Large-scale distribution of coccolithophores and Parmales in the surface waters of the Atlantic Ocean

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Coccolithophores and Parmales are important functional groups of calcified and siliceous marine nanophytoplankton. Large-scale biogeographic distributions of the two groups were investigated based on 71 samples that were collected in the Atlantic Ocean. Using a scanning electron microscope, a total of 48 taxa of coccolithophores and eight taxa of Parmales were recorded, with Emiliania huxleyi, Tetraparma pelagica *and* Triparma strigata *as the predominant forms. The highest abundances of coccolithophores (376×10^3 cells l^{-1}) and Parmales (624×10^3 cells l^{-1}) were observed in waters north-east of the Falkland Islands and the South Georgia Island, in close association with the Subantarctic Front and Polar Front, respectively. Three major biogeographic assemblages, i.e. the Falkland Shelf Assemblage, the Southern Ocean Assemblage and the Atlantic Ocean Assemblage, were revealed in cluster analysis. Additionally, canonical correspondence analysis indicated that temperature significantly affects the latitudinal patterns of the two algal groups. High abundances of Parmales were closely coupled with those of* E. huxleyi *in waters of the Southern Ocean with low temperature (<10°C). However, the number of coccolithophore species, along with the Shannon–Weaver diversity, significantly increased with elevated temperature, suggesting more diverse assemblages in tropical waters.*

Keywords: Abundance, Atlantic, coccolithophores, multivariate analysis, oceanic front, Parmales

INTRODUCTION

As primary producers, phytoplankton play crucial roles in marine food webs, biogeochemical cycles and carbon sequestration. The current trend of increasing sea surface temperature and acidification, caused by global warming, have greatly altered the phytoplankton composition, size spectrum and primary productivity in the oceans (Dutkiewicz et al., 2015). Irrespective of evolutionary response, by the end of this century, phytoplankton diversity in tropical waters will have declined by one third, coinciding with shrinking species ranges and poleward expansion (Thomas et al., 2012). In the past four decades, phytoplankton biomass and size structure have dramatically changed off the West Antarctic Peninsula due to regional climate change, with a 12% reduction in surface chlorophyll-*a* during austral summer and high latitude distribution (Montes-Hugo et al., 2009). However, recent findings showed an absence of regional warming since the late 1990s in the northern Antarctic Peninsula and the northern part of the Weddell Sea, where the annual mean sea ice concentration has significantly increased, due to the extreme natural internal variability of the regional atmospheric circulation (Turner et al., 2016). The decadal trend on sea ice change could have potential effects on the distribution pattern of phytoplankton, e.g. species shift, abundance fluctuation, community succession and even seasonal timing of blooms (Ardyna et al., 2014). Consequently, future phytoplankton changes will affect climate feedback mechanisms, e.g. amplifying arctic warming by 20%, through biogeophysical processes (Park et al., 2015).

In the nano- (2–20 μm) phytoplankton realm, coccolithophores (Haptophyta) are usually considered as an important calcifying functional group, since most of them can form calcified coccoliths by calcification inside the cell (Rost & Riebesell, 2004). On a global scale, around 20% of the marine primary production (Rousseaux & Gregg, 2014) and 20–80% of the carbonate flux (Honjo et al., 2008) are derived from these organisms. Living coccolithophores are sensitive to environmental changes on factors such as sea surface temperature and dissolved CO_2. Recent studies showed a poleward expansion of the key species *Emiliania huxleyi* (Winter et al., 2014) and an increase in the diversity of coccolithophore assemblages by 2100 using model prediction (O'Brien et al., 2016). However, it seems that coccolithophores are not always negatively affected by the rising temperature and CO_2, since evidence from the stratigraphic record indicates that their richness and speciation rate does increase during the warmer periods over geological time (Bown et al., 2004). Additionally, coccolithophores might have already been responding to rising atmospheric CO_2 partial pressures, as both laboratory measurements and filed observations demonstrate marked increase in calcification and coccolith mass at elevated CO_2 conditions (Iglesias-Rodriguez et al., 2008; Beaufort et al., 2011), which contradicts with the previous research (Riebesell et al., 2000).

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Parmales (Bolidophyceae) are a group of marine siliceous phytoplankton (Ichinomiya *et al.*, 2016), which are rare and often overlooked during sample checking because of the high latitude distribution and small cell size (2–5 μm). Parmales were first observed in the mid-1970s (Iwai & Nishida, 1976) and were originally recognized as cyst-like particles (Silver *et al.*, 1980) before their final confirmation as phytoplankton in the sectioned samples (Marchant & McEldowney, 1986). Although Parmales have been recorded in tropical waters (Kosman *et al.*, 1993; Bravo-Sierra & Hernández-Becerril, 2003), they are abundant in polar and subpolar waters and can form high cell abundances in spring before sinking to the pycnocline in summer (Konno & Jordan, 2012). Parmalean species, closely related to diatoms phylogenetically (Guillou *et al.*, 1999), can be discriminated by the shape and size of their silica plates (Booth & Marchant, 1987). However, the correct configuration of the silica plates was not realized until illustrations of collapsed cell walls were re-examined, and the plate terminology subsequently emended (Konno & Jordan, 2007).

Based on a four-month fishing trawl in the Atlantic Ocean and off the Antarctic Peninsula in 2014, we studied the biogeographic distributions of assemblages of coccolithophores and Parmales. By multivariate analysis, we found that the latitudinal patterns of these two groups of nanoplankton were primarily linked to the temperature gradient. Also, three major assemblages, being intimately associated with the oceanic provinces, were distinguished in the study region. Since the large-scale distribution of nanoplankton, especially of the microscopic Parmales, has been rarely reported in the Atlantic Ocean, this study provides species-level information on these organisms, which could be of great value to biogeochemical research and help modellers to more accurately predict future climate change.

MATERIALS AND METHODS

Sample collection

A total of 71 samples were collected by the trawler *LongTeng* in the Atlantic Ocean (ATO) during 28 May to 5 October 2014 (Figure 1A). The study area covers many oceanic provinces: NATR (North Atlantic Tropical Gyral Province), WTRA (Western Tropical Atlantic Province), SATL (South Atlantic Gyral Province), FKLD (Falklands Plateau and Argentine Shelf Province) and the Southern Ocean (SO) comprising SSTC, SANT, ANTA and APLR (Longhurst, 2007). In this study, the sampling sites at 1–12, 13–38 and 39–71 were located in the FKLD, SO and ATO, respectively.

Surface seawater samples were collected from ship water, which was connected directly to the sea via a pipe and supplied for research use by the scientific observers on board. Sub-samples (1–2 l) were vacuum filtered through 0.6 μm pore-size isopore polycarbonate filters (Millipore Corp.) under low pressure (<100 mmHg). Each membrane with filtered particles was then transferred to a plastic Petri dish and preserved at −20°C in the freezing store until analysis. Seawater temperature and bathymetric depth were measured by sensors attached to a Fish Finder (FCV-1200LM, FURUNO).

SEM observations

In the laboratory, a piece of the filter (∼0.5 cm²) was cut and attached to a stub using conductive double-sided adhesive tape, followed by coating with platinum using a magnetron sputter (MSP-1S, Shinkuu). Qualitative and quantitative analyses for coccolithophores and Parmales were performed at 4000× magnification using a tabletop scanning electron microscope (TM3000, Hitachi). Species-level taxonomy was based on the morphological characteristics of coccoliths and coccospheres for coccolithophores (Young *et al.*, 2003), and plate configurations for Parmales (Konno & Jordan, 2007; Konno *et al.*, 2007). Due to smaller cell size, images of dominant Parmales were obtained with a JSM-840 (JEOL) SEM after coating with platinum using an Ion Coater (Eiko-IB3). For statistical stability, at least 500 coccoliths, coccospheres and Parmales were counted in each sample. For low abundance, a minimum of 500 random selected areas were checked. Calculations of the final abundances were carried out using the previous literature (Bollmann *et al.*, 2002).

Statistical analysis

Species diversity was evaluated using the Shannon–Weaver Index (H', Shannon & Weaver, 1949) and Dominance (Y, Dufrene & Legendre, 1997). One-way ANOVA (SPSS 20.0) was performed to compare the means among the FKLD, SO and ATO. Using the program SMATR 2.0 (Warton *et al.*, 2006), a model II linear regression (Geometric Mean) was applied to explore the relationship between two variables. Cluster analysis (PRIMER 6.1) was used to measure the resemblance among the samples based on Bray–Curtis similarities (Group Average) after the fourth root of the original dataset.

Canonical correspondence analysis (CCA), a constrained ordination of the unimodal method, was used to estimate how much of the variation in the species distribution (response variables) could be attributed to changes in the environments (explanatory variables). Before the CCA, a detrended correspondence analysis (DCA) was conducted to assess the lengths of gradient in species data and to make the decision between unimodal and linear methods (Lepš & Šmilauer, 2003). Species with good species fits were selectively incorporated in the CCA, according to the percentage variance of species data explained by the first canonical axis in the ordination. Both CCA and DCA were realized in the CANOCO 4.5 software after $\log_{10}(x + 1)$-transformation of the species abundances and environmental parameters.

RESULTS

Sea surface temperature

During sample collection, sea surface temperature (SST) varied between −2.3 and 29.0°C, with the lowest and highest values being recorded in the adjoining waters of SOI (South Orkney Islands) and WTRA, respectively (Figure 1B). SST in the FKLD, SO and ATO were 2.7–15.0°C (mean ± SD, 8.1 ± 3.7°C), −2.3–14.8°C (1.5 ± 3.8°C) and 15.1–29.0°C (23.9 ± 4.0°C), respectively. The 40°S line clearly separated the warm and cool waters.

Species composition

A total of 48 taxa of living coccolithophores (including two subspecies, one variety and nine forms) and eight taxa of
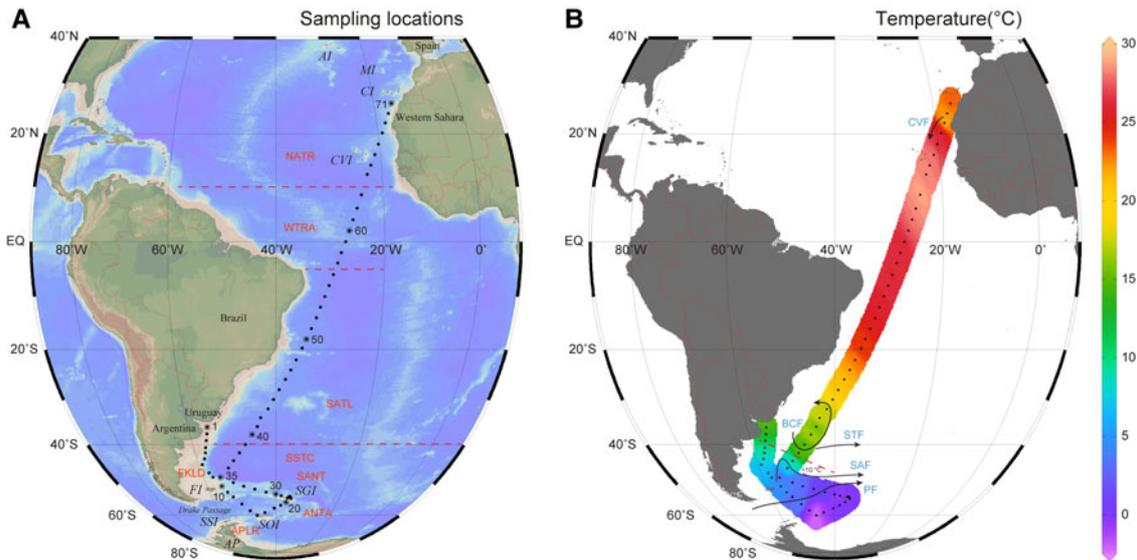
Fig. 1. Sampling sites in the Atlantic Ocean. (A) Sampling locations, AP, Antarctic Peninsula; SSI, South Shetland Islands; SOI, South Orkney Islands; SGI, South Georgia Island; FI, Falkland Islands; CVI, Cape Verde Islands; CI, Canary Islands; MI, Madeira Islands; AI, Azores Islands, red fonts indicate different oceanic provinces (after Longhurst, 2007); (B) Sea surface temperature, blue fonts indicate different fronts (after Peterson & Stramma, 1991; Peña-Izquierdo *et al.*, 2012), CVF, Cape Verde Front; BCF, Brazil Current Front; STF, Subtropical Front; SAF, Subantarctic Front; PF, Polar Front.

Parmales (including three subspecies and three forms) were recorded, with 19 taxa having frequencies of occurrence greater than 20% (Table 1). Of the 71 sampling sites, coccolithophores and Parmales were present at 69 (97.2%) and 45 (63.4%) sites, respectively. The most diverse coccolithophore species were documented at Site 59 (22 taxa), which was located in the tropical equatorial waters (Figure 2A). In contrast, the maximum number of parmalean species occurred in the cool SO waters at Site 32 (six taxa).

In the coccolithophore assemblages, the Order Syracosphaerales represented the largest group (23 taxa), with 12 taxa belonging to the Genus *Syracosphaera*. The dominant species were *Emiliania huxleyi*, *Gephyrocapsa oceanica* and *Gephyrocapsa ericsonii*, with the Dominance (Y) of 0.474, 0.011 and 0.010, respectively. Three forms of *E. huxleyi* (types A, B and C) and five forms of *Umbellosphaera tenuis* (types I, II, IIIa, IIIb and IV) existed in the surveyed waters (Figure 3A–I). It is noteworthy that the body coccoliths of *Algirosphaera robusta* in this study (Sites 39–41, 47 and 52) exhibited an unusual morphology with incomplete hoods, which had been previously recorded in the Yellow and East China Seas (see Figure 3 in Luan *et al.*, 2016). As for the Parmales assemblages, *Triparma laevis* was the most diverse species (five taxa), while *Tetraparma pelagica*, *Triparma strigata* and *Triparma laevis* f. *inornata* represented the dominant species (Figure 3J–L), in light of Y values of 0.087, 0.061 and 0.015, respectively.

Coccolithophore abundance

During the survey, the cell abundance of living coccolithophores ranged from absent at the far south Site 16 (60°S), to the maximum of 375.9×10^3 cells l^{-1} at Site 35 north-east of the FI (Falkland Islands), averaging 71.4×10^3 cells l^{-1}. The average cell abundances in the FKLD, SO and ATO were 62.2×10^3 cells l^{-1}, 87.5×10^3 cells l^{-1} and 67.9×10^3 cells l^{-1}, with no marked differences between any two of them (after ANOVA).

The species *E. huxleyi* was widespread in the surveyed waters (Figure 2C), and was predominant in the assemblages at most of the sampling sites. Its cell abundance varied between absent and 375.8×10^3 cells l^{-1} (on average 59.4×10^3 cells l^{-1}), accounting for an average of 75.4% of the total coccolithophores. The average *E. huxleyi* abundances in the FKLD, SO and ATO were 57.7×10^3 cells l^{-1}, 86.8×10^3 cells l^{-1} and 38.5×10^3 cells l^{-1}, with a significant difference between the SO and ATO ($P < 0.05$). The combined abundance of *Gephyrocapsa* taxa varied between absent and 213×10^3 cells l^{-1} (on average 5.7×10^3 cells l^{-1}), with the maximum at Site 69 in the Cape Verde Front (CVF) zone, and accounting for an average of 9.6% of the total. The average *Gephyrocapsa* abundances were 3.1×10^3 cells l^{-1}, 0.17×10^3 cells l^{-1} and 11.0×10^3 cells l^{-1} in the FKLD, SO and ATO, respectively.

Parmales abundance

The Parmales assemblages mainly inhabited the SO waters (Figure 2D), with an average cell abundance of 46.0×10^3 cells l^{-1} during the survey, ranging from absent to a maximum of 624×10^3 cells l^{-1} at Site 27 adjacent to the SGI (South Georgia Island). The average abundance in the SO waters was 122×10^3 cells l^{-1}, which was extremely high compared to that in the FKLD waters (0.52×10^3 cells l^{-1}, $P < 0.001$) and ATO waters (2.6×10^3 cells l^{-1}, $P < 0.001$). Parmales were absent in the whole WTRA, and were rare in the NATR (only being recorded at Sites 67 and 71) and SATL waters.

As for the dominant species, the average abundance of *T. pelagica* was 21.9×10^3 cells l^{-1}, with the highest value of 262×10^3 cells l^{-1} at Site 27, and accounting for an average of 47.2% of the total Parmales. The average *T. pelagica* abundance in the SO waters was 58.2×10^3 cells l^{-1}, in sharp contrast with 0.17×10^3 cells l^{-1} in the FKLD waters ($P < 0.001$) and 1.2×10^3 cells l^{-1} in the ATO waters ($P < 0.001$). The

Table 1. Taxonomic list of living coccolithophores and Parmales in the surface waters of the Atlantic Ocean, 2014.

Taxa	Frequency of occurrence (f_i, %)	Dominance (Y, >0.001)
Coccolithophores		
Coccolithales		
Calcidiscus leptoporus ssp. *leptoporus*	43.7	/
Coccolithus pelagicus ssp. *braarudii*	1.4	/
Oolithotus antillarum	12.7	/
Oolithotus fragilis	1.4	/
Umbilicosphaera anulus	9.9	/
Umbilicosphaera foliosa	25.4	0.001
Umbilicosphaera sibogae	22.5	/
Isochrysidales		
Emiliania huxleyi (types A, B & C)	95.8	0.474
Gephyrocapsa ericsonii	43.7	0.010
Gephyrocapsa oceanica	43.7	0.011
Syracosphaerales		
Acanthoica quattrospina	23.9	/
Algirosphaera robusta (a variety, Luan *et al.*, 2016)	7.0	/
Calciopappus rigidus	2.8	/
Calciosolenia brasiliensis	52.1	0.001
Calciosolenia murrayi	2.8	/
Cyrtosphaera lecaliae	4.2	/
Discosphaera tubifera	26.8	0.001
Michaelsarsia adriaticus	5.6	/
Michaelsarsia elegans	16.9	0.001
Palusphaera vandelii	21.1	/
Rhabdosphaera clavigera	11.3	/
Syracosphaera corolla	11.3	/
Syracosphaera dilatata	32.4	0.002
Syracosphaera marginaporata	1.4	/
Syracosphaera molischii	1.4	/
Syracosphaera nana	15.5	/
Syracosphaera nodosa	7.0	/
Syracosphaera ossa type 1	15.5	/
Syracosphaera ossa type 2	28.2	0.002
Syracosphaera prolongata	1.4	/
Syracosphaera pulchra	36.6	0.001
Syracosphaera rotula	4.2	/
Syracosphaera tumularis	2.8	/
Zygodiscales		
Helicosphaera carteri	11.3	/
Helicosphaera wallichii	9.9	/
Syracolithus confusus	1.4	/
Genera incertae sedis		
Umbellosphaera irregularis	35.2	0.001
Umbellosphaera tenuis type I	1.4	/
Umbellosphaera tenuis type II	1.4	/
Umbellosphaera tenuis type IIIa	1.4	/
Umbellosphaera tenuis type IIIb	28.2	0.001
Umbellosphaera tenuis type IV	40.8	0.004
Holococcolith-bearing taxa		
Calyptrolithophora papillifera	2.8	/
Helladosphaera cornifera	7.0	/
Homozygosphaera vercellii	9.9	/
Nannolith-bearing families		
Ceratolithus cristatus	1.4	/
Parmales		
Triparmaceae		
Tetraparma pelagica	47.9	0.087
Triparma columacea subsp. *alata*	1.4	/
Triparma laevis f. *inornata*	36.6	0.015
Triparma laevis f. *laevis*	2.8	/
Triparma laevis f. *longispina*	11.3	/
Triparma laevis subsp. *pinnatilobata*	2.8	/
Triparma laevis subsp. *ramispina*	2.8	/
Triparma strigata	39.4	0.061
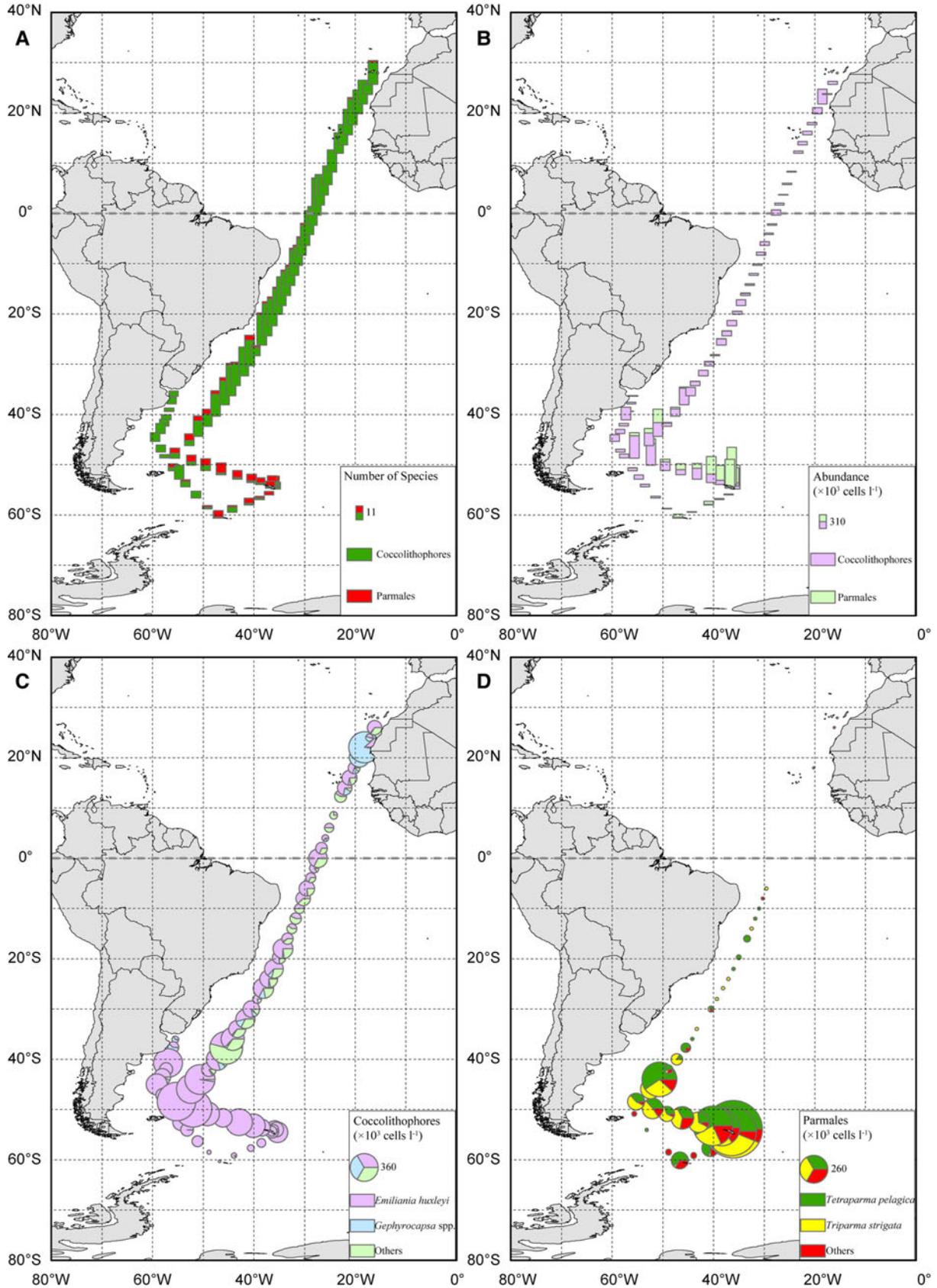
Fig. 2. Latitudinal distributions of coccolithophores and Parmales in the Atlantic Ocean.
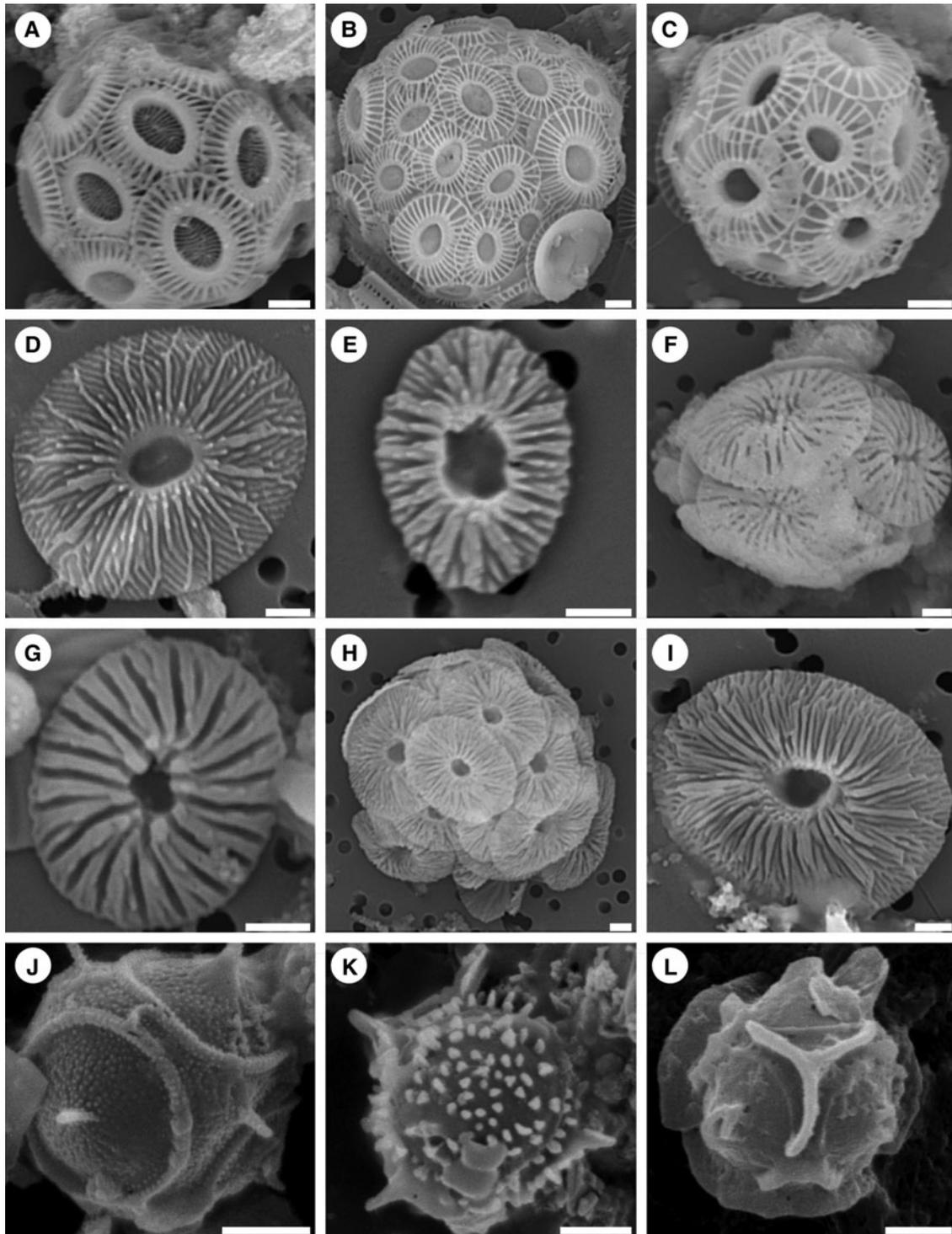
Fig. 3. Different morphotypes of coccolithophore species and dominant parmalean species in surveyed waters. (A) *Emiliania huxleyi* type A; (B) *E. huxleyi* type B; (C) *E. huxleyi* type C; (D) *Umbellosphaera tenuis* type I; (E) *U. tenuis* type II; (F) *U. tenuis* type IIIa; (G) *U. tenuis* type IIIb; (H) *U. tenuis* type IV (coccosphere); (I) *U. tenuis* type IV (coccolith); (J) *Tetraparma pelagica*; (K) *Triparma strigata*; (L) *Triparma laevis* f. *inornata*. Scale bars = 1 μm.

average abundance of *T. strigata* was 18.6×10^3 cells l^{-1}, with a maximum of 312×10^3 cells l^{-1} at Site 27, and accounting for an average of 32.6% of the total. Also, the average *T. strigata* abundance (49.5×10^3 cells l^{-1}) in the SO was significant higher than that in the FKLD (0, $P < 0.01$) and ATO (1.1×10^3 cells l^{-1}, $P < 0.001$). The combined abundance of *T. laevis* taxa was on average 5.4×10^3 cells l^{-1} (max. 53.7×10^3 cells l^{-1} at Site 30), with the dominant form

T. laevis f. *inornata* at 4.8×10^3 cells l^{-1} (max. 49.6×10^3 cells l^{-1} at Site 30).

Biogeographic assemblages

Based on the Bray–Curtis similarities of the species composition among the sampling sites, three major biogeographic assemblages were clarified on a 32.5 similarity level by
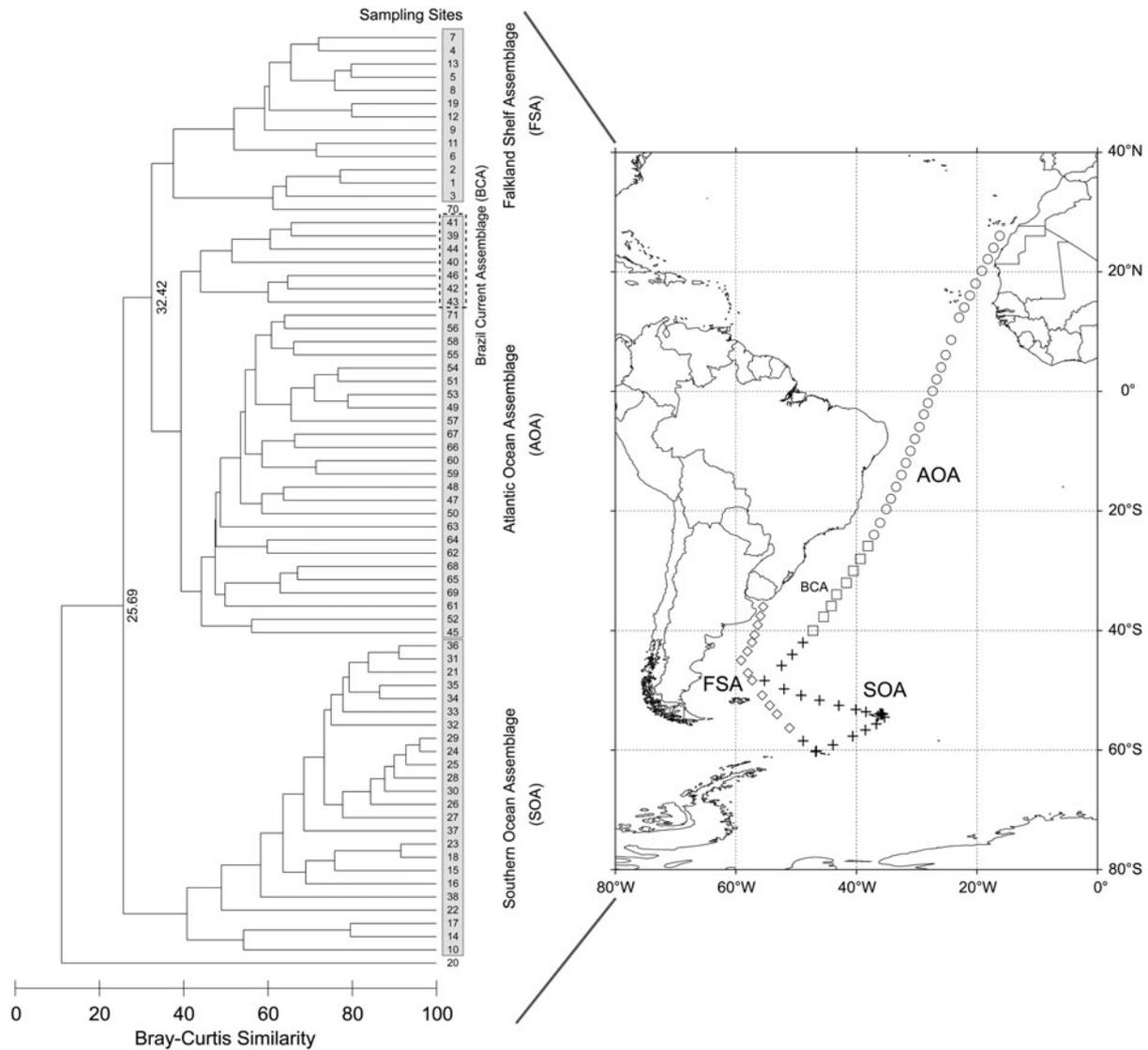
Fig. 4. Biogeographic distributions of three major assemblages based on cluster analysis. Left panel: dendrogram showing the similarities among the sampling sites; Right panel: spatial locations of the assemblages.

cluster analysis (Figure 4). They were the Falkland Shelf Assemblage (FSA), the Southern Ocean Assemblage (SOA) and the Atlantic Ocean Assemblage (AOA). It is noteworthy that our results precisely coincided with the geographically divided oceanic provinces (Longhurst, 2007). The FSA referred to the typical assemblage overlying on the Falklands plateau and Argentine shelf. Species characterizing these waters were: *E. huxleyi, G. oceanica* and *G. ericsonii*, as well as *Syracosphaera dilatata* and *Calciosolenia brasiliensis*. The SOA represented the taxa living in the cool SO waters, where the nanoplankton, in addition to *E. huxleyi*, were characterized by parmalean species, such as *T. pelagica, T. strigata* and *T. laevis* f. *inornata*. The AOA depicted the taxa living in the warm ATO waters, where the major taxa were *E. huxleyi, G. oceanica* and *G. ericsonii*, in combination with *U. tenuis* types IIIb and IV, *Umbellosphaera irregularis, S. dilatata* and *Syracosphaera ossa* type 2. Within the AOA, a minor group, the Brazil Current Assemblage (BCA), can be clearly distinguished. The BCA was primarily subjected to the Brazil Current Front (BCF), a convergence of the warm Brazil Current and cool Falklands Current.

Multivariate analysis

To clarify the species distribution of coccolithophores and Parmales in association with the ambient environment, multivariate analysis was applied in this study to distinguish how much of the variation in the species composition could be attributed to changes in the environmental factors (e.g. temperature, latitude and bathymetry). Since the DCA of the species data showed that the longest length of gradient (3.642, Table 2) was greater than 3.0, the constrained unimodal method of the CCA was appropriate for the current analysis.

The first two canonical axes together explained 18.8% of the variance in the species data and 93.6% of the variance in the species-environment relationship, with the first axis accounting for 12.8% and 63.8%, respectively. In the ordination chart (Figure 5), living coccolithophores and Parmales clearly formed two distinct groups. The position of individual species graphically illustrated their respective niche requirements. After the Monte Carlo permutation tests of significance, the independent explanation of species variation by

Table 2. Multivariate analysis results of DCA and CCA.

Axes	1	2	3	4
DCA results				
Eigenvalues	0.578	0.287	0.170	0.120
Lengths of gradient	3.642	2.993	2.221	1.973
Cumulative percentage variance of species data	14.8	22.1	26.5	29.5
CCA results				
Eigenvalues	0.501	0.234	0.051	0.300
Species-environment correlations	0.940	0.861	0.482	0.000
Cumulative percentage variance of species data	12.8	18.8	20.1	27.8
Cumulative percentage variance of species-environment relation	63.8	93.6	100.0	0.0
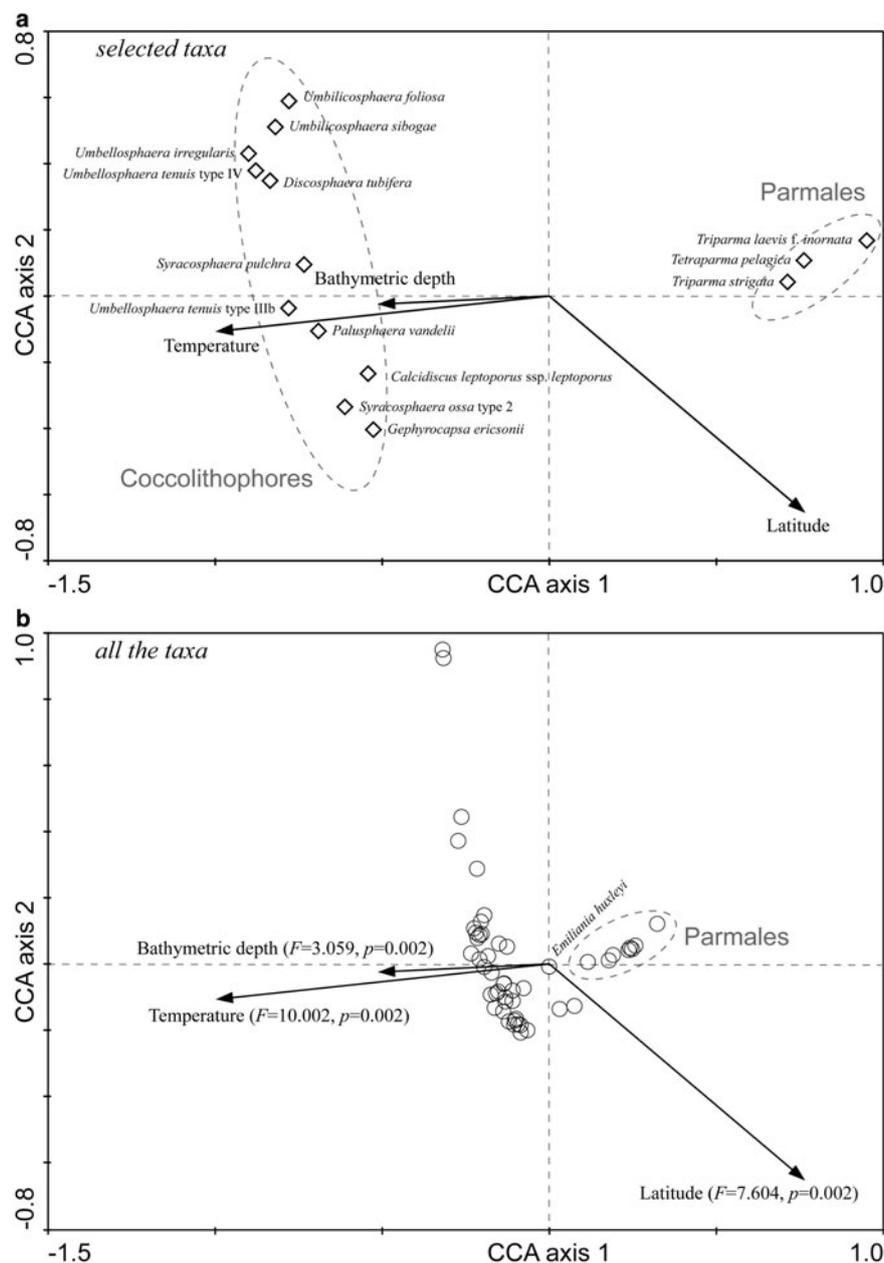
Fig. 5. CCA biplots showing the relationship between the species distribution and environmental factors. (A) Selected taxa according to the species fit; (B) All the taxa, *F* and *P* values in parentheses refer to the significance of environmental variables by Monte Carlo permutation tests under the reduced model.

Table 3. Summary of previous studies on biogeographic distributions of Parmales in distinct oceanographic settings.

Survey periods	Sampling regions	Number of taxa	Abundances ($\times 10^3$ cells l^{-1})	Major taxa
1974 (July)[1]	Aleutian Islands, North Pacific	/	140	*Tetraparma pelagica*
1978 (Feb.)[2]	Weddell Sea, SO	4	84 ± 17 (average); 586 (max.)	*Triparma laevis; Pentalamina corona*
1978 (May and June)[3]	Gulf of Alaska, subarctic North Pacific	9	4–700	*T. pelagica*
1980 (Feb.–Mar.)[4]	Weddell Sea (ice-edge region), SO	2	900	*T. pelagica; P. corona*
1983 (Mar.–Dec.)[5]	Kita-no-seto Strait, SO	12	/	*T. pelagica; T. laevis*
1983 (Dec.)–1984 (Jan.)[6]	Australian sector of the SO	6	100–226	*T. pelagica; Triparma strigata*
1996 (Jan.–Mar.)[7]	southern Indian sector of the SO (East Antarctica)	7	/	*T. pelagica; T. laevis; T. strigata; P. corona*
1999 (July–Aug.)[8]	Bering Sea, subarctic North Pacific	7	17	*T. pelagica; T. laevis; T. strigata*
1999 (Aug.)–2000 (Jan. and May)[9]	subarctic western Pacific	7	10–100	*T. pelagica*
2000 (Apr.) [10]	Gulf of Tehuantepec, Pacific of Mexico	2	40	*Tetraparma insecta; T. laevis* f. *mexicana*
2008 (Jan.–Feb.)–2009 (Mar.–Apr.)[11]	Scotia Sea, SO	/	1910 (max.)	*T. pelagica*
2009 (Mar.–Oct.)[12]	western North Pacific	6	100–570	*T. pelagica; T. laevis; T. strigata*
2014 (May–Oct.)[13]	SO, ATO	8	122 (SO average); 624 (max.)	*T. pelagica; T. laevis; T. strigata*

1. Nishida (1979); 2. Silver *et al.* (1980); 3. Booth *et al.* (1980); 4. Buck & Garrison (1983); 5. Takahashi *et al.* (1986); 6. Nishida (1986); 7. Waters *et al.* (2000); 8. Tanimoto *et al.* (2003); 9. Komuro *et al.* (2005); 10. Bravo-Sierra & Hernández-Becerril (2003); 11. Hinz *et al.* (2012); 12. Ichinomiya & Kuwata (2015); 13. this study.

temperature, latitude and bottom depth reached up to 49.5% ($F = 10.002$, $P < 0.01$), 38.8% ($F = 7.604$, $P < 0.01$) and 16.6% ($F = 3.059$, $P < 0.01$), respectively, all significantly contributing to the biogeographic distributions of coccolithophores and Parmales.

DISCUSSION

Biogeographic distributions of coccolithophores and Parmales

Although coccolithophores possess a wide range of ecological tolerance (Brand, 1994), the biogeographic distributions of this group of nanophytoplanton are subjected to various oceanic circulations and fronts in the ATO (Peterson & Stramma, 1991; Peña-Izquierdo *et al.*, 2012), such as the Subtropical Front (STF), Subantarctic Front (SAF), Polar Front (PF), BCF and CVF. In the frontal waters, the average abundance could reach up to as many as 82×10^3 cells l^{-1} (Boeckel & Baumann, 2008). Our results illustrated that high abundances of coccolithophores occurred in the northeast waters of the FI within the Falklands Current (Figure 2C), and were exactly confined in the SAF zone. A sharp contrast in temperature was detected between Site 35 ($3.3°C$) and Site 36 ($7.5°C$). The cool and nutrient-rich Antarctic waters, being mixed with the warm and oligotrophic Subtropical Gyre waters, facilitated the high abundance of living coccolithophores. It is similar in the North Atlantic, where high abundances of *G. oceanica* were observed in close coupling with the CVF (Figure 1B). Under the control of cool upwelling from the Canary Current, a $5.2°C$ drop was measured from Site 68 ($26.7°C$) to Site 69 ($21.5°C$).

The morphotypes within a species complex usually exhibited unequal ecological affinities. Fine-scale species-level

diversity has been studied in the South Atlantic waters, on species such as *Calcidiscus leptoporus, E. huxleyi* and *U. tenuis* (Boeckel & Baumann, 2008). In this study, we identified five types of *U. tenuis*, with types IIIb and IV as the predominant forms. Interestingly, these two morphotypes were absent in the cool and nutrient-replete waters of the FKLD and SO. On the contrary, the average abundances of *U. tenuis* types IIIb and IV in the ATO waters increased to 0.98×10^3 cells l^{-1} and 2.8×10^3 cells l^{-1}, associating with high frequencies of occurrence of 60.6% and 84.8%. This observation indicated that the two morphotypes had a preference for warm and oligotrophic open waters.

The latitudinal pattern and ecological zonation of living coccolithophores has been well established since the fundamental work in the Atlantic Ocean (McIntyre & Bé, 1967). However, the biogeographic knowledge on Parmales (formerly considered to be cysts) is almost blank before their algal nature was revealed (Marchant & McEldowney, 1986). So far, a number of microscopy works were carried out in both hemispheres (Table 3), e.g. the subarctic Pacific (Nishida, 1979; Booth *et al.*, 1980; Tanimoto *et al.*, 2003; Komuro *et al.*, 2005; Konno *et al.*, 2007; Ichinomiya & Kuwata, 2015), the Weddell Sea (Silver *et al.*, 1980; Buck & Garrison, 1983) and the SO (Nishida, 1986; Waters *et al.*, 2000; Hinz *et al.*, 2012), concentrating not only on the water columns, but also on the surface sediments (Zielinski, 1997). These surveys showed that the common abundance of Parmales, during both boreal and austral blooming seasons, can soar to $(4-900) \times 10^3$ cells l^{-1}, apart from a record abundance of 1910×10^3 cells l^{-1} in the Scotia Sea (Hinz *et al.*, 2012). Of the ∼20 taxa of Parmales (Konno *et al.*, 2007), *T. pelagica* is the most widespread species in various oceanographic settings (Table 3), except for the tropical waters, where distinct taxa exist, such as *Tetraparma insecta* and *T. laevis* f. *mexicana*. It is noteworthy that *Pentalamina corona* (Pentalaminaceae) seems solely occurring in the
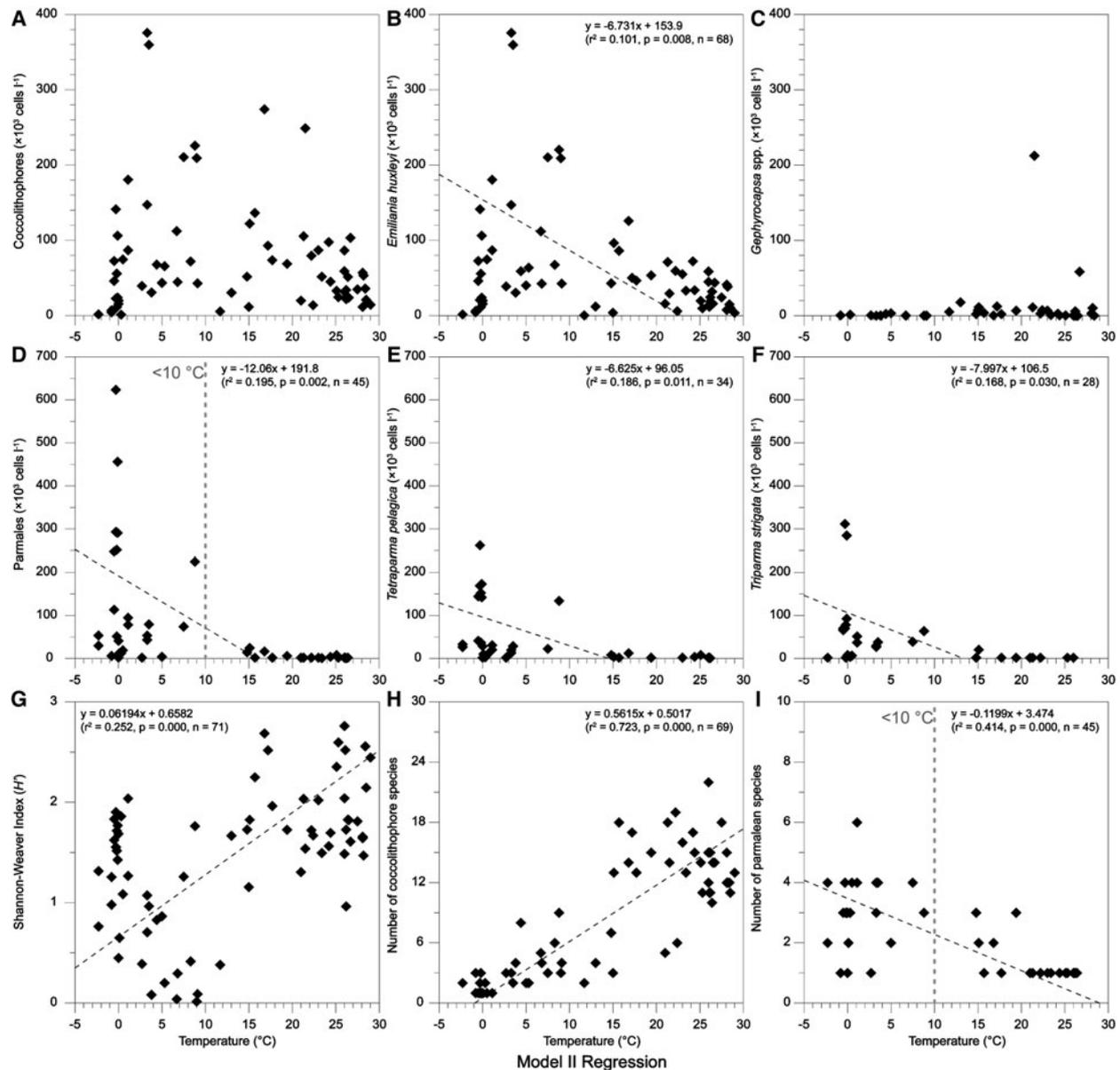
Fig. 6. Model II regressions of sea surface temperature with coccolithophores and Parmales.

coastal and ice-edge regions off the Antarctica, whereas it has not been recorded in the Pacific. Additionally, *T. laevis* may possess relatively big niche breadth, since many forms and subspecies have been described in diverse seawaters. Our results on Parmales in the SO were comparable to those previous reports, showing patchy distribution in the PF zone, where the Parmales were coupled with the occurrence of cool waters from the Antarctic Circumpolar Current.

Unlike the widespread distribution of coccolithophores, parmalean species seemed to be more restricted to cooler waters in higher latitudes (Figure 2B). However, metabarcoding technique also disclosed the subtropical existence of Parmales in the ATO (Ichinomiya *et al.*, 2016), which provided positive biogeographic information on these small organisms. Although in a very low level of abundance, in the present microscopy study, parmalean species were indeed observed in the subtropical waters of ATO, such as in the SATL (16 Sites) and NATR (two Sites, being affected

by the cool Canary Current). This suggests the ecological adaptation of Parmales in various oceanic environments.

Temperature affects the regional patterns

Temperature is considered as an important factor in controlling the phytoplankton distribution and productivity (Thomas *et al.*, 2012). Latitudinal patterns of the thermal limits of marine phytoplankton had been revealed in a synthetic study (Chen, 2015), which evaluated the various thermal breadths in different functional groups. As for coccolithophores and Parmales, although their abundances might be regulated by nutrient availability (Jordan, 2011) or zooplankton grazing (Urban *et al.*, 1993), it is evident that temperature is an important determinant in driving the large-scale patterns. Just like the CCA ordination results in this study (Figure 5), coccolithophores and Parmales were exactly intersected in two distinct groups by the thermal gradient.

Using a model II regression, the effects of temperature on assemblages of coccolithophores and Parmales were elucidated (Figure 6). Obviously, coccolithophores can survive in a wide range of temperature and hence maintain their high abundance, while the Parmales are restricted in a small range of temperature ($<10°C$). This difference might be caused by the low optimal growth temperature ($0–10°C$) in parmalean species, which had been previously verified both naturally in the field and in the growth experiments of individual species (Ichinomiya & Kuwata, 2015). Furthermore, a recent report indicated that the growth of Parmales was not limited by low silica concentration ($<1\ \mu mol\ l^{-1}$) even though in close genetic association with diatoms (Yamada et al., 2014).

Blooms of E. huxleyi had been observed in the north-east of the FI within the Great Calcite Belt ($40°–60°S$), in association with water temperatures between 5 and $15°C$ (Balch et al., 2014). In this study, high abundances of E. huxleyi were documented in the same geographic region (Figure 2C). Additionally, their abundance presented a negative correlation with increasing temperature (Figure 6B), with high abundance in waters $<10°C$. These findings suggested that natural E. huxleyi had adapted to a relatively low growth temperature. This can also be used to explain why the Parmales were closely coupled with E. huxleyi in this study. However, the number of coccolithophore species, together with the species diversity (H') of the whole nanoplankton, significantly increased with elevated temperature (Figure 6G, H), hence indicating more diverse assemblages in tropical waters, with mean increments of 127% (number) and 52% (diversity) in warmer waters ($>25°C$).

The oceanic warming has been dramatically impacting on the photosynthetic phytoplankton (Boyce et al., 2010). Model prediction showed that tropical assemblages will be more vulnerable to the increasing seawater temperature (Thomas et al., 2012). This study disclosed that temperature significantly affects the large-scale lateral patterns of nanophytoplankton in the Atlantic Ocean. Abundances of coccolithophores and Parmales have been closely coupling with oceanic fronts. Therefore, to get a better understanding of phytoplankton biogeography, further studies need to focus on the ecological response of various functional types in association with changing physico-chemical processes under the regional climate change.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/S0025315416001740.

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