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Research paper

Latitudinal distribution of extant fossilizable phytoplankton in the Southern Ocean: Planktonic provinces, hydrographic fronts and palaeoecological perspectives

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ABSTRACT

We present the combined abundance of all extant fossilizable planktonic groups (Dinoflagellates, Coccolithophores, Silicoflagellates, Diatoms, Parmales, Archaeomonads and micro-zooplankton) from surface waters collected along a latitudinal transect in the western Pacific sector of the Southern Ocean, ranging from ~48°S, offshore New Zealand, to ~70°S in the Ross Sea, Antarctica. Latitudinal shifts in species' distribution correspond with the Antarctic Circumpolar Current fronts and with the seasonal position of the ice-edge. Distinct bioprovinces are defined by clustering samples with a high degree of similarity. Our data confirm the importance of previously-defined taxa as palaeoceanographic proxies but also reveal some differences: the shift in dominance between the silicoflagellates genera *Dictyocha* and *Stephanocha*, used as a proxy of palaeo sea-surface temperatures, occurs slightly north of the Southern Sub-Antarctic Front rather than at the Polar Front; the shifts in abundance between the open-ocean diatom species *Fragilariopsis kerguelensis* and sea-ice related *F. curta* and *F. cylindrus*, as well as the drop in the coccolithophore *Emiliania huxleyi*, occur at the southern Antarctic Circumpolar Front rather than at the Polar Front. Finally, we introduce the Corona-index, based on the ratio of the coronatid to non-coronatid silicoflagellates species *Stephanocha speculum*, as a new proxy for sea-ice and we confirm the occurrence of abundant Archaeomonads and Parmales (*Triparma laevis* subsp. *ramispina*) in the marginal ice-edge zone.

1. Introduction

The Southern Ocean (SO) is an important High Nutrient Low Chlorophyll (HNLC) zone of the World's oceans, where phytoplankton growth is thought to be limited by the availability of iron in nutrient-replenished surface waters (De Baar, 1994). The SO plays a key role in the climate system: it influences global ocean circulation through the flow of the Antarctic Circumpolar Current (Orsi et al., 1995) and the formation of bottom waters in the Weddel and Ross Sea; it controls the distribution of nutrients in the upper oceans (Sarmiento et al., 2004) and is a key area for heat and CO_2 exchange with the atmosphere.

In the last decades, several international and national research projects targeted the SO as a key area to understand the mechanisms and consequences of recent climate change. Surveys of sea-surface temperature, salinity and upper ocean thermal structure, often coupled with surface water sampling through the ship's pump or the Continuous Plankton Recorder (Hosie et al., 2003), are routinely carried out as ancillary activities. Several latitudinal transects, located in different areas of the SO, and during different periods of the year, provide information on the lateral variability of physical and biological processes in the different sectors of the SO and contribute to the identification of seasonal patterns and inter-annual variation.

Biological zonation of the Southern Ocean is long recognized as one main goal of marine research (Deacon, 1982). Large-scale efforts for a bio-regionalization of the oceans (Grant et al., 2006) showed the importance of the hydrographic control on the patterns of biological production. Light availability, macro- and micro-nutrients are identified as key factors controlling phytoplankton processes in the Southern Ocean (Boyd, 2002), with water column stability, temperature and the extent and variability of sea-ice also playing an important role in structuring the Antarctic marine ecosystems. Grazing pressure is a further factor that controls phytoplankton standing stocks. After the first pioneer work on diatoms (Ehrenberg, 1844), early works (Hart, 1934, 1942; Halldal, 1953; Husted, 1958; Beklemishev, 1964; Hasle, 1969) showed the biogeographic distribution and seasonality of the main phytoplankton species in the Southern Ocean. Although most early and following studies were focused on diatoms (among others Husted, 1958; Fenner et al., 1976; Hasle, 1976; Burckle et al., 1987), several studies targeting all phytoplankton groups (Kopczyńska et al., 1986, 1998, 2007; Froneman et al., 1995; Ehnert and McRoy, 2007; Gomi et al.,

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2007; Chang et al., 2013; Patil et al., 2013) pointed out the importance of latitudinal gradients in defining the biogeographic distribution of single species and the role of the PF as an important hydrographic boundary. The influence of sea-ice on the composition of extant phytoplankton was also highlighted (El-Sayed and Taguchi, 1981; Buck and Garrison, 1983; Bianchi et al., 1992; Garrison et al., 1993; Leventer, 1998; Wright and van den Enden, 2000; Kang et al., 2001).

In the long-range geological record, bioprovincialism appears as an important feature, with different species making an important contribution in high- or low-latitude settings, thus requiring the creation of distinct biostratigraphic schemes for different latitudinal provinces. In sub-polar marine settings, the palaeo-biogeography of distinct species or species groups is used as a palaeoenvironmental tool to infer the latitudinal shift in position and/or gradient of hydrographic fronts. In the SO, fluctuations in the abundance of calcareous nannofossil species (Flores et al., 1999; Findlay and Flores, 2000; Findlay and Giraudeau, 2002; Fenner and Di Stefano, 2004), in the proportion of silicoflagellate species (Ciesielski, 1974) and diatom assemblages (among others Burckle, 1984; Pichon et al., 1987, 1992; Labeyrie et al., 1996; Zielinski and Gersonde, 1997; Crosta et al., 1998; Zielinski et al., 1998; Gersonde and Zielinski, 2000; Gersonde et al., 2005) along sedimentary successions are used to the define the latitudinal shifts of the PF and/or the distribution of sea-ice on glacial–interglacial time scales.

The latitudinal distribution of extant fossilizable species in relation to frontal hydrography in the SO has been addressed only sectorially, through the analysis of specific groups such as coccolithophores (Hasle, 1960; McIntyre et al., 1970; Nishida, 1986; Findlay and Giraudeau, 2000; Cubillos et al., 2007; Böckel and Baumann, 2008; Gravalosa et al., 2008; Mohan et al., 2008; Saavedra-Pellitero et al., 2014; Malinverno et al., 2016), diatoms (Hasle, 1976; Smetacec et al., 2002; Tremblay et al., 2002; Cefarelli et al., 2010; Olguín and Alder, 2011) and silicoflagellates (van der Spoel and Hallegraeff, 1973; Malinverno, 2010) but detailed comprehensive information on the main fossilizable phytoplankton groups is still scarce (Eynaud et al., 1999; Hinz et al., 2012) and incomplete.

The aim of this work is to increase our knowledge on the biogeography of all extant fossilizable phytoplankton species, i.e. Coccolithophores, Silicoflagellates, Diatoms, Dinoflagellates, Parmales and Archaeomonads, through the analysis of their distribution along a latitudinal gradient in surface waters. Identification at the lowest possible taxonomic level and the use of morphotypes allow overcoming the limitation of broadly-distributed species.

Although our data are restricted to one transect, one season and the surface layer, statistical analysis of species/morphotype's distribution allowed to define distinct biogeographic provinces, which correlate with upper the ocean thermal structure and hydrographic fronts of the ACC, satellite-detected Chl-a data and published surface macronutrients from the same transect. The palaeoceanographic applications of species/morphotypes' distribution in relation to frontal hydrography are discussed.

The analysed transect, located in the western Pacific sector of the SO, crosses the PF at 62.8°S, much to the south than in other circum-Antarctic areas, and reaches until ~70°S in the Ross Sea, Antarctica, through a corridor in the pack-ice belt.

2. Oceanographic setting

2.1. Physical oceanography

The Southern Ocean is characterized by the eastward flow of the ACC, driven by the westerly winds which flow between 45–55°S (Orsi et al., 1995 and references therein). The ACC is bound to the north by the Subtropical Front (STF), which separates it from the warmer and saltier waters of the subtropics, and to the south by the southern boundary (Bdy), which separates it from the coastal circulation driven by the cyclonic Ross Sea Gyre (Orsi et al., 1995). Different fronts within the ACC are identified as bands of enhanced latitudinal property gradients in surface waters and by pronounced isopycnal tilt throughout the deep water column. The Subantarctic Front (SAF) and Polar Front (PF) carry out most of the transport of the ACC and are associated with strong surface currents (Orsi et al., 1995; Nowlin et al., 1977). An additional front, the Southern ACC Front (sACCf), is identified on the basis of the subsurface temperature signature (Orsi et al., 1995). Its position is often very close to the Bdy. Although the ACC flow is driven by atmospheric forcing through westerly winds, its path is strongly controlled by bottom topography (Gordon et al. 1978) so that the fronts are located at different latitudes across the different zonal sectors of the SO. Campanelli et al. (2011) described the characteristics and latitudinal position of the ACC fronts along our transect from New Zealand to the Ross Sea (Fig. 1):

- the SAF, as defined by a sharp temperature gradient at depths of 300 or 400 m (Belkin and Gordon 1996 and Orsi et al., 1995, respectively) is here split in two branches: the Northern SAF (NSAF) corresponds with a thermal gradient in the range 4–7 °C at 300 m and occurs at 51.7°S, while the Southern SAF (SSAF) is associated with a thermal gradient in the range 3–4 °C at 300 m and occurs at 58.6°S. While the NSAF position is stable in time, over the continental slope at the southern edge of the Campbell Plateau (see also .kml map), the SSAF position is not controlled by bottom topography and is strictly related to the development of meander features (Budillon and Rintoul, 2003; Campanelli et al., 2011), probably influenced by the interaction with the southern tip of the Campbell Plateau (Yaremchuk et al., 2001).
- the PF, as defined by the subsurface temperature minimum of 2 °C at depth above 200 m (Orsi et al., 1995) and a 2 °C gradient in SST, is located at 62.8°S, but has been found to oscillate by up to 2° of latitude on a seasonal and interannual basis, due to the lack of a topographic constrain. When the same track has been crossed several times during the same season, the PF has been found southward from November to February (Budillon and Rintoul, 2003; Campanelli et al., 2011).
- the sACCf, as defined by temperatures below 0° at the sub-surface (<150 m) temperature minimum and by temperatures above 1.8 °C in the deeper (>500 m) temperature maximum (Orsi et al., 1995), is located at 63.6°S. Its position is stable in time and strictly constrained, in the area of our transect, by the steep northern flank of the SE Indian/Pacific–Antarctic Ridge.

Within these fronts, the water masses show more uniform characteristics, with more gradual changes in physical properties and can be therefore described as distinct zones (Orsi et al., 1995). From north to south, these are (Fig. 1):

- the Subantarctic Zone (SAZ) between the STF and the SSAF: in this sector of the Southern Ocean, it is divided by the NSAF into a northern SAZ (nSAZ) and a southern SAZ (sSAZ);
- the Polar Frontal Zone (PFZ) between the SAF and the PF;
- the Antarctic Zone (AZ) from the PF to the Antarctic continent. The sACCf and the Bdy lay within the AZ and correspond with the winter and summer position of the sea-ice limit, respectively. South of the Bdy the circulation is dominated by the Ross gyre, a cyclonic clockwise feature driven by the interaction with the westward coastal flow. Within the AZ, the seasonal waxing and waning of sea-ice defines different hydrographic conditions, that we sampled along our transect:
- the permanently open ocean zone (POOZ), between the PF and the winter sea-ice (WSI) limit;
- the seasonal ice zone (SIZ) including the marginal ice-edge zone (MIZ) at the edge of the retreating pack-ice belt. During the cruise, we crossed the “corridor” of open water that develops seasonally into the belt of pack ice at the entrance of the Ross Sea (PNRA,