii	*Pappsphaera borealis*
Coronosphaera sp.	*Pappsphaera lepida*
Cyrtosphaera aculeata	*Pappsphaera thomsenii*
	Pappsphaera sp. Type 1

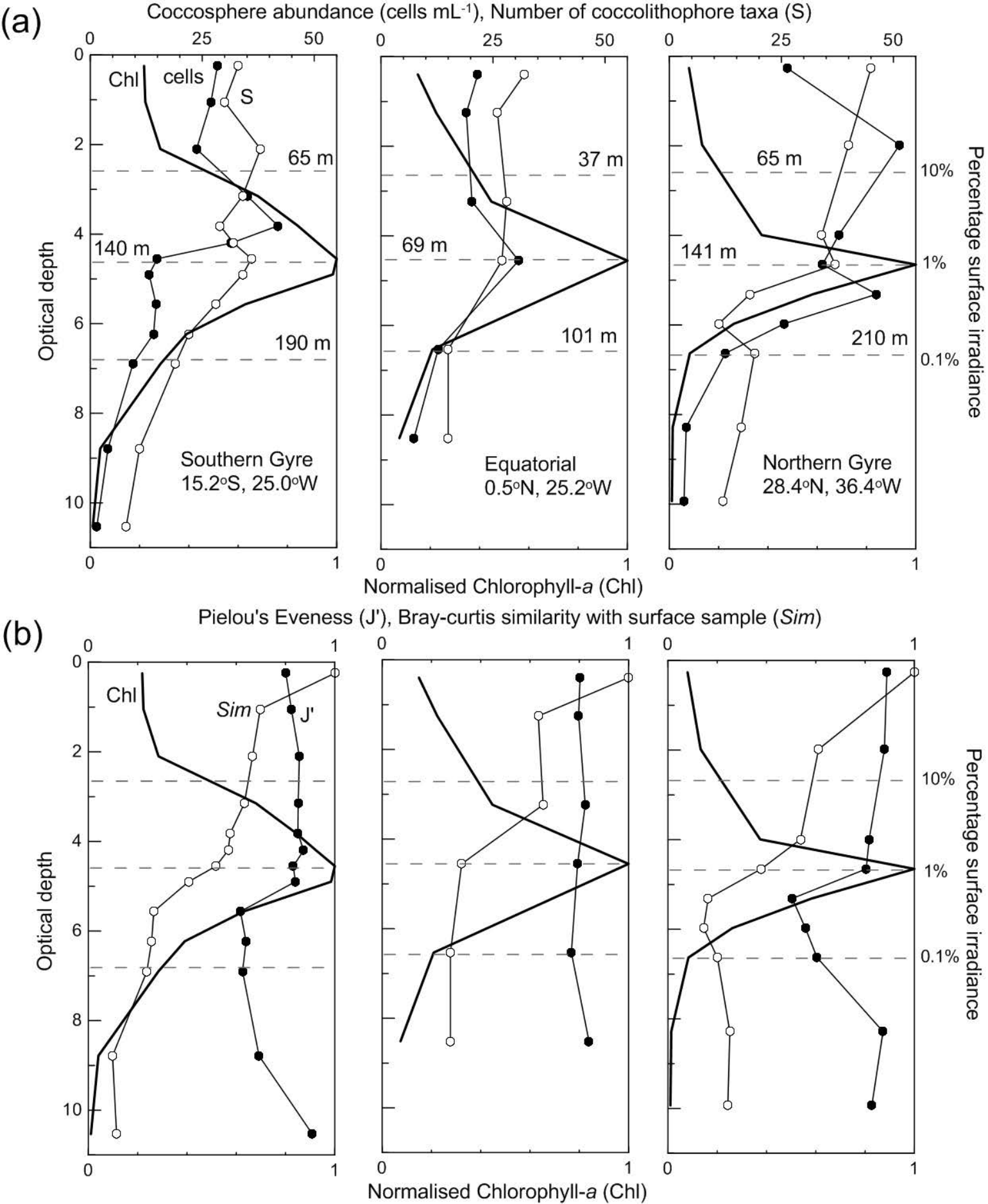
Species name	**Species name**
Papposphaera sp. Type 2	*Syracosphaera pirus*
Papposphaera sp. Type 4	*Syracosphaera prolongata*
Papposphaera sp.	*Syracosphaera protrudens*
Picarola margalefii	*Syracosphaera pulchra*
Placorhombus ziveriae	***Syracosphaera pulchra* HOL *pirus***
Pleurochrysis carterae var. *carterae*	***Syracosphaera pulchra* HOL *oblonga***
Pleurochrysis roscoffensis	*Syracosphaera rotula*
Polycrater galapagensis	*Syracosphaera tumularis*
***Polycrater* sp. 'ladle like'**	*Syracosphaera hastata*
***Polycrater* sp.**	*Syracosphaera didyma*
Pontosphaera syracusana	*Syracosphaera castellata*
Poricalyptra aurisinae	*Syaracosphaera reniformis*
Poricalyptra gaarderiae	*Syracosphaera squamosa*
Poricalyptra isselii	*Syracosphaera leptolepis*
Poricalyptra magnaghii	*Syracosphaera* sp.
Poritectolithus maximus	*Tetralithoides quadrilaminata*
Poritectolithus poritectum	*Turrilithus latericioides*
Reticulofenestra parvula	*Umbellosphaera irregularis*
Reticulofenestra sessilis	*Umbellosphaera tenuis*
Rhabdosphaera clavigera	*Umbilicosphaera anulus*
Rhabdosphaera xiphos	*Umbilicosphaera hulburtiana*
Solisphaera spp	*Umbilicosphaera sibogae*
Scyphosphaera apsteinii	***Zygosphaera amoena***
Sphaerocalyptra quadridentata	Undescribed heterococcolithohore A
***Sphaerocalyptra* sp.1**	Undescribed coccolithophore
***Sphaerocalyptra* sp.3**	**Undescribed holococcolithophore**
***Sphaerocalyptra* sp.**	
Syracolithus ponticuliferus	
Syracolithus schilleri	
***Syracolithus* sp. A**	
Syracosphaera ampliora	
Syracosphaera anthos	
***Syracosphaera anthos* HOL**	
Syracosphaera bannockii	
***Syracosphaera bannockii* HOL**	
Syracosphaera borealis	
Syracosphaera corolla	
Syracosphaera delicata	
Syracosphaera dilatata	
Syracosphaera epigrosa	
Syracosphaera exigua	
Syracosphaera florida	
Syracosphaera halldalii	
Syracosphaera histrica	
Syracosphaera lamina	
Syracosphaera marginaporata	
Syracosphaera molischii	
Syracosphaera nana	
***Syracosphaera nana* HOL**	
Syracosphaera nodosa	
Syracosphaera noroitica	
Syracosphaera ossa	

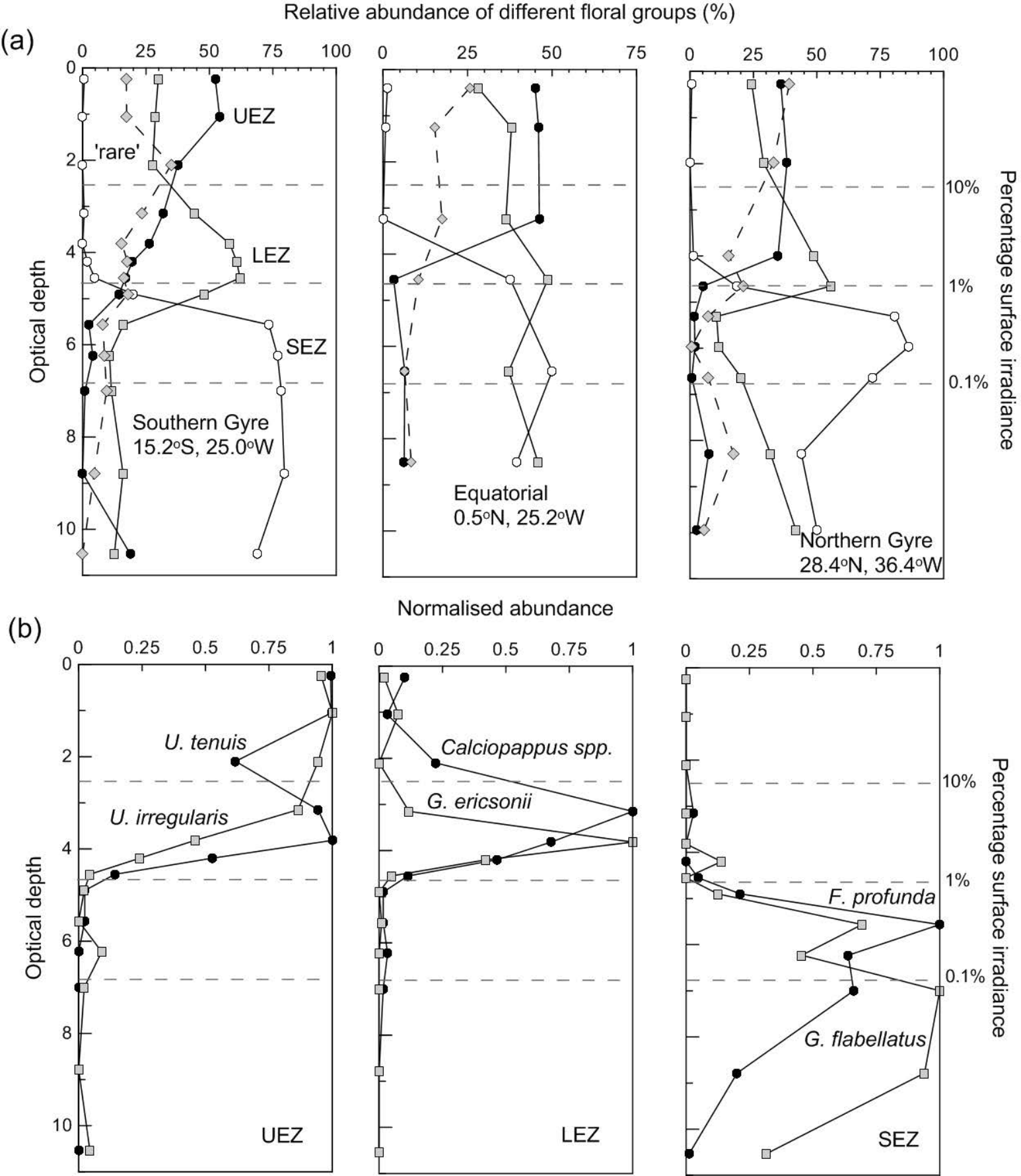

(a)
TMP
NG
EQ
SG
TMP
AMT-12
AMT-14
50
25
0
-25
-50
-54
-36
-18
0
Latitude
Longitude
20
10
5
3
2
1
0.5
0.2
0.1
0.01
MODIS Chl-a (mg m-3)

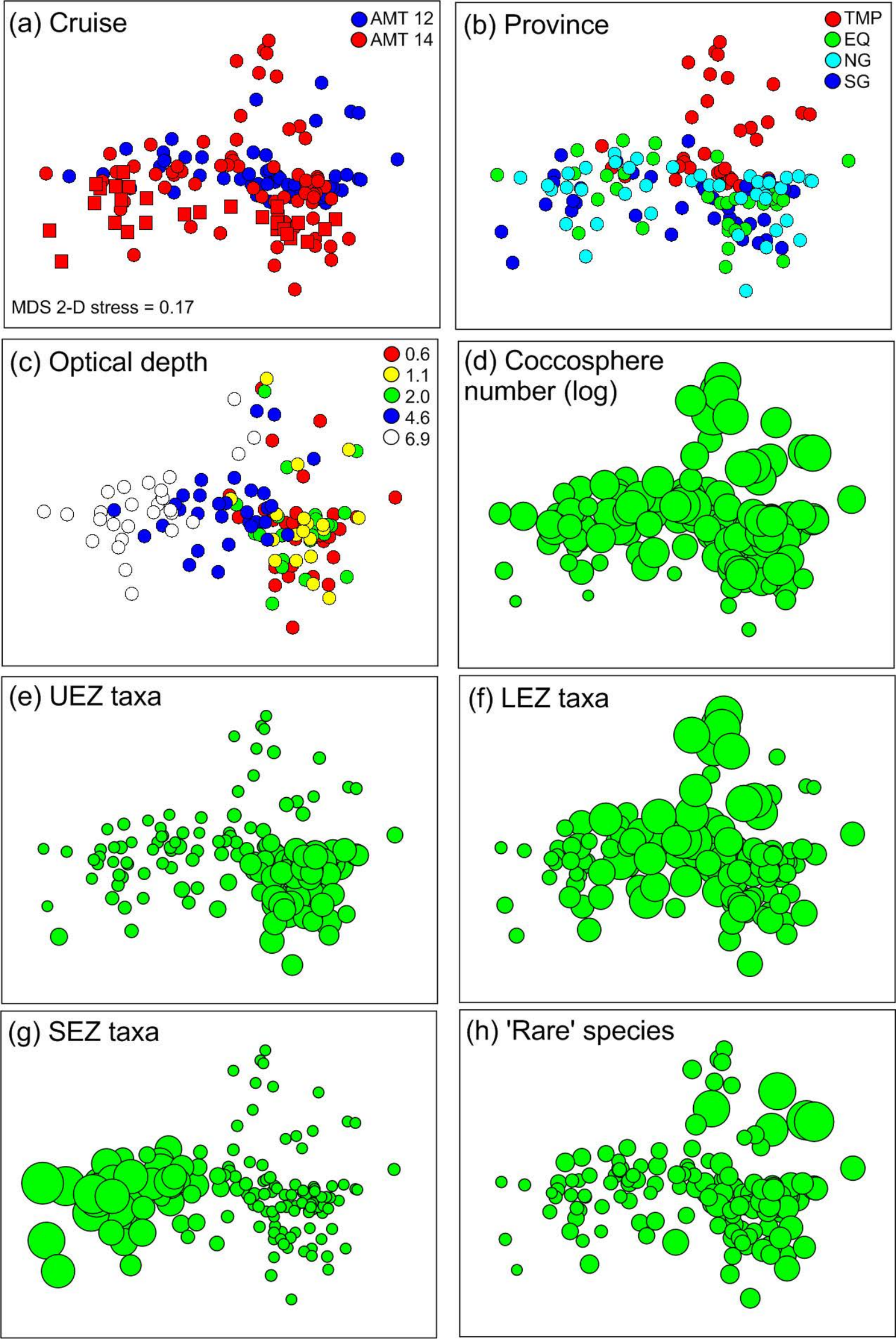

(b)
TMP
NG
EQ
SG
TMP
AMT-15
AMT-17
50
25
0
-25
-50
-54
-36
-18
0
Longitude

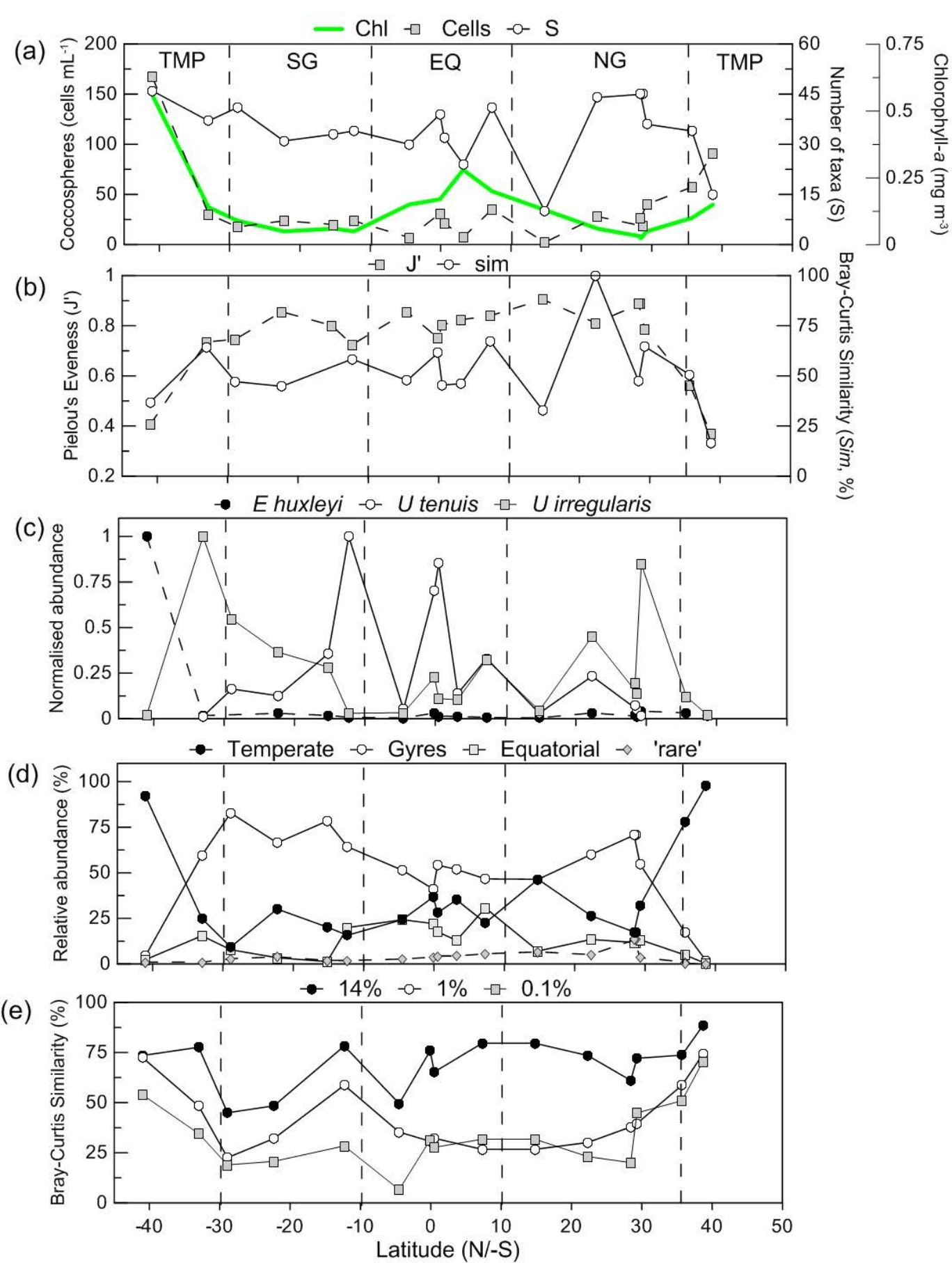

Latitude (-S/N)
-50
-40
-30
-20
-10
0
10
20
30
40
50
Depth (m)
0
50
100
150
200
TMP
AMT-12
AMT-14
Zeup
SG
EQ
NG
TMP
-50
-100
-150
-200
0.2
0.3
0.2
0.2
0.4
0.3
0.2
1
5
1
5
1
5
1

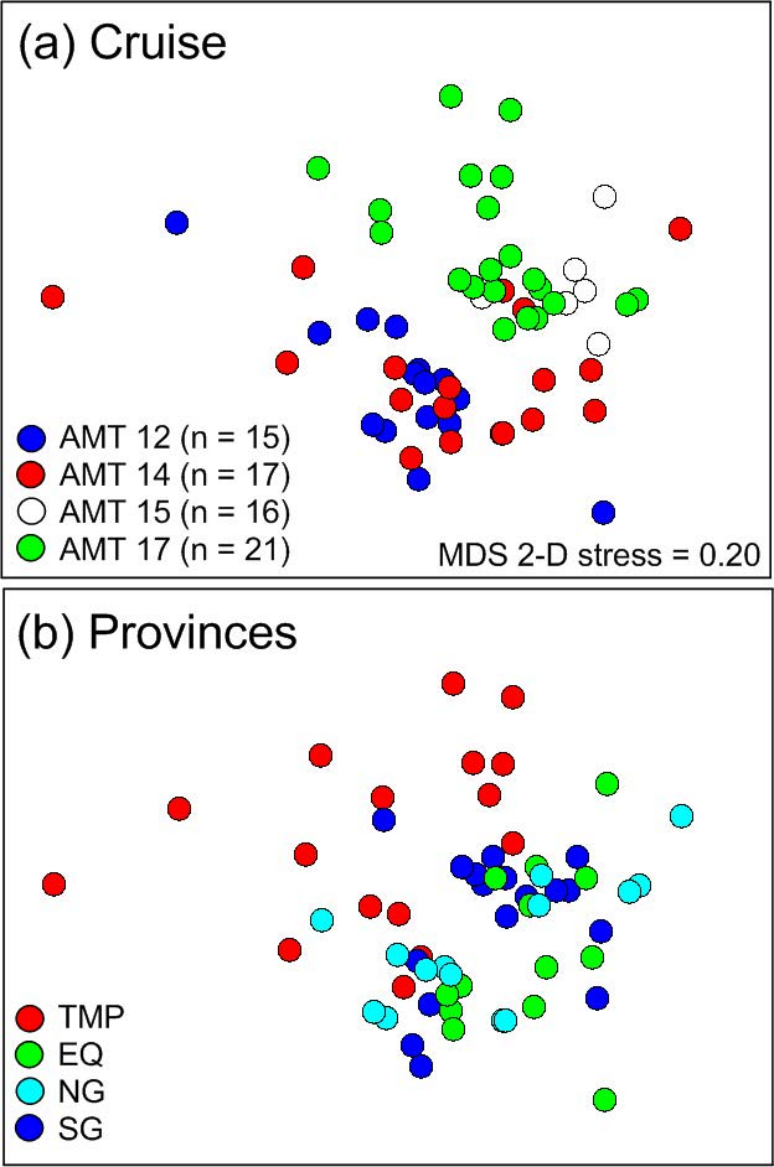

Cumulative Species Richness
75
60
45
30
15
0
(a)
(b)
(c)
1.8
3.6
5.4
7.2
7.2
13.8
21.1
28.3
15.1
30.2
45.2
60.2
Rep 1
Rep 2
Rep 3
Rep 4
Stub 1
Stub 2
Stub 3
Stub 4
Stub 1
Stub 2
Stub 3
Stub 4
AMT 14, CTD 71, 31 m
Stub 4 recounts
AMT 14, CTD 71, 31 m
Multiple stubs
AMT 12, CTD 26, 120 m
Multiple stubs

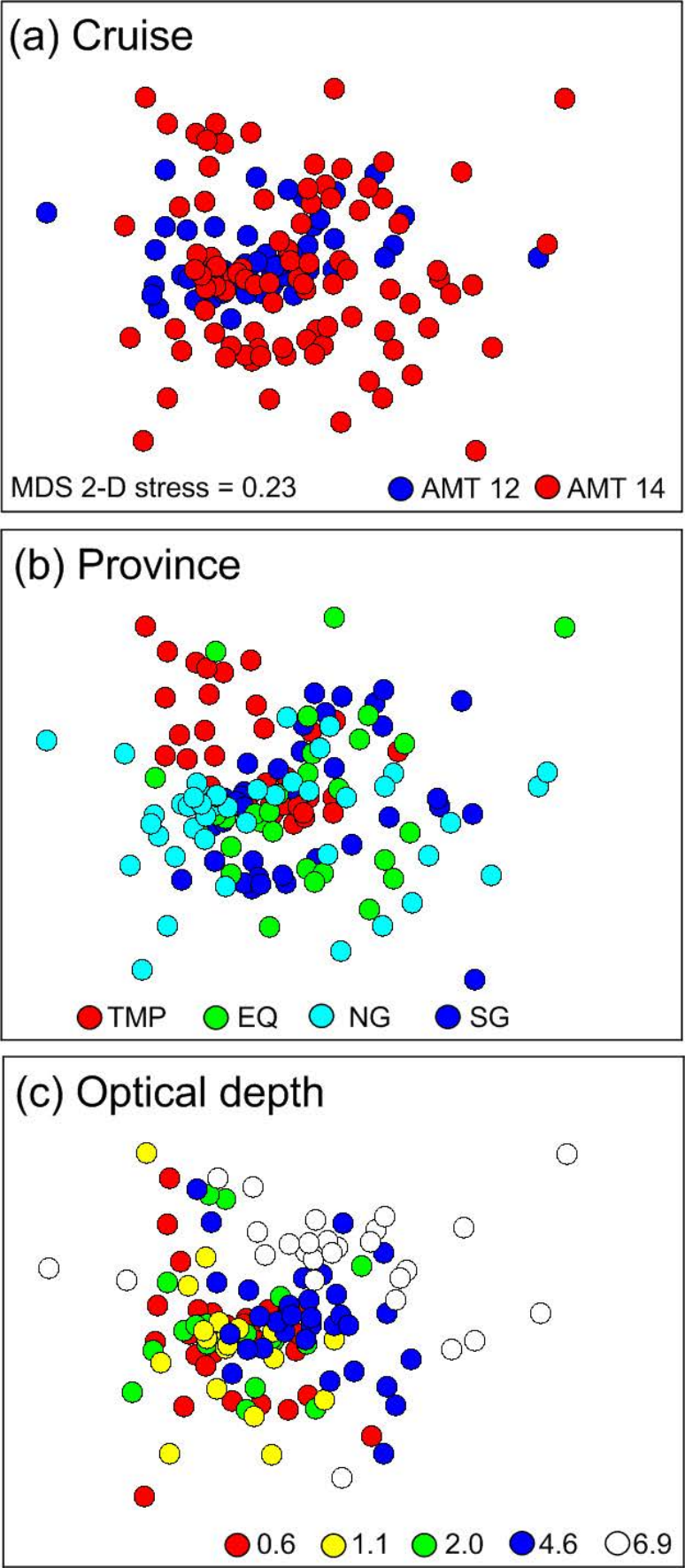

(a)
Coccosphere abundance (cells mL-1), Number of coccolithophore taxa (S)
Chl
cells
S
65 m
140 m
190 m
Southern Gyre
15.2°S, 25.0°W
37 m
69 m
101 m
Equatorial
0.5°N, 25.2°W
65 m
141 m
210 m
Northern Gyre
28.4°N, 36.4°W
Optical depth
Percentage surface irradiance
10%
1%
0.1%
Normalised Chlorophyll-a (Chl)
(b)
Pielou's Eveness (J'), Bray-curtis similarity with surface sample (Sim)
Chl
Sim
J'
Optical depth
Percentage surface irradiance
10%
1%
0.1%
Normalised Chlorophyll-a (Chl)

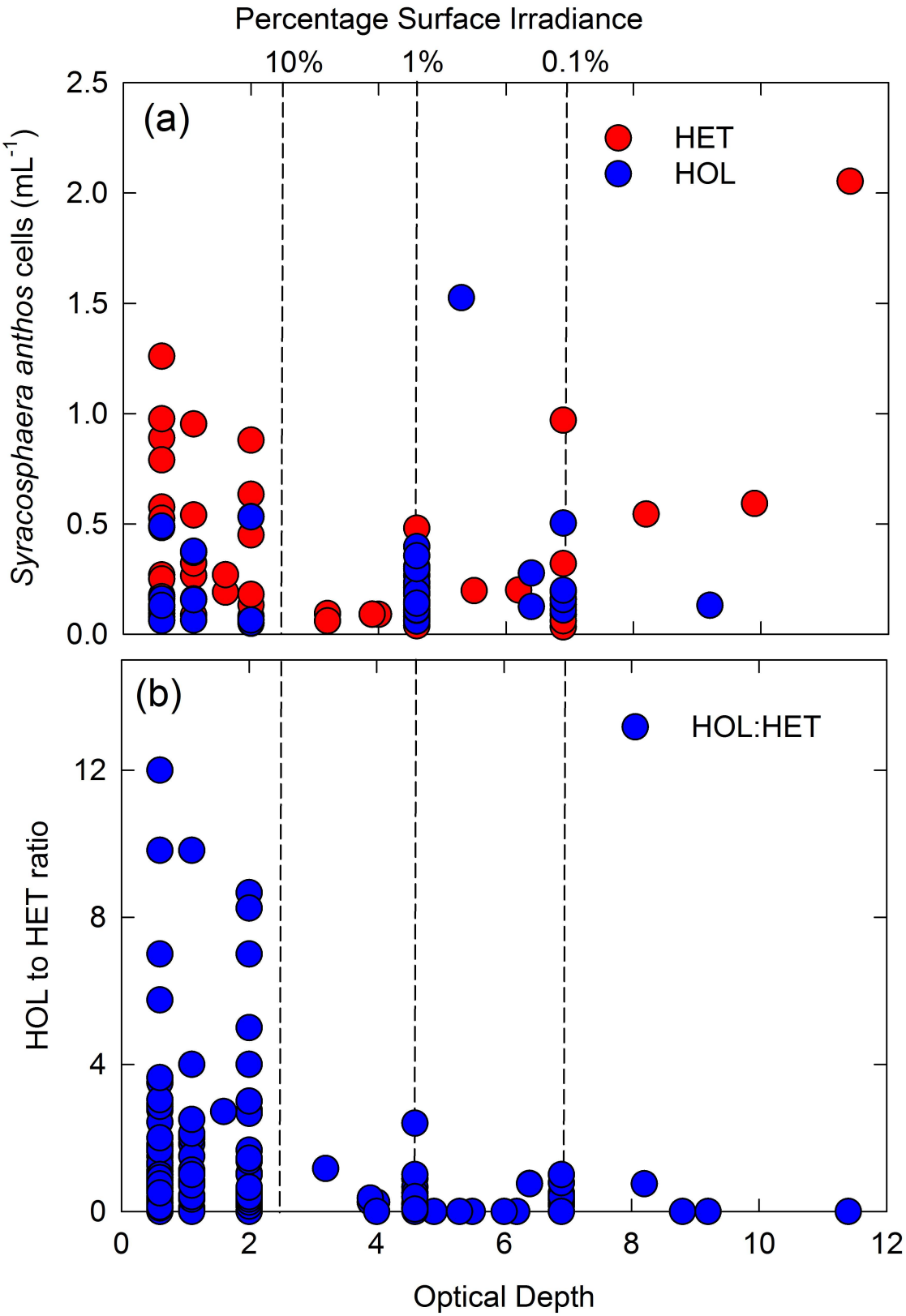

Relative abundance of different floral groups (%)
(a)
0
25
50
75
100
Optical depth
UEZ
'rare'
LEZ
SEZ
Southern Gyre
15.2°S, 25.0°W
Equatorial
0.5°N, 25.2°W
Northern Gyre
28.4°N, 36.4°W
10%
1%
0.1%
Percentage surface irradiance
Normalised abundance
(b)
0
0.25
0.5
0.75
1
U. tenuis
U. irregularis
Calciopappus spp.
G. ericsonii
F. profunda
G. flabellatus
UEZ
LEZ
SEZ


(a) Cruise
AMT 12
AMT 14
MDS 2-D stress = 0.17
(b) Province
TMP
EQ
NG
SG
(c) Optical depth
0.6
1.1
2.0
4.6
6.9
(d) Coccosphere number (log)
(e) UEZ taxa
(f) LEZ taxa
(g) SEZ taxa
(h) 'Rare' species


(a)
Chl
Cells
S
TMP
SG
EQ
NG
TMP
Coccospheres (cells mL-1)
Number of taxa (S)
Chlorophyll-a (mg m-3)
(b)
J'
sim
Pielou's Eveness (J')
Bray-Curtis Similarity (Sim, %)
(c)
E huxleyi
U tenuis
U irregularis
Normalised abundance
(d)
Temperate
Gyres
Equatorial
'rare'
Relative abundance (%)
(e)
14%
1%
0.1%
Bray-Curtis Similarity (%)
Latitude (N/-S)


(a) Cruise
AMT 12 (n = 15)
AMT 14 (n = 17)
AMT 15 (n = 16)
AMT 17 (n = 21)
MDS 2-D stress = 0.20
(b) Provinces
TMP
EQ
NG
SG


(a) Cruise
MDS 2-D stress = 0.23
AMT 12
AMT 14
(b) Province
TMP
EQ
NG
SG
(c) Optical depth
0.6
1.1
2.0
4.6
6.9


Percentage Surface Irradiance
10%
1%
0.1%
(a)
HET
HOL
Syracosphaera anthos cells (mL-1)
2.5
2.0
1.5
1.0
0.5
0.0
(b)
HOL:HET
HOL to HET ratio
12
8
4
0
0
2
4
6
8
10
12
Optical Depth