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Plankton community response to Saharan dust fertilization in subtropical waters off the Canary Islands

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Abstract

The plankton community response to natural fertilization caused by the Saharan dust was studied in the Canary Islands waters during winter–spring 2010. For this, a weekly sampling was carried out to characterize the pico-, nano- and microplankton communities. During this period several dust events were identified from atmospheric suspended matter and metal composition. Temperatures above 19 °C in the mixed layer, high stratification and a very low concentration of chlorophyll *a*, indicated the absence of the characteristic late winter bloom during this year. However, relatively high primary production rates were measured, probably fuelled by nutrient release from the deposited atmospheric dust. In fact, this winter–spring was one of the most intense dust periods during the last years and Saharan dust events were identified in every month. The effect of the Saharan dust over the plankton community mainly consisted in the enhancement of primary producers, mostly diatoms, and the increase of the mesozooplankton stock, whereas cyanobacteria and autotrophic picoeukaryotes were negatively affected. These results suggest that the Saharan dust deposition would be partly fuelling the primary production in these oligotrophic waters of the northeast Atlantic, and could be especially significant during stratified periods, when the atmospheric dust would be the most important nutrient source.

1 Introduction

The productivity of the oceans is largely determined by nutrient availability for autotrophic organisms living in the euphotic zone, even in ecosystems plenty of macronutrients. In this sense, it is now rather clear that the iron deficiency limits primary production in the so-called high nutrient low chlorophyll (HNLC) ecosystems from polar to tropical regions (Boyd et al., 2007). In oligotrophic waters, iron is not the only factor limiting phytoplankton growth as macronutrients are also scarce and nitrogen, phosphorus or manganese could also be limiting elements (Schluter, 1998). Therefore, primary productivity is stimulated when nutrients are available for phototrophic organisms. This was observed in the oligotrophic gyre of the North Pacific (McAndrew et al., 2007; Mahaffey et al., 2012) where a positive response of phytoplankton biomass and primary production was found when nutrient-replete deep water was added to surface water. Similarly, the experimental addition of Saharan dust, releasing iron, phosphate, nitrate and silicate, has resulted in the stimulation of primary productivity in low nutrient low chlorophyll waters (Bonnet et al., 2005; Herut et al., 2005; Duarte et al., 2006; Marañón et al., 2010).

Atmospheric deposition is one of the major sources of limiting nutrients to the open ocean, mainly iron (Duce and Tindale, 1991; Jickells, 1999) but also, in a lesser extent, nitrogen and phosphorus (Donaghay et al., 1991; Guerzoni et al., 1999; Duarte et al., 2006). In this sense, the Sahara desert is the most important dust source for the world's oceans, particularly in the North Atlantic. The Saharan dust contents high values of crustal elements as silicate, aluminum, manganese or iron (Goudie and Middleton, 2001; Viana et al., 2002), as well as nitrate and phosphorus (Bonnet et al., 2005; Herut et al., 2005; Duarte et al., 2006). The release of nutrients from Saharan dust has a positive effect over phytoplankton growth that has been experimentally observed (Bonnet et al., 2005; Herut et al., 2005; Duarte et al., 2006; Marañón et al., 2010). However, the effect of the Saharan dust deposition in the field has been rarely studied and is still not clear. The enhanced biological response after a dust storm was observed by Bishop et al. (2002) based on in situ particulate organic carbon and chlorophyll data in HNLC waters in the North Pacific. Also in oligotrophic waters of South China Sea, chlorophyll *a* concentration was significantly increased during heavy dust deposition years (Wang et al., 2012). However, Chami et al. (2012) showed a negative effect of dust on primary production in the subtropical Atlantic Ocean and they ascribed it to the attenuation of PAR radiation produced by the dust aerosol layer in the atmosphere. In the Mediterranean Sea, a relationship between phytoplankton and dust was only observed when atmospheric events coincided with the stratified season (Eker-Develi et al., 2006; Volpe et al., 2009). Hence, it has been hypothesized (Guerzoni et al.,

1999) that Saharan dust would only have a major influence on primary production at local and short time scales, just when an atmospheric deposition event takes place.

There is another key factor regulating the biological response when nutrients are available, the control exerted by grazers (Donaghay et al., 1991; Landry et al., 1997). Microzooplankton grazing has been pointed out as the principal mechanism limiting phytoplankton growth in both artificial iron injections (Landry et al., 2000a, b; De Baar et al., 2005; Boyd et al., 2007; Henjes et al., 2007) and dust addition experiments (Herut et al., 2005; Marañón et al., 2010). Thereby, larger diatoms are the most favored organisms when primary production is artificially induced (Landry et al., 2000b; De Baar et al., 2005; Boyd et al., 2007; Henjes et al., 2007), because of their higher growth rates and a lower grazing pressure compared to prokaryotic algae (Landry et al., 2000a, b; Henjes et al., 2007). Furthermore, although mesozooplankton grazing is also enhanced (Bollens and Landry, 2000; Tsuda et al., 2007), its impact upon primary production seems to be low (Tsuda et al., 2005). The coupling between phytoplankton and their grazers, as well as predation of mesozooplankton upon microzooplankton, and the composition of the planktonic community are essential aspects determining the flux of organic matter from the euphotic zone to deeper waters. In this sense, the community biomass change observed from nano- to microplankton and the success of diatoms in artificial fertilization (De Baar et al., 2005; Boyd et al., 2007) would favor a higher carbon export flux. However, if the microbial loop is enhanced, the major carbon respiration occurs in surface waters and a less effective export of carbon takes place (Azam et al., 1983; Legendre and Le Fèvre, 1995). This has been observed in the equatorial Pacific after the increase in primary production promoted by iron addition. The coupled response between phytoplankton growth and microzooplankton grazing maintained the usual low carbon export scenario of these waters (Landry et al., 2000a).

The Canary Islands are located in the eastern subtropical North Atlantic within the Canary Current and close to the Sahara desert. In these oligotrophic waters, a quasi-permanent thermocline prevents the entrance of nutrients in the mixed layer, and only the cooling of surface waters during the winter erodes the thermocline and allows the increment of nutrient concentrations in the upper water column stimulating a higher phytoplankton growth (De León and Braun, 1973; Braun, 1980). In this scenario, the high iron inputs produced by the frequent African dust events reaching these stratified waters (Sarthou et al., 2007) could be a major factor affecting primary production, especially during winter, because of the highest intensity of the events (Viana et al., 2002). Therefore, the Canary Islands are a suitable place to study the effect of Saharan dust deposition in the ocean, not only because of their location in oligotrophic waters and their proximity to the most important dust source, but also because their distant position from intense anthropogenic influences.

In this work, we studied the in situ effect of the Saharan dust deposition on the planktonic community within the oligotrophic waters of the northeast Atlantic Ocean (Canary Islands) during the winter–spring 2010.

2 Material and methods

A weekly sampling was carried out in the Canary Islands waters to the north of Gran Canaria Island from February to June 2010, on-board the R/V *Atlantic Explorer*. Four stations 10 nautical miles equidistant (Fig. 1) were sampled from the surface to 300 m depth. Pressure, salinity, temperature and fluorescence were measured using a SBE25 CTD and a Turner Scufa Fluorometer coupled to an oceanographic rosette equipped with six 4 L Niskin bottles. Seawater samples were taken at the mixed layer (20 m) to characterize the pico-, nano- and microplankton communities. A SBE19 plus CTD was eventually used during some cruises because of the main CTD failure. From temperature data, the mixed layer depth (MLD) was calculated as the level with a temperature difference of 0.5 °C from the 10 m depth (Cianca et al., 2007).

Sea surface temperature was obtained from the Deep Sea Buoy Network dataset (REDEXT, http://www.puertos.es/oceanografia_y_meteorologia/redes_de_medida/index.html, last access: April 2013) belonging to Puertos del Estado (Spanish Government). Hourly data were taken at 3 m depth by a SeaWatch buoy located to the northwest of Gran Canaria (28.20° N, 15.80° W, Fig. 1) from December 2009 to June 2010.

Chlorophyll *a* (Chl *a*) was measured by filtering 500 mL of seawater through a 25 mm Whatman GF/F filter and freezing it at −20 °C until its analysis at the laboratory. The extraction procedure consisted in placing the filter in 90 % acetone at −20 °C in the dark, during at least 20 h, and following the acidification method by Strickland and Parsons (1972). Pigments were measured on a Turner Designs 10 A Fluorometer, previously calibrated with pure Chl *a* (Yentsch and Menzel, 1963). From these data at 20 m, fluorescence in the whole profile was converted to Chl *a* (Chl $a = -0.001 + 26.05 \cdot \text{fluorescence}$, $r^2 = 0.65$, $p < 0.001$ for the SBE19plus and Chl $a = 0.001 + 0.21 \cdot \text{fluorescence}$, $r^2 = 0.12$, $p > 0.05$ for the SBE25) as an indicator of phytoplankton biomass. The relationship between fluorescence and Chl *a* for the SBE25 was not significant because of the scarcity of data and the fact that all concentrations measured using that sensor were very low. However, it was the only way to obtain chlorophyll data for all cruises in May and until June, 9. Average Chl *a* concentration was calculated without station 1 as a significant difference (Kruskal–Wallis test, $p < 0.001$) was found between this coastal station and the stations 2, 3 and 4.

Picoplanktonic organisms (0.2–2 µm) were sampled in 1.6 mL tubes, fixed immediately with 100 µL of 20 % paraformaldehyde, incubated at 4 °C during half an hour, frozen in liquid nitrogen, and finally kept at −80 °C until further analysis. Samples were analyzed later by Flow Cytometry using a FACScalibur Cytometer (Beckton and Dickinson). Side scatter (SSC) and fluorescence parameters were obtained to distinguish between autotrophic picoeukaryotes (APE), cyanobacteria (*Prochlorococcus*, Pro, and *Synechococcus*, Syn) and heterotrophic prokaryotes (HP). Samples were run until 10 000 events were reached or after 2 min at high speed to measured phototrophic organisms (APE, Pro and Syn), and at low speed for HP samples which were pre-stained with SYTO-13.

Auto- and heterotrophic nanoflagellates (ANF and HNF) were fixed using 540 µL of 25 % glutaraldehyde in a tube containing 45 mL of seawater and kept at 4 °C in dark until the sample was filtered onto a 0.6 µm black polycarbonate filter placed over a backing filter and stained by diamidino-2-phenylindole (DAPI) for five minutes. The filter was immediately mounted on a microscope slide with low-fluorescence immersion oil and kept at −20 °C until its analysis by epifluorescence microscopy with a Zeiss Axiovert 35 microscope (Haas, 1982).

Microplanktonic organisms were kept in 500 mL dark bottles fixed with 1.5 mL of acid lugol and analyzed afterwards by the Utermöhl technique, settling a 100 mL subsample for 48 h in a composite chamber. The bottom chamber was then examined by an inverted Zeiss Axiovert 35 microscope to identify the main microplanktonic groups: diatoms (Dia), dinoflagellates (Din), ciliates (Cil), and copepod nauplii or copepodites (Cop). Only samples from station 3 at 20 m were analyzed.

The abundance of organisms obtained by flow cytometry was converted to biomass using the carbon conversion factor of: 17 $\mathrm{fg\,C\,cell^{-1}}$ given by Bode et al. (2001) for HP, 29 $\mathrm{fg\,C\,cell^{-1}}$ for Pro, 100 $\mathrm{fg\,C\,cell^{-1}}$ for Syn (Zubkov et al., 2000) and 1500 $\mathrm{fg\,C\,cell^{-1}}$ for APE (Zubkov et al., 1998). After biovolume estimation by microscopy, nanoflagellates were converted to carbon using the factor of 220 $\mathrm{fg\,C\,\mu m^{-3}}$ for HNF (Borsheim and Bratbak, 1987) and the equation $0.433(\mathrm{BV})^{0.863}$ $\mathrm{pg\,C\,cell^{-1}}$ for ANF (Verity et al., 1992). Finally, the microplanktonic abundance was converted to biomass from total biovolume data obtained directly by microscopy for the most abundant cells or from previous measurements in these waters (A. Ojeda, unpublished data). If these data were not available, an average size from the literature for every organism or group (Tomas, 1997; Horner, 2002; Ojeda, 2006, 2011) was assumed, fitting them to the suitable shape following Hillebrand et al. (1999). The corresponding parameters were used for Dia ($\log a = -0.541$, $b = 0.811$ for $V < 3000\,\mu\mathrm{m}^3$; $\log a = 0.933$, $b = 0.881$ for $V > 3000\,\mu\mathrm{m}^3$), Din ($\log a = -0.353$, $b = 0.864$) and Cil ($\log a = -0.639$, $b = 0.984$ for aloricate ciliates; $\log a = -0.168$, $b = 0.841$ for tintinnids) to obtain the biovolume to biomass conversion factor given by Menden-Deuer and Lessard (2000) ($\log \mathrm{pg\,C\,cell^{-1}} = \log a + b \cdot \log V$). Some species were not taken into account to calculate the microbial biomass because of the impossibility of finding their size range or biovolume in the literature, but these species were always practically negligible in terms of abundance.

The average biomass was calculated taking into account the four stations sampled for pico-, nano- and microplankton as no statistical differences were found for any of the groups (Kruskal–Wallis test, $p > 0.05$).

Primary production (PP) was measured using the ^{13}C method (Hama et al., 1983) only in station 2 at 20 m depth. Water samples were transferred to 2 L polycarbonate bottles previously rinsed with 10 % HCl and distilled-deionized water and $NaH^{13}CO_3$ was added at about 10 % of total inorganic carbon in the ambient water. The samples were incubated for between 6 and 22 h depending on the cruise, in a tank on-deck. Running surface seawater and appropriate meshes simulated in situ temperature and light intensity. Initial and final particulate organic carbon (POC), and particulate material used for isotopic analysis were filtered through precombusted (5 h, 450 °C) GF/F filters. The filters were frozen and stored at −20 °C until analysis. POC was measured using a CHN analyzer (Carlo Erba EA 1108) and isotopes in a mass spectrometer equipped with an elemental analyzer (Flash EA 11 ThermoFinnigan with Deltaplus).

Atmospheric total suspended particulate matter (TSM) was collected from November 2009 to June 2010 using a high volume sampler pumping system (MCV), at a flow rate of 50 $m^3 h^{-1}$ and onto Whatman GF/A 20 cm × 25 cm fiberglass filters. Each sampling period started at 08:00 LT and lasted 24 h. Three collectors were located in the northeast of the island (Fig. 1) and placed 10 m above the ground. For Fe, Al and Mn analysis, the filters were treated with nitric and hydrochloric acid, according to the Beyer modified method (López-Cancio et al., 2008). These elements were determined by atomic emission spectrophotometry using an inductively coupled plasma optical emission spectrometer (Perkin Elmer 3200 DV).

The zooplankton sampling procedure is explained in detail elsewhere (Herrera et al., 2013). Briefly, organisms were captured in vertical hauls with a double WP-2 net equipped with 100 µm mesh nets. One of the samples was used for measuring biomass as dry weight using a standard protocol (Lovegrove, 1966). The average zooplankton biomass was calculated from the four stations data as no statistical differences were found (Herrera et al., 2013).

3 Results

A highly stratified water column was characteristic during the whole period from March to June 2010. Temperature and potential density were above 19 °C and 26.4 $\mathrm{kg\,m^{-3}}$, respectively, in the upper 100 m layer (Fig. 2a and b). Average MLD ranged between 110 m in March to 36 m in June, with no differences among stations (Kruskal–Wallis test, $p > 0.05$). The absence of intense mixing in the surface waters resulted in very low values of Chl *a*, even at the deep chlorophyll maximum (DCM) where the highest chorophyll concentration was 0.5 $\mathrm{\mu g\,L^{-1}}$ at the end of March (Fig. 2c).

Saharan dust events were identified in every month from TSM data, from November 2009 to July 2010 (Fig. 3a). The highest value ($521 \pm 71\ \mathrm{\mu g\,m^{-3}}$) was reached during March, coinciding with the maximum concentrations of aluminum, iron and manganese (Fig. 3a and b). However, metal concentrations as high as in March were measured in January, although TSM only reached $104 \pm 68\ \mathrm{\mu g\,m^{-3}}$. Less intense TSM peaks also coincided with relative maxima in metal concentrations, but the magnitude of the increment was not proportional in all cases. In May, an intense peak of aluminum was found without observing a similar increase of iron or manganese. In June, a rather high value of iron concentration was reached without observing a parallel increase in aluminum or manganese. Nevertheless, a significant correlation (Spearman $r > 0.41$, $p < 0.001$) was found for TSM and the three metals.

In spite of the quite low Chl *a* concentration observed at 20 m from February to June (Figs. 2c and 4), rather high values of PP were found at the end of March ($4.8 \pm 0.6\ \mathrm{\mu g\,C\,L^{-1}\,h^{-1}}$) and in May and June (Fig. 4), reaching rates up to $5.9 \pm 1.3\ \mathrm{\mu g\,C\,L^{-1}\,h^{-1}}$ (see Sect. 4). However, most of the autotrophic organisms kept extremely low biomass, as it was showed for Chl *a* (Figs. 2c and 4). Pico- and nanophytoplankton biomass accounted for less than 1 $\mathrm{\mu g\,C\,L^{-1}}$ (Fig. 5a and b) except at the end of March and April for autotrophic ANF, and at the beginning of May for Pro. Similarly, Dia biomass was rather low (Fig. 5c) only reaching 1 µg C L^{-1} in April and May. Only Din accounted for more than 1 µg C L^{-1} during the sampling period, peaking at the end of March and April, and in June (Fig. 5c).

Heterotrophic biomass was also quite low with a slightly higher contribution of HP, whose biomass was more than 1.5 µg C L^{-1} from mid March to June, while HNF and Cil did not reach this value except at the end of April for HNF (Fig. 5b and d).

The relationship between autotrophic and heterotrophic biomass was always below 1 (Table 1), although ratios including microplankton (A : H) were always higher than those in which only pico- and nanoplankton were taken into account ($A_{\mathrm{Pico,ANF}} : H_{\mathrm{HP,HNF}}$).

The effect of dust upon the planktonic community was estimated for the dust deposition event observed on 18 March. For that, the difference between parameters, before (two samplings before) and after (two samplings after) this date was calculated. Negligible and non-significant changes (t test, $p > 0.05$) in Chl *a* were measured (Fig. 6a). By opposite, PP displayed a positive although non-significant change (t test, $p > 0.05$). The response of the different planktonic groups considered was quite different, finding an increase in biomass for the majority of groups (Fig. 6a), with the exception of APE and Syn that showed a significant negative change (APE: t test, $p < 0.01$; Syn: t test, $p < 0.05$) in both biomass and abundance (Fig. 6b). Only HP and Din increased their abundance, while the other groups did not show any measurable change. The largest positive responses were observed for Meso and Din, but they were statistically significant only for the former. In the case of phytoplankton, the only significant positive change (t test, $p < 0.05$) was the Dia increase in biomass (Fig. 6a), although this change was not found in abundance (Fig. 6b).

These observed changes in abundance and biomass entailed considerable relative changes in planktonic groups (Fig. 7a and b). ANF and Meso biomass increased more than 100 % (Fig. 7a), but the response was not significant for nanoflagellates (t test, $p > 0.05$), which additionally decreased in abundance (Fig. 7b). The highest relative change was observed for Dia biomass which supposed an increment of 1309 ± 576 %, despite its abundance decreased by 10 ± 57 % (Fig. 7a and b). However, the considerable enhancement of PP rate of 138 ± 208 % was not significant (*t* test, $p > 0.05$). On the other hand, the negative effect of the dust event upon APE and Syn supposed a reduction in their biomass and abundance of 72 ± 73 and 65 ± 92 %, respectively.

4 Discussion

Sea surface temperature data obtained since January 2010 (Fig. 2a) confirmed the higher temperatures before our sampling, precluding the development of the bloom as temperature in the mixed layer, and consequently stratification was higher before February. Thus, the characteristic late winter bloom (De León and Braun, 1973; Braun, 1980; Arístegui et al., 2001) did not take place during the 2010 year, given the high stratification (Fig. 2a and b) and the low Chl *a* concentration measured (Figs. 2c and 4). These low values of phytoplankton biomass were common for all autotrophic organisms (Fig. 5) but extremely low for cyanobacteria and picoeukaryotes comparing to previous years in the area (Schmoker and Hernández-León, 2013). Biomass was also lower than in previous years for both HNF and Cil. Only Din biomass was considerable and dominated microplanktonic biomass during the whole period (Fig. 5c). Despite the low biomass values for both autotrophs and heterotrophs, the last dominated during the whole period (A : H < 1, Table 1), which seem to be a common feature in the North Atlantic gyre waters when Chl *a* is below 0.1 $\mu g L^{-1}$ (Buck et al., 1996).

The microplankton biomass data shown here should be taken with caution because in many cases no direct size measurements were made by microscopy, and a quite wide range was used from the literature to calculate an average biovolume for dinoflagellates and diatoms groups or species. Furthermore, comparison with previous years must be taken with caution as different carbon conversion factors were used. Nevertheless, these sources of error do not affect the aim of this study, i.e. the possible change on the composition of the planktonic community through a natural dust fertilization episode. Hence, if the same error is assumed in all data, no influence should be expected in the relative change of different organisms.

In addition to unusual hydrographic and biological properties, 2010 was one of the most intense dust periods during the last years, especially in March (Aerosol Optical Thickness data collected by the Moderate Resolution Imaging Spectroradiometer, MODIS, from NASA Earth Observations Project, http://earthobservatory.nasa.gov/, last access: April 2013). This was also observed in frequent dust events occurred over Gran Canaria Island during the whole period studied. Furthermore, the most intense event took place in March, when the TSM concentration reached the highest value (Fig. 3). The presence of significant concentrations of iron, aluminum and manganese in dust and their correlation with TSM confirmed the crustal nature of the dust and its Saharan origin (Viana et al., 2002). This fact, together with the strong water column stratification observed during this winter (Fig. 2) suggests that the major source of nutrients to the surface waters in this area during the period studied was the atmospheric deposition of Saharan dust. In this sense, it is important to note the location of the sampling site, to the north of the islands, away from intense mesoscale activity prevalent leeward (Arístegui et al., 1994; Barton et al., 2004) which could be an important source of nutrients into the mixed layer (Barton et al., 1998). Moreover, Cianca et al. (2007) showed that in subtropical waters of the northeast Atlantic (European Station for Time Series, ESTOC) nitrate concentration remained low ($< 0.5\,\mu$M) at potential densities below 26.4 $\mathrm{kg\,m^{-3}}$, and it increased significantly above that isopycnal surface. During our sampling, the MLD was never deeper than the 26.4 $\mathrm{kg\,m^{-3}}$ isopycnal surface (Fig. 8), hence, it is unlikely that a substantial nutrient input occurred through physical mixing. Surprisingly, nutrient concentrations measured during the study period (Benavides et al., 2013) showed rather high values for nitrate+nitrite (0.3–0.6 µM) and exceptionally high for phosphate (0.5–2.5 µM). These concentrations are higher than previous measurements at the time-series ESTOC station (Neuer et al., 2007) and at the northeast subtropical gyre (Marañón et al., 2000, 2003). One possible source of nitrogen could be the nitrogen fixation, which could be favored by high temperatures and stratification. However, it was not the case as low fixation rates were measured on average by Benavides et al. (2013) during the sampling period. Therefore, the more plausible explanation is the Saharan dust release of high quantities of nitrate and phosphorus as it has been measured in other studies (Bonnet et al., 2005; Herut et al., 2005; Duarte et al., 2006). In the case of silicate, a nutrient also contained in Saharan dust (Goudie and Middleton, 2001; Viana et al., 2002), rather low concentrations (0.02–0.03 µM) were measured by Benavides et al. (2013). We suggest this could be the result of diatom uptake, as silicate concentration was minimum in March (Benavides et al., 2013), when diatom biomass increased (Fig. 6).

The effect over the plankton community was unequal, as it was shown for the heavy dust deposition during March. A negligible change in Chl *a* was observed in contrast to the positive change in PP after the event (Fig. 6a). This is consistent with experimental results when Saharan dust was added to oligotrophic waters of the Atlantic (Marañón et al., 2010) and the Mediterranean (Bonnet et al., 2005). In both cases little changes in phytoplankton biomass were observed. Contrary, a considerable response in primary production was measured. Marañón et al. (2010) used dust concentrations that mimicked a high atmospheric deposition event, obtaining an increment in PP rates of 1–1.5 $\mu g\,C\,L^{-1}\,d^{-1}$, which supposed a mean relative change of 25 % in PP. After the simulation of a medium dust event, Bonnet et al. (2005) found a positive change of 48 % in PP rates. In our case, a higher average increment (up to 140 %) in PP was measured (Fig. 7b), accounting for an increase of 14 $\mu g\,C\,L^{-1}\,d^{-1}$ (Fig. 7a), consistent with the results from Herut et al. (2005). They measured an increment of more than 9 $\mu g\,C\,L^{-1}\,d^{-1}$ in PP in experiments adding Saharan dust. However, they argued that in the field, the likely low nutrient release during an atmospheric event would promote a minor phytoplankton response, as they measured in situ a very low increase in Chl *a* after a dust storm. In any case, as it has been shown here, PP could be enhanced in spite of any change in Chl *a* was measured. Although the enhancement of PP is consistent with experimental results, absolute rates (Fig. 4) of PP measured here are much higher than maximum rates found in these waters by De

León and Braun (1973) during a characteristic late winter bloom (2.4–3.3 $\mu g\,C\,L^{-1}\,h^{-1}$). Moreover, our mean rates (3.25 $\mu g\,C\,L^{-1}\,h^{-1}$) are 7-fold over mean rates measured at BATS station (0.45 $\mu g\,C\,L^{-1}\,h^{-1}$) during the same period (BATS interactive data access, http://bats.bios.edu/index.html, last access: July 2013). The difference is not expected to result by a methodological issue, as good agreement has been described between the ^{13}C isotopic technique and the ^{14}C method (Slawyk et al., 1977; Hama et al., 1983). On the other hand, high PP rates resulted from the extremely high POC concentrations measured within incubation bottles and used to compute them. Actually, the POC concentrations measured at the ML (data not shown), were in many cases much higher than previous measurements in this area (Alonso-González et al., 2009). These authors measured concentrations around 4 µM in the surface waters at the northeast of the Canary Islands. Our data showed a high variability ranging between 0.99 to 25.66 µM (7.47±7.85 µM) and reaching values higher than 4 µM during March, May and June. Unfortunately, we are not able to explain the cause behind these POC values, so that the PP rates should be considered only as an estimate of relative autotrophic activity and not as absolute values.

The relative increase in PP after the dust deposition event was probably promoted by diatoms as they were clearly the most favored planktonic group in terms of biomass (Figs. 6a and 7a). This is a common feature in ocean fertilization experiments (De Baar et al., 2005; Boyd et al., 2007) because of their higher growth rates compared to prokaryotic algae during the release of iron (Landry et al., 2000a), and the lower grazing pressure upon them (Landry et al., 2000a, b; Henjes et al., 2007). In this study, diatom biomass showed a remarkable increment of 1310 % (Fig. 7a), whereas their abundance diminished by 11 % (Fig. 7b). It was likely due to the appearance of *Chaetoceros* sp. (Fig. 9), which despite their low abundance supposed between 60 and 99 % of total biomass when diatom peaks were observed (Fig. 5c). This increase of larger diatoms has also been observed in artificial fertilization experiments (De Baar et al., 2005). Contrary, a significant negative response was observed for APE and Syn after 18 March (Figs. 6 and 7). Their biomass and abundance reduction suggests a higher grazing pressure after the event or a possible negative effect of dust over these organisms. Grazing has been pointed out as a major process controlling primary producers, even when phytoplankton growth is enhanced (Landry et al., 2000a, b; De Baar et al., 2005; Herut et al., 2005; Boyd et al., 2007; Henjes et al., 2007; Marañón et al., 2010). Moreover, microzooplankton are major grazers in these subtropical waters (Calbet and Landry, 2004), and an increment was found for all heterotrophic organisms (Figs. 6 and 7). Thus, it is not surprising that prokaryotic algae would be under a higher grazing pressure than diatoms, the latter favored by either the fertilization effect as well as lower grazing. On the other hand, a toxic effect of dust has been previously suggested for cyanobacteria (Marañón et al., 2010) and demonstrated for APE and Syn (Paytan et al., 2009). However, there was not a substantial increase in copper, the element associated to toxicity, for the period of the heavy dust event in March in comparison with the average concentration during the rest of the year (Supplement). Thus, it is not likely that picophytoplanktonic organisms would be affected by dust toxicity.

The mesozooplankton response was also significant after the dust event on 18 March, increasing their biomass by more than 100 %. Actually, mesozooplankton increased not only their biomass but also their metabolic activity after that event (Herrera et al., 2013). This effect was previously described in the Canary Islands waters by Hernández-León et al. (2004), who measured an increase in biomass, gut fluorescence and potential respiration (ETS activity) of these organisms after a Saharan dust storm. This enhancement has been reported previously by Boyd et al. (2007) after the enrichment promoted by mesoscale iron experiments, although not in all cases.

5 Summary

In summary, our results showed that the Canary Islands waters were continuously affected by the Saharan dust deposition during the period studied. Dust fertilization was evident by the high atmospheric iron, and nitrate and phosphate concentrations found in the mixed layer. Therefore, after the heavy dust event observed in March, the smaller but numerous dust events in April, May and June would potentially reinforced the fertilization effect of the atmospheric deposition. It is also remarkable the high iron concentration measured during January, when this metal remained at high levels practically during the whole month showing that considerable quantities of iron could be reaching this area and fertilizing these waters although the measured particle concentration (TSM) in the air was not high. Finally, the response of the planktonic community consisted, on one hand, in the enhancement of primary producers, mostly diatoms, and mesozooplanktonic organisms, as it has been observed before. On the other hand, picophytoplankton seemed to be negatively affected, but if this effect was directly caused by dust or indirectly by grazing losses remains unknown. This unequal effect upon autotrophs, favoring diatoms instead the small autotrophs, could also enhanced the biological pump due to a higher carbon export flux resulted from diatom sedimentation. Hence, the Saharan dust deposition would be partly fuelling the primary production in these oligotrophic waters and could also enhanced the carbon export, especially during stratified periods, when it would be the most important nutrient source. Nevertheless, further research is needed to better understand the potential influence of this process in the subtropical northeast Atlantic. In this sense, an intensive temporal sampling would help to properly quantify the rapid response of the different planktonic groups in the field, especially in subtropical waters, given the complexity and quickness of the biological interactions.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/10/17275/2013/bgd-10-17275-2013-supplement.pdf.

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Table 1. Mean (±SD) autotrophs : heterotrophs (A : H) ratio at the mixed layer from February to June 2010. Monthly ratios are shown for pico- and nanoplankton ($A_{\mathrm{Pico,ANF}} : H_{\mathrm{HP,HNF}}$) and including microplankton (Dia, Cil, Din) considering 50 % Din as autotrophs and 50 % as heterotrophs (A : H). Biomass in $\mu g\,C\,L^{-1}$.

Month	$A_{\mathrm{Pico,ANF}} : H_{\mathrm{HP,HNF}}$	A : H
Feb	0.66 (±0.00)	0.78 (±0.00)
Mar	0.58 (±0.29)	0.67 (±0.14)
Apr	0.49 (±0.14)	0.77 (±0.11)
May	0.78 (±0.34)	0.81 (±0.13)
Jun	0.57 (±0.08)	0.69 (±0.09)

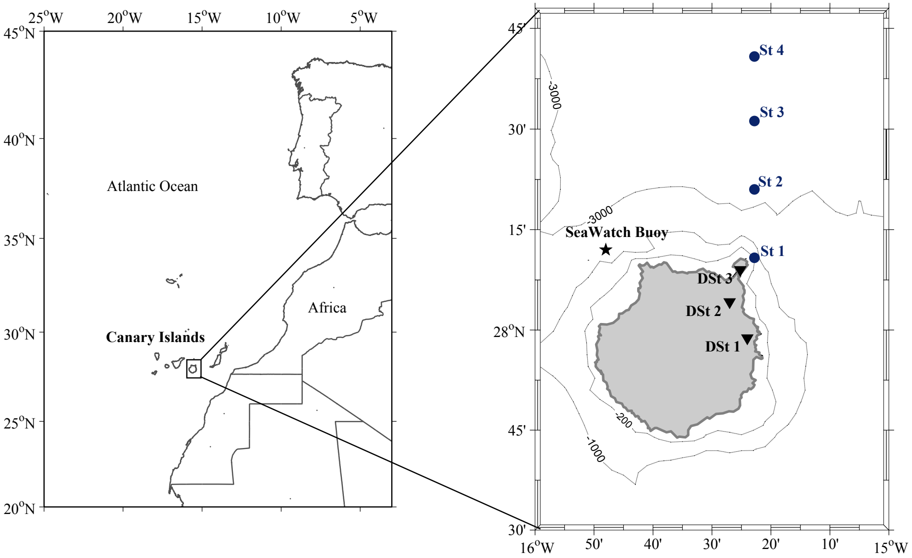

Fig. 1. Location of the four oceanographic stations (St) at the north of Gran Canaria Island (Canary Islands) and the three dust stations (DSt) in the northeast of the island. SeaWatch buoy position is also plotted.

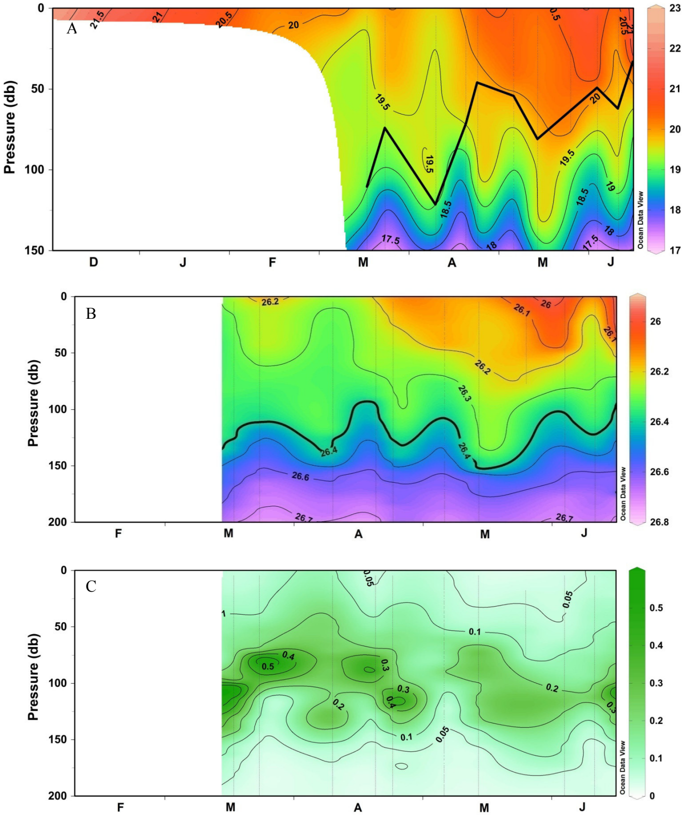

Fig. 2. Temporal variability of temperature (**A**, °C), potential density (**B**, $\mathrm{kg\,m^{-3}}$) and Chl *a* (**C**, $\mathrm{\mu L\,m^{-1}}$) from surface to 150 db for temperature and 200 db for others. MLD is drawn in the upper panel (black solid line). Data correspond to station 3, from February to June 2010. CTD data were available after 17 March. Before that time sea surface temperature is showed since December 2009 (SeaWatch Buoy data).

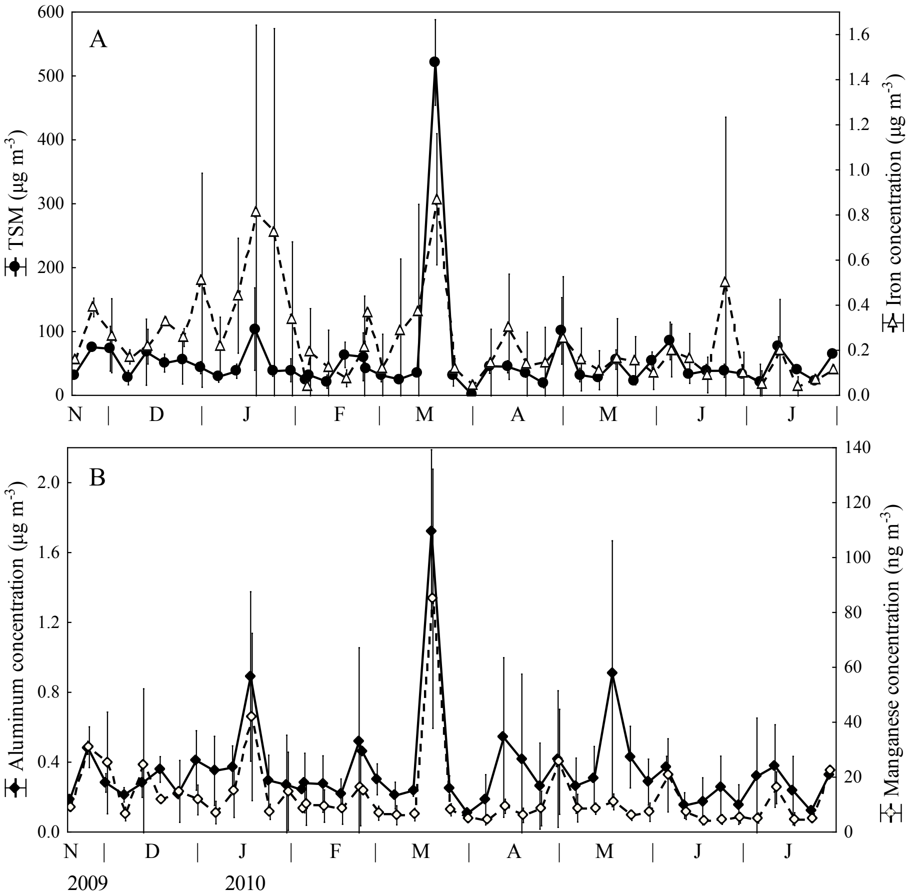

Fig. 3. Atmospheric total suspended matter (TSM, $\mu g\,m^{-3}$) and iron concentration (**A**, $\mu g\,m^{-3}$) and aluminum ($\mu g\,m^{-3}$) and manganese concentration (**B**, $ng\,m^{-3}$), from November 2009 to July 2010. TSM, Fe, Al and Mn data showed as average and standard deviation.

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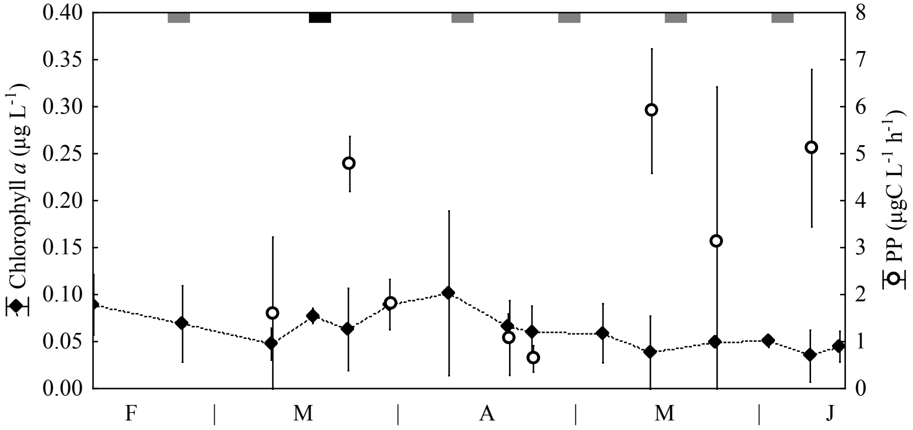

Fig. 4. Average (±SD) Chl *a* concentration ($\mu g\,L^{-1}$) and primary production (PP, $\mu g\,C\,L^{-1}\,h^{-1}$) measured at the mixed layer (20 m) from February to June 2010. Dust deposition is marked at the top with grey rectangles for relative low dust events, and a black rectangle for the highest dust event in March.

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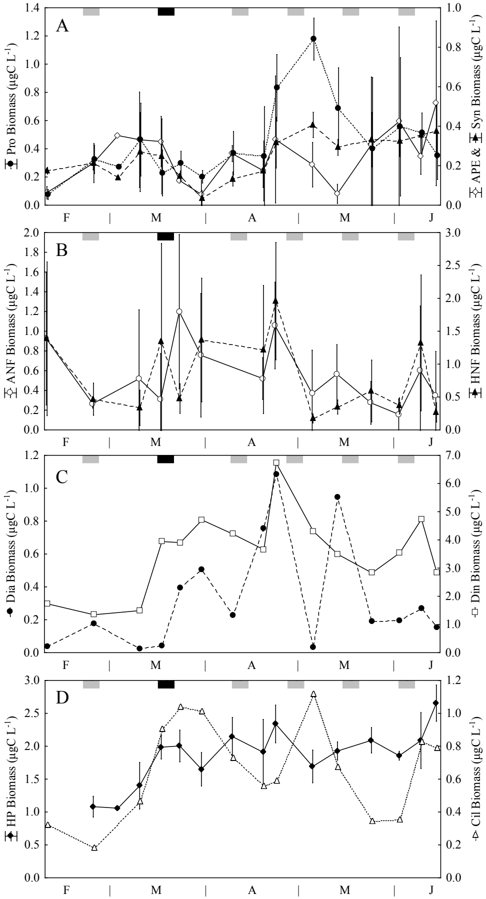

Fig. 5. Average (±SD) biomass ($\mu g\,C\,L^{-1}$) of APE, Syn, Pro **(A)**, ANF, HNF **(B)**, Dia, Din **(C)**, HP and Cil **(D)** during the study period in 2010. Dust deposition is marked at the top with grey rectangles for relative low dust events, and a black rectangle for the highest dust event in March.

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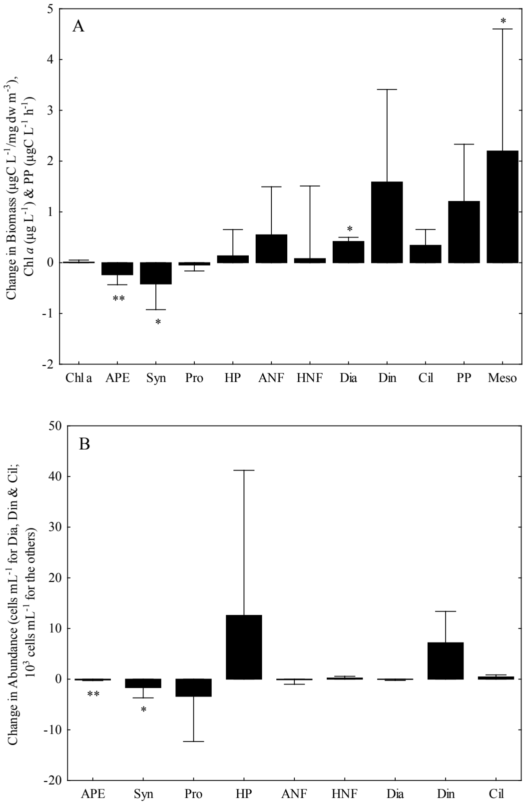

Fig. 6. Average change (+SD) in biomass (μg C L^{-1} for pico-, nano- and microplankton; mg DW m^{-3} for mesozooplankton), Chl *a* (μg L^{-1}) and PP (μg C L^{-1} h^{-1}) **(A)**, and in abundance (cells mL^{-1} for Dia, Din and Cil; 10^3 cells mL^{-1} for the others) **(B)** after the deposition event in March. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

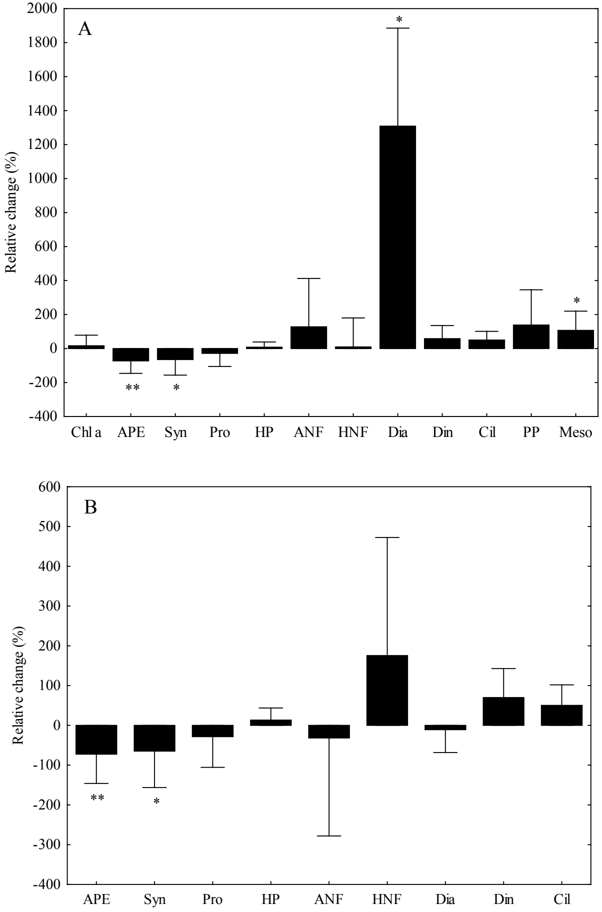

Fig. 7. Average relative change (%, +SD) in biomass, Chl *a* and PP **(A)**, and in abundance **(B)** after the dust event on 18 March. Relative change was calculated as $(A - B/B) \cdot 100$, where *A* and *B* are the average values for every parameter after and before the event, respectively.

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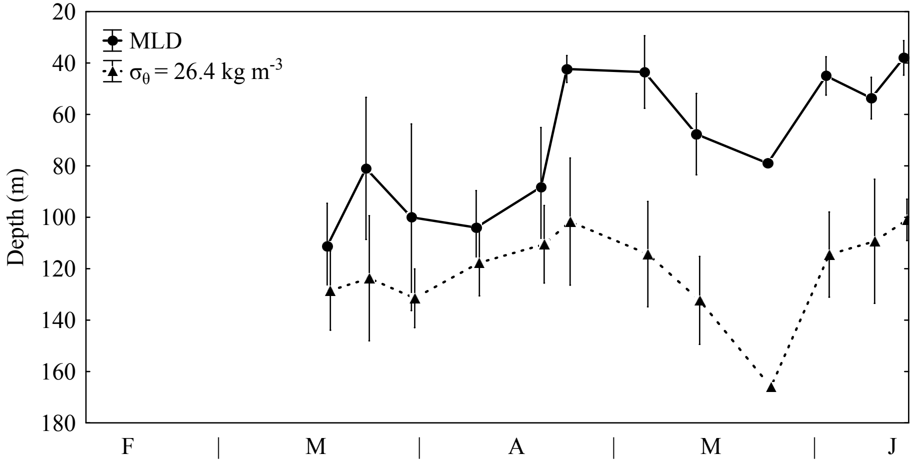

Fig. 8. Temporal variability of the average mixed layer depth (MLD) and the average depth of the isopycnal surface 26.4 kg m^{-3} from March to June 2010. Average and standard deviation for the four stations.

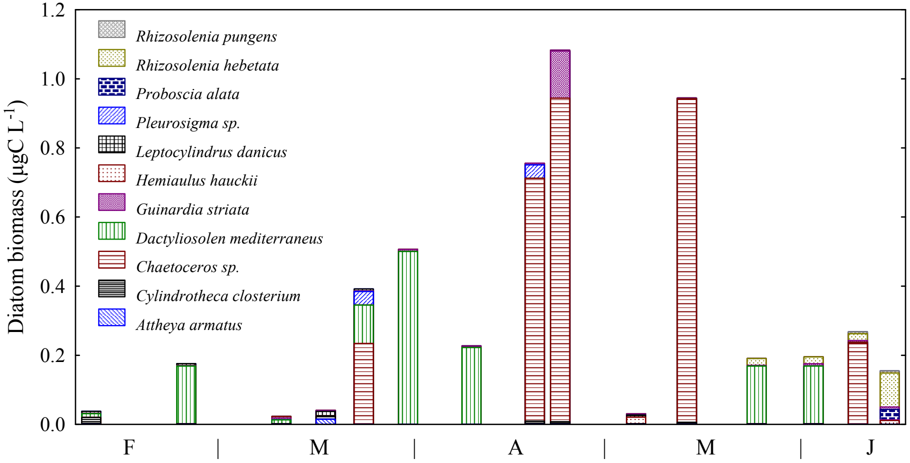

Fig. 9. Temporal variability of diatom biomass (µg C L^{-1}) and the contribution of different species during the period studied in 2010.