

# Environmental influence on phytoplankton communities in the northern Benguela ecosystem

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## ABSTRACT

An investigation of surface phytoplankton communities was undertaken on the shelf of the northern Benguela upwelling ecosystem during austral autumn (May) and spring (September) using microscopic identification and CHEMTAX analysis of pigment biomarkers on latitudinal transects at 20°S and 23°S up to 70 nautical miles offshore, and on a zigzag grid located between these transects. During May 2014, warmer, more saline water with a shallower upper mixed layer corresponding to periods of less intense offshore Ekman transport was encountered on the shelf. Satellite imagery indicated high biomass extending for a considerable distance from the coast, and CHEMTAX indicated diatoms dominating at most of the stations (52-92%), although dinoflagellates were dominant at some inshore localities (57-74%). Species of *Chaetoceros*, *Bacteriastrium* and *Cylindrotheca* were the most abundant, with *Pseudonitzschia* seriata-group abundance being particularly high at a number of stations. In September 2014, more intense wind forcing resulted in a deeper upper mixed layer and stronger upwelling of colder, less saline water. Elevated phytoplankton biomass was confined close to the coast where diatoms accounted for most of the population (54-87%), but small flagellates such as prasinophytes, haptophytes and cryptophytes, and the cyanobacterium *Synechococcus*, dominated the communities (58-90%) further away from the coast. It is hypothesized that stronger upwelling and deeper vertical mixing in September 2014 were not conducive for wide-spread diatom growth, and that small flagellates populated the water column by being entrained from offshore onto the shelf in the upwelled water that moved in towards the coast.

**Keywords:** Phytoplankton, Pigments, Species, Hydrography, Benguela upwelling ecosystem

## Introduction

The Benguela ecosystem off southwest Africa is one of the major upwelling systems in the world's ocean and is characterised by cold nutrient-rich water and high plankton productivity on the continental shelf (Nelson and Hutchings 1983; Shannon and Nelson 1996; Hutchings et al. 2009). The northern region of the ecosystem is located off Namibia (17°-29°S) and upwelling is driven by intense along-shore southeasterly winds, facilitated by low eddy activity and a shallow mixed layer on a relatively wide shelf (Lachkar and Gruber 2012). There are seasonal fluctuations in the wind field and the climatology indicates peaks in wind stress during April-May and August-September (Louw et al. 2016). There is a consequent seasonality in upwelling and surface water temperatures, with lower surface temperatures in the period June to October and higher surface temperatures during December to May (Louw et al. 2016).

In response to changing upwelling conditions, phytoplankton biomass is highly variable on the Namibian shelf. Previous investigations by Estrada and Marrasé (1987) demonstrated patchy distributions of phytoplankton, with chlorophyll *a* levels of 20 mg m<sup>-3</sup> at various localities near the coast in 15°-16°C water. Barlow et al. (2001) measured 0.3-18.5 mg m<sup>-3</sup> on the shelf south of Walvis Bay in winter, with the high levels being observed at shallow stations, while chlorophyll *a* ranging from 18.4 mg m<sup>-3</sup> near the coast (11°-12°C water) to 0.6 mg m<sup>-3</sup> 100 km offshore (16°-17°C water) were observed during a spring

54 survey between 19°S and 25°S (Barlow et al. 2006). In a recent 12 year *in situ* study on a transect at 23°S  
55 in the centre of the Namibian upwelling system, Louw et al. (2016) observed that major blooms where  
56 chlorophyll *a* was >18 mg m<sup>-3</sup> occurred in 5 of the 12 years and minor blooms (10-13 mg m<sup>-3</sup>) were  
57 observed every year. Maxima usually developed inshore each year with peaks in April (autumn), August  
58 (winter) and December (summer). The forcing mechanisms driving these patterns are complex and  
59 include dynamic variability in wind, temperature, mixing, stratification and thermocline development, and  
60 nutrient availability. Similar changes in chlorophyll *a* occur in the upwelling ecosystem off central Chile  
61 where Anabalón et al. (2016) observed seasonal variability at a coastal site with two maxima of 8-10 mg  
62 m<sup>-3</sup> in the spring (October) and summer (January). In the upwelling system off central Oregon Du et al.  
63 (2015) also noted that peaks in chlorophyll *a* of 15-20 mg m<sup>-3</sup> occurred in the boreal summer months of  
64 July and August.

65  
66 Phytoplankton composition of diatoms and dinoflagellates was originally identified by microscopy in the  
67 1960's (Kollmer 1962, 1963) and by Kruger (1980), who also noted many small flagellates that were  
68 difficult to identify and quantify by microscopy. More recently community structure has also been  
69 elucidated using pigment indices and a spring survey during 2000 by Barlow et al. (2006) indicated  
70 diatoms dominating closer to the coast, while small flagellates were generally more prominent in the  
71 offshore communities. Pigments have been useful to characterize phytoplankton populations in the  
72 southern Benguela ecosystem, where fucoxanthin, peridinin and zeaxanthin are biomarkers of diatoms,  
73 dinoflagellates and cyanobacteria, respectively. 19'-Hexanoyloxyfucoxanthin (haptophytes), 19'-  
74 butanoyloxyfucoxanthin (pelagophytes), chlorophyll *b* (prasinophytes) and alloxanthin (cryptophytes) are  
75 useful biomarkers for the small flagellates (Barlow et al. 2001, 2005, Fishwick et al. 2006). Microscopy  
76 revealed that the small flagellates in the 2000 spring survey were dominated by *Emiliania huxleyi*, while a  
77 substantially calcified *E. huxleyi* morphotype was also observed inshore immediately succeeding the  
78 decline in the coastal diatom blooms (Henderiks et al. 2012).

79  
80 Investigations on succession have demonstrated a transition from dinoflagellates, coccolithophores and  
81 microflagellates in newly upwelled water to diatom dominance in matured upwelled water, and a change  
82 from diatoms to dinoflagellates in aged water (Hansen et al. 2014). In a complementary study in  
83 shipboard mesocosms, it was found that diatoms dominated in newly upwelled water, but autotrophic and  
84 heterotrophic dinoflagellates were then dominant at the matured stage (Wasmund et al. 2014). Water  
85 types were originally defined for the southern Benguela ecosystem where newly upwelled water had  
86 temperatures of <10°C and nitrate concentrations of 15-30 mmol m<sup>-3</sup>, matured upwelled water  
87 temperatures were 10-15°C and nitrate levels were 2-15 mmol m<sup>-3</sup>, while aged water contained low  
88 concentrations of nitrate (<2 mmol m<sup>-3</sup>) and temperatures of 12-16°C (Barlow 1982a). Communities were  
89 observed to be in an active phase of growth in newly upwelled and mature water but were in a slow-  
90 growing phase in aged water. A study by Louw et al. (2017) noted that the diatom genus, *Pseudo-*  
91 *nitzschia*, occurs frequently on the central Namibian coast and blooms developed in mature water when  
92 there was a decrease in wind stress and upwelling.

93  
94 The high phytoplankton biomass off Namibia has sustained higher trophic levels and a rich marine  
95 fishery, but there has been a decline in commercial fish catches mainly due to overfishing (Finney et al.  
96 2010). Furthermore, global climate change may have an impact on the Benguela ecosystem through  
97 atmospheric forcing (Bakun et al. 2010) and negatively affect both environmental and plankton patterns  
98 with consequent repercussions for the fragile fisheries industry. Under a warming scenario, phytoplankton  
99 composition could shift from diatom dominance to mixed communities where small flagellates and  
100 prokaryotes might contribute a greater proportion to the biomass, or perhaps become dominant under  
101 certain conditions. This would have an impact on zooplankton communities and Verheye et al (2016)  
102 report a shift from large to smaller zooplankton in the Benguela ecosystem since the mid-1990s, which in  
103 turn is likely to have an impact on higher trophic levels such as pelagic and demersal fish. The  
104 contribution of flagellates and prokaryotes to phytoplankton populations in the contemporary Namibian  
105 ecosystem is not well understood and an opportunity arose to examine community structure in more detail  
106 during two research cruises on the central shelf during May and September 2014. The approach was to

107 collect surface samples for phytoplankton pigments and analyse the detailed pigment data using the  
108 statistical technique of CHEMTAX (Mackey et al. 1996; Higgins et al. 2011). CHEMTAX yields  
109 information about the contribution to the total chlorophyll *a* (TChl<sub>a</sub>) by the various flagellates mentioned  
110 above as well as the diatoms, dinoflagellates and prokaryotes (Higgins et al., 2011). Samples for  
111 microscopic analysis were also taken to elucidate details of the dominant diatom and dinoflagellate  
112 species. The objective was to examine the changing proportions of diatoms, dinoflagellates, flagellates  
113 and prokaryotes in surface waters at the time of the research cruises, and assess the impact of different  
114 seasonal environmental conditions on community structure.

## 116 **Methods**

### 118 *Hydrography and sampling*

120 The research cruises were undertaken on the Namibian shelf during 9-15 May and 8-13 September 2014  
121 respectively. Hydrographic measurements and sampling were conducted on latitudinal transects located at  
122 20°S and 23°S at 8-9 stations varying from 2-70 nm (nautical miles) from the coast (Figure 1). In  
123 addition, further measurements and sampling were conducted at stations on a zigzag grid (ZZ1-ZZ14)  
124 located between 20°S and 23°S (Figure 1). The water column was profiled for temperature and salinity  
125 utilizing a Seabird CTD that was maintained regularly and calibrated according to the manufacturer's  
126 instructions. Nutrient samples (50 ml) were drawn from the CTD rosette bottles at 10 m or 20 m depth  
127 intervals on the 20°S and 23°S transects only, filtered on board, and stored frozen for later analysis ashore  
128 using standard auto-analyser techniques (Mostert 1983). Surface seawater samples within the upper 2-5 m  
129 (200 ml) were taken for species identification only at the 20°S and 23°S stations and preserved with 5 ml  
130 of 40% formaldehyde (Thronsen 1978). Further surface samples were drawn for pigment analysis (1000  
131 ml) at the 20°S and 23°S stations, and at the ZZ stations, and filtered through GFF filters that were stored  
132 frozen at -80°C for analysis ashore. The depth of the upper mixed layer ( $Z_m$ ) was determined as the depth  
133 where the local change in density was  $\geq 0.03 \text{ kg m}^{-3}$  using density profiles and a threshold gradient  
134 criterion (Thomson and Fine 2003).

136 Ekman transport at 20°S and 23°S was computed from daily NCEP-DOE Reanalysis 2 meridional wind  
137 vectors according to Lamont et al. (2017). Wind vectors were rotated to account for the orientation of the  
138 coastline and wind stress was computed using the non-linear drag coefficient defined by Large and Pond  
139 (1981) and modified by Trenberth et al. (1990) for low wind speeds. Ekman transport ( $\text{m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$   
140 of coastline) was then computed, with positive values indicating offshore transport (upwelling), and negative  
141 values representing onshore transport (downwelling). Daily values were summed to provide an estimate  
142 of the monthly cumulative offshore Ekman transport at 20°S and 23°S. Standard monthly-averaged  
143 chlorophyll *a* data and Sea Surface Temperature (SST) from MODIS-Aqua (v2018.0), at 4.5 km spatial  
144 resolution (NASA 2018), was downloaded for May and September 2014 from the Ocean Biology  
145 Processing Group (OBGP) at NASA's Goddard Space Flight Center (GSFC;  
146 <http://oceancolor.gsfc.nasa.gov>). It was difficult to obtain clear enough satellite images of daily or  
147 weekly-averaged chlorophyll *a* and SST due to extensive cloud cover and fog along the Namibian coast  
148 and shelf and therefore only monthly-averaged images were found to be suitable.

### 150 *Phytoplankton identification*

152 Species identification and counts were performed with a Zeiss Axiovert 200 inverted light microscope  
153 (Utermöhl 1958). Prior to counting, formalin-preserved samples were settled in a 25 ml chamber for 24 h.  
154 Concentrations of cells were calculated using the equation of Utermöhl (1958) and counting of at least  
155 400 cells with a precision of  $\pm 10\%$ . Where species occurred in low concentrations, 50–200 cells were  
156 counted, providing a precision of 15–30% for quantitative estimates (Andersen and Thronsen 2004).

## 160 *Pigment analysis and CHEMTAX*

161  
162 Pigments were extracted in 90 % acetone, aided by the use of ultrasonication, clarified by centrifugation  
163 and filtration, and analysed by HPLC (ThermoScientific Accela) using a Waters Symmetry C8 column  
164 (150 x 2.1 mm, 3.5  $\mu\text{m}$  particle size, thermostated at 25°C) according to Zapata et al. (2000). Pigments  
165 were detected at 440 and 660 nm and identified by retention time and on-line diode array spectra.  
166 Monovinyl chlorophyll *a* standard was obtained from Sigma-Aldrich Ltd and other pigment standards  
167 were purchased from the DHI Institute for Water and Environment, Denmark. Quality assurance  
168 protocols followed Van Heukelem and Hooker (2011). The method separates divinyl and monovinyl  
169 chlorophyll *a*, zeaxanthin and lutein, but does not resolve divinyl and monovinyl chlorophyll *b*. Limits of  
170 detection were of the order of 0.001 mg m<sup>-3</sup>.

171  
172 To determine community composition, pigment data was analysed by CHEMTAX (Mackey et al. 1996)  
173 following Higgins et al. (2011), with chemotaxonomic groups being identified according to Jeffrey et al.  
174 (2011). An assumption made using CHEMTAX is that the pigment:chlorophyll *a* ratios are constant  
175 across all the samples within each analysis. Therefore analysis was performed separately for each cruise  
176 such that all samples for May 2014 were run together, and then all samples for September 2014 were run  
177 together. Pigment starting ratios were obtained from Higgins et al. (2011) and Table 1 indicates the  
178 identified functional groups and the various starting and output ratios for each group. To ease the  
179 presentation of the chemotaxonomic data, diatoms-1 and -2 were combined into a collective diatom  
180 group, and prasinophytes-1 and -3 were combined into a collective prasinophyte group. Data for  
181 chlorophytes is not presented as CHEMTAX indicated that the contribution of this group was very low.

182  
183 CHEMTAX outputs are the fraction of chlorophyll *a* attributed to each functional group specified in the  
184 matrix. The HPLC method separated monovinyl chlorophyll *a* allomer, monovinyl chlorophyll *a*,  
185 monovinyl chlorophyll *a* epimer and chlorophyllide *a*, and in CHEMTAX the sum of all 4 was used as  
186 the total chlorophyll *a* concentration (TChla). Chlorophyllide *a* was included as it can be generated from  
187 artificial degradation of chlorophyll *a* by chlorophyllase activity during sample handling and extraction  
188 when diatoms are present (Jeffrey and Hallegraeff 1987). The software may not discover the best global  
189 solution if it encounters local minima in the process. To circumvent this possibility, multiple starting  
190 points were used. Sixty-nine further pigment ratio tables were generated by multiplying each cell of the  
191 initial table by a randomly determined factor F, calculated as:

$$192 \quad F = 1 + S \times (R - 0.5)$$

193 where S is a scaling factor of 0.7, and R is a random number between 0 and 1 generated using the  
194 Microsoft Excel RAND function (Wright et al., 2009). Each of the 69 ratio tables was used as the starting  
195 point for a CHEMTAX optimization. The solution with the smallest residual was used for the estimated  
196 taxonomic abundance.

## 197 **Results**

### 200 *Hydrography*

201  
202 Monthly-averaged satellite images are presented to set the geographic and hydrographic context for the  
203 study area, indicating that warmer water prevailed during May 2014 compared to cooler water conditions  
204 in September 2014 (Figure 1a and c). The chlorophyll *a* image for May 2014 revealed high levels along  
205 the coast between 25°S and 19°S, with an offshore extension to the ZZ stations (Figure 1b). In September  
206 2014, chlorophyll *a* was elevated inshore from Walvis Bay to Toscanini, with patchy lower  
207 concentrations between 20°S and 21°S (Figure 1d). Levels were much lower further offshore between  
208 23°S and 20°S.

209  
210 Daily offshore Ekman transport showed a decreasing trend during the cruise period in May 2014, with  
211 values decreasing from 130 m<sup>3</sup> s<sup>-1</sup> 100 m<sup>-1</sup> on 9 May to 18 m<sup>3</sup> s<sup>-1</sup> 100 m<sup>-1</sup> on 13 May at 20°S, increasing  
212 slightly to 55 m<sup>3</sup> s<sup>-1</sup> 100 m<sup>-1</sup> by 15 May (Figure 2a). Similarly, Ekman transport decreased from 163 m<sup>3</sup> s<sup>-1</sup>

213  $100 \text{ m}^{-1}$  on 9 May to  $11 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  on 12 May at  $23^\circ\text{S}$ , then increasing to  $51 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  by 15  
214 May (Figure 2b). In contrast, the opposite pattern was observed during the cruise in September 2014, with  
215 offshore Ekman transport increasing from  $5 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  on 8 September to  $98 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  on 10  
216 September at  $20^\circ\text{S}$ , and then fluctuating between 30 and  $70 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  during 11-13 September  
217 (Figure 2c). Ekman transport also increased from  $32 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  on 8 September 2014 to 170, 138 and  
218  $142 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  on 10, 11 and 12 September respectively at  $23^\circ\text{S}$  (Figure 2d). Monthly values of  
219 cumulative offshore Ekman transport at  $23^\circ\text{S}$  indicated that upwelling-favourable winds during  
220 September 2014 ( $4003 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$ ) were nearly twice the intensity of that in May 2014 ( $2295 \text{ m}^3 \text{ s}^{-1}$   
221  $100 \text{ m}^{-1}$ ). The difference in monthly cumulative offshore Ekman transport at  $20^\circ\text{S}$  was less, being 2424  
222  $\text{m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  in September 2014 compared to  $1520 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$  in May 2014, but still indicating  
223 greater offshore transport in the spring.

224  
225 *In situ* surface temperature and salinity data indicated warmer, more saline waters at the surface on the  
226  $20^\circ\text{S}$  and  $23^\circ\text{S}$  transects during May 2014. Along  $20^\circ\text{S}$ ,  $15\text{-}16^\circ\text{C}$  water was observed inshore at the  
227 surface and  $18\text{-}19^\circ\text{C}$  offshore between 40 and 70 nm (Figure 3a), while at  $23^\circ\text{S}$  surface temperatures were  
228  $14\text{-}15^\circ\text{C}$  inshore and  $15\text{-}17^\circ\text{C}$  offshore (Figure 3b). Surface salinities of 35.4-35.5 inshore and 35.5-35.6  
229 offshore (40-70 nm) were noted for the  $20^\circ\text{S}$  transect (Figure 4a), while salinities of 35.2-35.3 prevailed  
230 across the  $23^\circ\text{S}$  transect in May 2014 (Figure 4b). The estimated depth of the upper mixed layer varied  
231 from 25-75 m along  $20^\circ\text{S}$  and was  $<50$  m on  $23^\circ\text{S}$  (Figures 3, 4). Lower surface temperatures and  
232 salinities were observed in September 2014, with  $12\text{-}13^\circ\text{C}$  water close inshore on  $20^\circ\text{S}$ ,  $13\text{-}14^\circ\text{C}$  from 2-  
233 30 nm, and  $14\text{-}15^\circ\text{C}$  between 30 nm and 70 nm (Figure 3c). Along  $23^\circ\text{S}$ , surface temperatures were  $11.5\text{-}$   
234  $13^\circ\text{C}$  inshore up to 25 nm from the coast and  $13\text{-}15^\circ\text{C}$  further offshore (Figure 3d). Surface salinities of  
235 35.1-35.2 were noted from the coast to 40nm on  $20^\circ\text{S}$  and 35.2-35.3 beyond 40 nm (Figure 4c), while  
236 salinities of 34.9-35.0 were measured out to 50 nm on  $23^\circ\text{S}$  and 35.0-35.1 between 50 and 70 nm (Figure  
237 4d). Upper mixed layers were  $<50$  m on  $20^\circ\text{S}$  in September 2014, but varied from 15-100 m on  $23^\circ\text{S}$   
238 (Figures 3 and 4).

239  
240 Two longitudinal transects were designated for the ZZ stations, a coastal transect for the odd numbered  
241 stations, and an offshore transect for the even numbered stations (Figure 1). Surface temperatures were  
242 uniform at  $14^\circ\text{C}$  along the coastal transect in May 2014 (Figure 5a) and varied from  $12.5\text{-}14^\circ\text{C}$  in  
243 September 2014 (Figure 5c). Salinity was 35.3-35.4 in May 2014 and 35.1-35.2 in September 2014 (data  
244 not shown). The upper mixed layer on this coastal transect was 17-18 m in May 2014, but only 3 m at  
245 ZZ1, and varied between 5 m and 30 m in September 2014 (Figure 5a, c). Surface temperatures were  
246 higher along the offshore ZZ transect, being  $16\text{-}17^\circ\text{C}$  in May 2014 (Figure 5b) and  $14\text{-}15^\circ\text{C}$  in September  
247 2014 (Figure 5d). Surface salinity varied from 35.3-35.5 in May 2014 and was lower in September 2014  
248 at 35.0-35.2 (data not shown). Mixed layer depths on the offshore ZZ transect were  $<50$  m during both  
249 May and September 2014 (Figure 5b, d).

### 251 *Phytoplankton species*

252  
253 Only the dominant species of diatoms and dinoflagellates on the  $20^\circ\text{S}$  and  $23^\circ\text{S}$  transects are listed in  
254 Table 2 as a more detailed account of all species will be reported elsewhere. The criterion for dominance  
255 was selected as the highest abundance for 1-3 species at each station compared to other species that had  
256 lower abundances. Dominant cell counts varied widely, however, and examples are the 30 nm station on  
257  $20^\circ\text{S}$  in May 2014 where abundance was  $1.39\text{-}2.67 \times 10^6 \text{ cells L}^{-1}$ , while at the 50 nm station on  $23^\circ\text{S}$ , cell  
258 counts were  $1.05\text{-}1.14 \times 10^3 \text{ cells L}^{-1}$  (Table 2).

259  
260 Diatoms were dominated by various species on each transect and the *Pseudo-nitzschia* seriata-group,  
261 *Chaetoceros curvisetus* and *Chaetoceros debilis* were the most abundant up to 30 nm on  $20^\circ\text{S}$  during May  
262 2014. *Thalassiosira gravida*, *Bacteriastrum delicatulum*, *Bacteriastrum hyalinum*, *Cylindrotheca*  
263 *closterium*, *Pseudo-nitzschia* seriata-group, *Rhizosolenia robusta* and a *Thalassiosira* sp were the  
264 dominant diatoms from 40-70 nm, with the particular details for each station presented in Table 2. These  
265 species were also the dominant diatoms on  $23^\circ\text{S}$  in May 2014 and the *Pseudo-nitzschia* seriata-group was

266 particularly dominant at six of the nine stations (Table 2). The dominant dinoflagellates on the 20°S  
267 transect included *Ceratium* spp., *Prorocentrum micans*, *Corythodinium tessellatus*, *Gyrodinium* spp.,  
268 *Protoperidinium pallidum* and *Protoperidinium* spp., although unidentified dinoflagellates were also  
269 present at some of the stations. For 23°S, *Prorocentrum micans*, *Protoperidinium* spp. and *Scrippsiella*  
270 *trochoidea* were the dominant species, but the abundance of naked dinoflagellates and unidentified  
271 dinoflagellates appeared to be greater on this transect (Table 2).

272  
273 A change in diatom species was observed in September 2014 where the dominant species on 20°S were  
274 *Thalassiosira gravida*, *Pseudo-nitzschia* seriata-group, *Thalassiosira rotula*, *Leptocylindrus danicus*,  
275 *Thalassiosira anguste-lineata*, *Chaetoceros decipiens* and *Chaetoceros didymus*, with varying  
276 abundances between stations (Table 2). Different species were generally dominant on 23°S that included  
277 *Skeletonema japonica*, *Navicula* spp., *Pseudo-nitzschia* delicatissima-group, *Chaetoceros curvisetus*,  
278 *Chaetoceros constrictus*, *Chaetoceros convolutes*, *Chaetoceros atlanticus* and *Pseudo-nitzschia* seriata-  
279 group (Table 2). There was also a general change in dinoflagellates for September 2014 and *Gyrodinium*  
280 spp., *Gymnodinium* spp., *Protoperidinium* spp., *Scrippsiella trochoidea*, *Noctiluca scintillans*, *Ceratium*  
281 *furca*, *Dinophysis fortii*, *Prorocentrum triestinum* and *Dinophysis acuminata* were the dominant species  
282 on 20°S. Four of these dinoflagellates were also dominant on 23°S in addition to *Prorocentrum triestinum*  
283 and *Protoperidinium oblongum* (Table 2). Unidentified dinoflagellates were also present in significant  
284 numbers at some stations on both the 20°S and 23°S transects.

## 285 286 **CHEMTAX**

287  
288 The pattern of community structure as determined by CHEMTAX is presented together with surface  
289 temperature and nutrient data in Figures 6 to 9. Surface temperatures on the 20°S transect were 15°-18°C  
290 in May 2014 compared to 13°-14.5°C in September 2014 and there was a general decrease in the  
291 concentrations of nitrates and silicates from inshore to offshore, although they did not appear to reach  
292 limiting levels of <1 mmol m<sup>-3</sup> (Barlow et al. 2006) as all concentrations were >2 mmol m<sup>-3</sup> (Figure 6a,  
293 d). TChla concentrations ranged from 1.1-3.4 mg m<sup>-3</sup> in May 2014, but was more variable in September  
294 2014 where TChla was 2.2-8.0 mg m<sup>-3</sup> at inshore stations and 0.8-2.6 mg m<sup>-3</sup> between 10 and 70 nm  
295 offshore (Figure 6b, e). Phytoplankton communities in May 2014 were dominated by dinoflagellates at  
296 the 2, 10 and 20 nm stations (57-74%) and by diatoms at the 30-70 nm stations (71-92%), with the small  
297 flagellate (haptophytes, pelagophytes, cryptophytes, prasinophytes) and prokaryote (*Synechococcus*)  
298 groups contributing <20% (Figure 6c). The diatom proportion was 45-88% at the 2-60 nm stations in  
299 September 2014, but the flagellate contribution was 76% at the 70 nm station, with prasinophytes  
300 accounting for at least half (Figure 6f).

301  
302 On the 23°S transect, surface temperatures were also higher in May 2014 (14°-16.5°C) than September  
303 2014 (12°-14.5°C), with highly variable nitrate and silicate concentrations that were >2 mmol m<sup>-3</sup> (Figure  
304 7a, d). TChla levels were 1.2-2.4 mg m<sup>-3</sup> across the transect in May 2014 and 0.8-2.2 mg m<sup>-3</sup> in  
305 September 2014 (Figure 7b, e). Diatoms dominated the populations on the transect in May 2014 (47-  
306 78%), although dinoflagellates and pelagophytes contributed 24% and 21% respectively at the 2 nm  
307 station and dinoflagellates 29% at 30 nm (Figure 7c). Flagellates were dominant in September 2014 (56-  
308 100%) although diatoms were 55% at the 20 nm station (Figure 7f). Prasinophytes accounted for most of  
309 the flagellates at the 2-50 nm stations, *Synechococcus* contributed 42% and 30% at 40 nm and 50 nm,  
310 while haptophytes contributed 32% at the 70 nm station.

311  
312 No nutrient data was available for the ZZ stations but surface temperatures were 13.9°-14.7°C at the  
313 inshore ZZ stations in May and 12.4°-13.7°C in September 2014 (Figure 8a, d). The highest TChla levels  
314 were observed at the southern ZZ1 station in both May (4.5 mg m<sup>-3</sup>) and September 2014 (7.7 mg m<sup>-3</sup>),  
315 with lower TChla at the other inshore ZZ stations (Figure 8b, e). Dinoflagellates were generally the  
316 dominant phytoplankton group (47-70%) in May 2014 (Figure 8e), but in September 2014 the diatoms  
317 were mostly dominant (33-73%) together with some of the flagellates (Figure 8f). Prasinophytes

318 contributed 28-45% at the ZZ1, 3, 5 and 7 stations, and cryptophytes were 19-32% at the ZZ 11 and 13  
319 stations (Figure 8f).

320  
321 Temperatures at the offshore ZZ stations were higher in May (16.0°-17.0°C) compared to September 2014  
322 (14.2°-15.2°C) (Figure 9a, d), and overall surface waters at these offshore stations were also warmer than  
323 at the inshore stations during both months. TChla at these offshore stations was 1.2-10.2 mg m<sup>-3</sup> in May  
324 2014 but lower in September (0.7-1.5 mg m<sup>-3</sup>; Figure 9b, e). Diatoms dominated 52-92% at all stations in  
325 May 2014 (Figure 9e) but the flagellates were collectively more dominant (59-97%) in September 2014  
326 (Figure 9f). While the diatoms were dominant at ZZ2 (57%), the haptophytes and prasinophytes  
327 contributed 13-50% and 12-44% respectively at the other offshore stations, and the *Synechococcus*  
328 proportion was 9-23% at some of these stations (Figure 9f).

## 329 330 Discussion

331  
332 Previous studies in the southern Benguela ecosystem identified three stages in the evolution of upwelled  
333 water, namely newly upwelled water, matured water and aged water (Barlow 1982a, 1982b; Brown and  
334 Hutchings 1987). More recently, in a study of phytoplankton succession in the northern Benguela,  
335 Hansen et al. (2014) developed more suitable hydrographic criteria for these stages for the northern  
336 Benguela. Applying the criteria of Hansen et al. (2014) to the current data indicated that the water masses  
337 in May 2014 were in a late mature to aged stage on the 20°S, 23°S and ZZ transects. This is in agreement  
338 with the offshore Ekman transport that exhibited a decreasing pattern during the May cruise period, and  
339 implied that the sampling was conducted during the declining phase of an upwelling event. During  
340 September 2014, the Hansen et al. (2014) criteria suggested that the water was in a newly upwelled stage,  
341 with a tendency towards the mature stage at the outer three stations on 20°S and 23°S. This corresponded  
342 well with the offshore Ekman transport that displayed an increasing pattern during the cruise period in  
343 September, implying that sampling took place during the early phase of an upwelling event.

344  
345 Hansen et al. (2014) observed diatom dominance in matured upwelled water, with a decline in diatoms  
346 and a succession to domination by dinoflagellates in the later stage of aged water. The CHEMTAX  
347 analysis of pigment data in this study indicated that diatoms were also dominant in aged water at most of  
348 the stations during May 2014, although dinoflagellates were dominant at the three inshore stations on  
349 20°S and at the inshore ZZ stations (Figures 6 and 8). Mixed populations of nanoflagellates,  
350 coccolithophores and dinoflagellates were observed in newly upwelled water by Hansen et al. (2014).  
351 Similarly, small flagellates tended to be dominant in the newly upwelled water during September 2014,  
352 although diatoms and dinoflagellates were present in lower proportions. Prasinophytes and haptophytes  
353 contributed the greater proportion of the nanoflagellate component, and there was also a substantial  
354 proportion of the prokaryote *Synechococcus* (Figures 7 and 9). Thus, even though this investigation could  
355 only provide a “snapshot” of two stages of upwelling, there are similarities between the results of Hansen  
356 et al. (2014) for August-September 2011 and the observations here for May and September 2014.  
357 Although only surface characteristics are reported, Barlow et al. (2006) demonstrated that these  
358 communities are representative of the population within the water column for stations closer to the coast,  
359 but for stations towards the shelf edge the dominance of small flagellates in the upper mixed layer usually  
360 decreased at deeper depths where diatoms tended to be more dominant.

361  
362 While CHEMTAX analysis was useful for indicating change in the bulk proportion of phytoplankton  
363 groups, microscopy provided details about the differences in species of diatoms and dinoflagellates  
364 between the two periods of investigation. The dinoflagellates in May 2014 were mostly unidentified  
365 species that included naked dinoflagellates, but more identifiable species were observed in September  
366 2014. For the diatoms, species of *Chaetoceros*, *Bacteriastrum* and *Cylindrotheca* were dominant during  
367 May 2014, with *Pseudo-nitzschia* seriata-group abundance being particularly high at a number of stations  
368 on the 20°S and 23°S transects (Table 2). In contrast, dominant diatoms in September 2014 included  
369 species of *Thalassiosira* and *Leptocylindrus*, with *Chaetoceros* and *Pseudo-nitzschia* species at a few  
370 stations. Hansen et al. (2014) also noted that *Pseudo-nitzschia* seriata-group was abundant in mature

371 upwelled water, together with species of *Chaetoceros* and *Thalassiosira*, but dinoflagellates of the order  
372 Gymnodiniales were dominant in aged water. Interestingly, small phytoplankton characterized the inshore  
373 newly upwelled water in August-September 2011 where *Emiliania huxleyi* and species of *Phaeocystis*,  
374 *Pyramimonas* and *Pseudopedinella* contributed a high percentage (Hansen et al. 2014). The prevalence of  
375 *Pseudo-nitzschia* species in Namibian waters (Kollmer 1963; Kruger 1980; Hansen et al. 2014) is of  
376 concern because they can be toxic to higher trophic levels. A 14 year study on the 23°S transect revealed  
377 blooms of *Pseudo-nitzschia* occurring in 13-16°C water, with the climatology showing an increase during  
378 austral summer, while a maximum can be attained during May-July (Louw et al. 2017). *Pseudo-nitzschia*  
379 blooms occurred during periods of low wind stress and weak upwelling (Louw et al. 2017),  
380 complementing the observations in this study where high *Pseudo-nitzschia* cell counts were observed  
381 under conditions of decreasing Ekman transport in May 2014.

382  
383 This investigation indicated that small phytoplankton groups were more prominent on the Namibian shelf  
384 in September 2014 than in May 2014, particularly the prasinophytes, haptophytes and *Synechococcus*  
385 (Figures 6-9). Colder, lower salinity, nutrient sufficient water prevailed in September 2014 that was  
386 characterized as being in the first stage of newly upwelled water. Under these environmental conditions, it  
387 might be expected that diatoms would dominate as observed by Barlow (1982b) and Brown and  
388 Hutchings (1987) in the southern Benguela. However, these early studies did not evaluate the contribution  
389 of small phytoplankton cells as has been done for the northern Benguela by Hansen et al. (2014).  
390 CHEMTAX showed that although diatoms accounted for a greater proportion of the biomass on the 20°S  
391 transect and at the ZZ inshore stations in September 2014, this was not the case for the 23°S transect and  
392 the ZZ offshore stations (Figures 7 and 9). High phytoplankton biomass was confined much closer to the  
393 coast in September 2014 and there were patches of elevated chlorophyll *a* in the vicinity of 20°S (Figure  
394 1d). But TChla was lower on the 23°S transect and at the offshore ZZ stations (Figures 1d, 7 and 9) and  
395 the flagellate groups were more dominant. The upper mixed layer was deeper on the 23°S transect and at  
396 the offshore ZZ stations (Figures 3d, 4d, 5d), indicating stronger vertical mixing, driven by stronger wind  
397 conditions in September 2014 (Figure 2d). Diatoms tend to flourish and bloom when the upper mixed  
398 layer is shallow and the water column is more stratified during periods of lower wind stress and reduced  
399 Ekman transport as in May 2014 (Figures 2b, 3b, 4b, 5b), resulting in elevated phytoplankton biomass  
400 that can extend for a considerable distance offshore, as illustrated in Figure 1b.

401  
402 Prominent contribution by small flagellates to phytoplankton biomass in upwelling systems is not unusual  
403 and could be considered a general feature. Crespo et al. (2011) estimated that nanoflagellates accounted  
404 for 62-80% of the integrated biomass in both coastal and oceanic domains off northwest Iberia during a  
405 spring upwelling event. A similar pattern has also been observed in the Humboldt upwelling system off  
406 northern Chile where Iriarte et al. (2000) observed that nano- and picophytoplankton contributed 80% to  
407 primary production and 63% to TChla in summer, and 67% to both in the winter. A 2 year temporal study  
408 at a coastal site in central Chile by Bottjer and Morales (2007) demonstrated that nanoflagellates were the  
409 dominant component of the phytoplankton community during all seasons, contributing up to 80% to the  
410 autotrophic biomass in the upper 50 m during both upwelling and downwelling periods. In comparison,  
411 the average proportion of flagellates (including *Synechococcus*) along the 20°S transect off Namibia  
412 increased from 13% in May to 28% in September 2014, while the average proportion on the 23°S transect  
413 was 27% in the May and 72% during the September cruise. The average proportion for the ZZ inshore  
414 stations increased from 23% in May to 42% in September 2014, with the average at the ZZ offshore  
415 stations being 16% and 74% in the May and September respectively. It appears therefore that small  
416 flagellates contribute substantially to phytoplankton biomass on the central shelf of Namibia, as reported  
417 for the other upwelling ecosystems.

418  
419 Overall, there are important differences in physical, geochemical and biological processes between the  
420 upwelling ecosystems of the southern Pacific and southern Atlantic eastern ocean margins (3°-40°S)  
421 (Mackas et al. 2006). There is strong ENSO activity in the Pacific, while “Benguela Ninos” occur with  
422 decadal frequency in the Atlantic. In addition, strong coastal trapped waves are a feature in both  
423 ecosystems, although this occurs intra-seasonally in the Pacific. While hypoxia, oxygen minimum layers

424 and denitrification are a feature of the Pacific margin, there is a mismatch of time scales between phyto-,  
425 zoo- and meroplankton in the Atlantic margin. Trophic efficiency is higher in the southeastern Pacific,  
426 leading to greater fish production, but in contrast fish yield is lower in the southeastern Atlantic (Mackas  
427 et al. 2006).

428  
429 Previously, small flagellates were observed to be more dominant at the Namibian shelf edge and on the  
430 slope (Barlow et al. 2006) and it is hypothesized that these flagellates were entrained in the upwelled  
431 water that moved inshore and up the shelf towards the coast in September 2014. The water column was  
432 not sufficiently stratified at the time of sampling for diatoms to have proliferated, and therefore the small  
433 flagellates that had populated the water column were observed to be more dominant on the 23°S transect  
434 and at the offshore ZZ stations. Barange and Pillar (1992) proposed a conceptual model of cross-shelf  
435 circulation during active and quiescent phases of upwelling, and suggested that during active upwelling,  
436 shelf circulation is characterised by seaward transport of surface waters, but the flow at depth is onshore,  
437 following isopycnal surfaces. Such a transport mechanism would account for the mid-shelf observation of  
438 flagellate communities, which are more common in the offshore regions. With the stronger vertical  
439 mixing in September 2014, it is likely that flagellate communities were mixed down to a depth where  
440 they were entrained in the onshore flow. Evidence of this transport mechanism can be seen in the vertical  
441 salinity distribution along 23°S, where higher salinity water occurring at the surface between 60 and 70  
442 nm from the coast appears to be subducted and advected shoreward below the upper mixed layer (Figure  
443 4).

444  
445 The prominence of small flagellates in contemporary upwelling ecosystems raises questions about their  
446 future role in the marine food web. The food chain in the Benguela ecosystem has been considered to be  
447 relatively simple, with mesozooplankton grazing on larger diatoms and dinoflagellates,  
448 macrozooplankton grazing on phytoplankton and mesozooplankton, small pelagic fish (anchovies,  
449 sardines) consuming predominately zooplankton, and larger fish such as hake feeding on small fish  
450 (Jarre-Teichmann et al. 1998; Hutchings et al. 2009). Besides the observation in this study,  
451 nanoflagellates have also been observed to be prominent in the southern Benguela ecosystem,  
452 predominantly offshore on the continental slope, but also on the shelf together with diatoms (Mitchell-  
453 Innes and Winter 1987; Barlow et al. 2005; Lamont et al. 2014). This implies that microzooplankton  
454 grazing probably plays an important role in the food web, grazing on the nanoflagellates and in turn being  
455 grazed by the mesozooplankton (Jarre-Teichmann et al. 1998). Thus the food web in the Benguela  
456 ecosystem is probably more complex than previously thought since this microbial loop most likely plays  
457 an important role. If there is a decline in upwelling-favourable winds due to climate change (Bakun et al.  
458 2010), then it is likely that offshore Ekman transport would decrease along the Namibian shelf, as well as  
459 along the west coast of South Africa, leading to less or no upwelling of nutrient-rich water into the  
460 euphotic zone, with a consequent low abundance of diatoms and the dominance of nano- and  
461 picophytoplankton. The overall phytoplankton production and biomass are then likely to be lower than  
462 contemporary levels and the microbial loop would then become a key component of the food web. Meso-  
463 and macrozooplankton production and biomass could also decrease, with a resulting synergetic effect of  
464 upwelling changes and the role of the microbial loop over the biomass of small pelagic fish and larger  
465 demersal species such as hake.

466  
467 Indeed, a substantial decrease in upwelling-favourable winds in the Northern Benguela has been observed  
468 in recent years (Lamont et al., 2017), and this corresponds to positive linear sea surface temperature  
469 trends suggestive of warming (Jarre et al., 2015). However, the impact of this longer-term reduction in  
470 upwelling and warming of surface waters has not yet been clearly discerned as satellite records of surface  
471 chlorophyll *a* show a seemingly contradictory trend, with higher values in recent years (Jarre et al., 2015),  
472 while zooplankton trends are in agreement with a warming scenario and show an overall decrease in  
473 abundance and a shift in dominance by smaller species (Verheye et al., 2016). Modifications in the food  
474 web structure will have important implications for the commercial fisheries of Namibia and South Africa,  
475 and therefore current ecosystem- and fisheries-based management in each country needs to be reviewed

476 and adjusted accordingly in consideration of the possible changes in water properties and plankton  
477 interactions.

478  
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**Table 1**  
Pigment:chlorophyll *a* starting and output ratios for the CHEMTAX analysis of HPLC pigments. Starting ratios derived from Higgins et al. (2011). Chla-chlorophyll *a*; Chlb-chlorophyll *b*; MgDVP-Mg-2,4-dinyl pheoporphyrin *a*<sub>5</sub> monomethyl ester; Chlc1-chlorophyll *c*<sub>1</sub>; Chlc2-chlorophyll *c*<sub>2</sub>; Chlc3-chlorophyll *c*<sub>3</sub>; Per-peridinin; But-19'-butanoyloxyfucoxanthin; Fuc-fucoxanthin; Neo-neoxanthin; Viol-violaxanthin; Pras-prasincoxanthin; Hex-19'-hexanoyloxyfucoxanthin; Allo-alloxanthin; Zea-zeaxanthin; Anth-antheraxanthin; Asta-astaxanthin; Lut-lutein; Chlc2-MGDG1-chlorophyll *c*<sub>2</sub>-monogalactosyldiacylglyceride ester [18:4/14:0]; Chlc2-MGDG2- chlorophyll *c*<sub>2</sub>-monogalactosyldiacylglyceride ester [14:0/14:0].

Group	Chla	Chlb	Mg DVP	Chlc1	Chlc2	Chlc3	Per	But	Fuc	Neo	Viol	Pras	Hex	Allo	Zea	Anth	Asta	Lut	Chlc2- MG DG1	Chlc2- MG DG2
<b>Starting Ratios</b>																				
Diatoms-1	1	0	0	0.087	0.18	0	0	0	0.775	0	0	0	0	0	0	0	0	0	0	0
Diatoms-2	1	0	0	0	0.284	0.083	0	0	0.998	0	0	0	0	0	0	0	0	0	0	0
Dinoflagellates	1	0	0.006	0	0.22	0	0.56	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptophytes	1	0	0	0	0.2	0	0	0	0	0	0	0	0	0.38	0	0	0	0	0	0
Pelagophytes	1	0	0	0.01	0.275	0.23	0	0.66	0.78	0	0	0	0	0	0	0	0	0	0	0
Haptophytes	1	0	0.009	0	0.21	0.18	0	0.04	0.31	0	0	0	0.47	0	0	0	0	0	0.09	0.103
Prasinophytes-1	1	0.631	0.008	0	0	0	0	0	0	0.072	0.138	0	0	0	0.026	0.023	0	0.057	0	0
Prasinophytes-3	1	0.73	0.062	0	0	0	0	0	0	0.063	0.054	0.25	0	0	0.058	0.021	0	0.021	0	0
Chlorophytes	1	0.32	0	0	0	0	0	0	0	0.066	0.049	0	0	0	0.032	0.014	0.012	0.17	0	0
Cyanobacteria (Synechococcus)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.64	0	0	0	0	0
<b>May 2014</b>																				
Diatoms-1	1	0	0	0.135	0.148	0	0	0	0.761	0	0	0	0	0	0	0	0	0	0	0
Diatoms-2	1	0	0	0	0.222	0.133	0	0	0.482	0	0	0	0	0	0	0	0	0	0	0
Dinoflagellates	1	0	0.005	0	0.212	0	0.776	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptophytes	1	0	0	0	0.187	0	0	0	0	0	0	0	0	0.257	0	0	0	0	0	0
Pelagophytes	1	0	0	0.008	0.236	0.241	0	0.840	0.759	0	0	0	0	0	0	0	0	0	0	0
Haptophytes	1	0	0.007	0	0.189	0.188	0	0.034	0.357	0	0	0	0.630	0	0	0	0	0	0.061	0.066
Prasinophytes-1	1	0.427	0.008	0	0	0	0	0	0	0.060	0.153	0	0	0	0.018	0.023	0	0.055	0	0
Prasinophytes-3	1	0.980	0.082	0	0	0	0	0	0	0.060	0.069	0.120	0	0	0.076	0.026	0	0.017	0	0
Chlorophytes	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyanobacteria (Synechococcus)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.832	0	0	0	0	0
<b>September 2014</b>																				
Diatoms-1	1	0	0	0.088	0.101	0	0	0	0.513	0	0	0	0	0	0	0	0	0	0	0
Diatoms-2	1	0	0	0	0.258	0.109	0	0	0.851	0	0	0	0	0	0	0	0	0	0	0
Dinoflagellates	1	0	0.008	0	0.154	0	0.742	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptophytes	1	0	0	0	0.168	0	0	0	0	0	0	0	0	0.368	0	0	0	0	0	0
Pelagophytes	1	0	0	0.008	0.194	0.293	0	0.763	0.819	0	0	0	0	0	0	0	0	0	0	0
Haptophytes	1	0	0.012	0	0.323	0.299	0	0.042	0.397	0	0	0	0.793	0	0	0	0	0	0.133	0.129
Prasinophytes-1	1	0.601	0.008	0	0	0	0	0	0	0.063	0.096	0	0	0	0.028	0.029	0	0.045	0	0
Prasinophytes-3	1	0.687	0.069	0	0	0	0	0	0	0.064	0.054	0.129	0	0	0.056	0.018	0	0.014	0	0
Chlorophytes	1	0.315	0	0	0	0	0	0	0	0.088	0.046	0	0	0	0.042	0.019	0.015	0.215	0	0
Cyanobacteria (Synechococcus)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.642	0	0	0	0	0

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**Table 2**  
Dominant diatom and dinoflagellate species at the surface for each station on the 20°S and 23°S transects during May and September 2014. *Pseudo-nitzschia* seriata-gr indicates *Pseudo-nitzschia* seriata-group. *Pseudo-nitzschia* delicatissima-gr indicates *Pseudo-nitzschia* delicatissima-group.

May	Diatoms	Cells L <sup>-1</sup>	Dinoflagellates	Cells L <sup>-1</sup>	September	Diatoms	Cells L <sup>-1</sup>	Dinoflagellates	Cells L <sup>-1</sup>
20°S 2	<i>Pseudo-nitzschia</i> seriata-gr <i>Chaetoceros curvisetus</i>	14.89x10 <sup>3</sup> 11.45x10 <sup>3</sup>	<i>Ceratium</i> spp <i>Prorocentrum micans</i> Unidentified dinoflagellates	5.47x10 <sup>3</sup> 4.58x10 <sup>3</sup> 3.43x10 <sup>3</sup>	20°S 2	<i>Thalassiosira gravida</i>	21.33x10 <sup>4</sup>	<i>Gyrodinium</i> spp	4.35x10 <sup>3</sup>
					20°S 5	<i>Thalassiosira gravida</i> <i>Pseudo-nitzschia</i> seriata-gr	84.45x10 <sup>4</sup> 22.63x10 <sup>4</sup>	<i>Gymnodinium</i> spp <i>Gyrodinium</i> spp <i>Protoperidinium</i> spp	7.33x10 <sup>3</sup> 6.18x10 <sup>3</sup> 5.38x10 <sup>3</sup>
20°S 10	<i>Chaetoceros curvisetus</i> <i>Pseudo-nitzschia</i> seriata-gr	13.40x10 <sup>4</sup> 66.44x10 <sup>3</sup>	<i>Ceratium</i> spp	14.04x10 <sup>3</sup>	20°S 10	<i>Thalassiosira gravida</i> <i>Thalassiosira rotula</i>	77.92x10 <sup>4</sup> 28.73x10 <sup>4</sup>	<i>Gyrodinium</i> spp <i>Scrippsiella trochoidea</i> <i>Noctiluca scintillans</i>	28.98x10 <sup>3</sup> 10.88x10 <sup>3</sup> 10.31x10 <sup>3</sup>
20°S 20	<i>Chaetoceros debilis</i> <i>Pseudo-nitzschia</i> seriata-gr <i>Chaetoceros curvisetus</i>	24.51x10 <sup>4</sup> 24.40x10 <sup>4</sup> 10.65x10 <sup>4</sup>	<i>Ceratium</i> spp	42.92x10 <sup>3</sup>	20°S 20	<i>Thalassiosira rotula</i> <i>Leptocylindrus danicus</i>	82.71x10 <sup>3</sup> 60.94x10 <sup>3</sup>	Unidentified dinoflagellates	4.12x10 <sup>3</sup>
20°S 30	<i>Pseudo-nitzschia</i> seriata-gr <i>Chaetoceros curvisetus</i> <i>Chaetoceros debilis</i>	2.67x10 <sup>6</sup> 2.08x10 <sup>6</sup> 1.39x10 <sup>6</sup>	Unidentified dinoflagellates	9.16x10 <sup>3</sup>	20°S 30	<i>Leptocylindrus danicus</i> <i>Thalassiosira gravida</i> <i>Thalassiosira anguste-lineata</i>	32.21x10 <sup>4</sup> 28.73x10 <sup>4</sup> 27.64x10 <sup>4</sup>	<i>Ceratium furca</i> Unidentified dinoflagellates <i>Dinophysis fortii</i>	10.66x10 <sup>3</sup> 6.53x10 <sup>3</sup> 6.30x10 <sup>3</sup>
20°S 40	<i>Thalassiosira gravida</i> <i>Bacteriastrum delicatulum</i>	69.42x10 <sup>4</sup> 35.17x10 <sup>4</sup>	<i>Corythodinium tessellatus</i> <i>Gyrodinium</i> spp	1.14x10 <sup>3</sup> 1.14x10 <sup>3</sup>	20°S 40	<i>Pseudo-nitzschia</i> seriata-gr <i>Leptocylindrus danicus</i> <i>Thalassiosira gravida</i>	76.18x10 <sup>3</sup> 74.01x10 <sup>3</sup> 39.18x10 <sup>3</sup>	Unidentified dinoflagellates <i>Prorocentrum triestinum</i>	30.24x10 <sup>3</sup> 23.94x10 <sup>3</sup>
20°S 50	<i>Bacteriastrum delicatulum</i> <i>Pseudo-nitzschia</i> seriata-gr	1.62x10 <sup>6</sup> 88.44x10 <sup>4</sup>	Unidentified dinoflagellates <i>Protoperidinium pallidum</i>	8.02x10 <sup>3</sup> 3.43x10 <sup>3</sup>	20°S 50	<i>Thalassiosira gravida</i> <i>Leptocylindrus danicus</i>	10.40x10 <sup>4</sup> 85.57x10 <sup>3</sup>	Unidentified dinoflagellates	4.12x10 <sup>3</sup>
20°S 60	<i>Bacteriastrum hyalinum</i>	97.15x10 <sup>4</sup>	<i>Protoperidinium</i> spp	2.29x10 <sup>3</sup>	20°S 60	<i>Thalassiosira gravida</i> <i>Chaetoceros decipiens</i> <i>Chaetoceros didymus</i>	78.36x10 <sup>3</sup> 53.61x10 <sup>3</sup> 53.61x10 <sup>3</sup>	<i>Scrippsiella trochoidea</i> <i>Dinophysis acuminata</i> Unidentified dinoflagellates	9.28x10 <sup>3</sup> 6.18x10 <sup>3</sup> 6.18x10 <sup>3</sup>
20°S 70	<i>Bacteriastrum delicatulum</i>	2.16x10 <sup>6</sup>	Unidentified dinoflagellates	2.29x10 <sup>3</sup>	20°S 70	<i>Thalassiosira gravida</i>	14.43x10 <sup>3</sup>	Unidentified dinoflagellates <i>Prorocentrum triestinum</i>	11.34x10 <sup>3</sup> 8.25x10 <sup>3</sup>
23°S 2	<i>Cylindrotheca closterium</i>	36.66x10 <sup>4</sup>	Naked dinoflagellates <i>Prorocentrum micans</i>	12.60x10 <sup>3</sup> 5.72x10 <sup>3</sup>	23°S 2	<i>Skeletonema japonica</i> <i>Navicula</i> spp	20.62x10 <sup>3</sup> 12.60x10 <sup>3</sup>	<i>Prorocentrum triestinum</i>	1.14x10 <sup>3</sup>
23°S 5	<i>Cylindrotheca closterium</i> <i>Pseudo-nitzschia</i> seriata-gr <i>Bacteriastrum hyalinum</i>	73.32x10 <sup>3</sup> 37.81x10 <sup>3</sup> 29.78x10 <sup>3</sup>	Unidentified dinoflagellates <i>Protoperidinium</i> spp	10.31x10 <sup>3</sup> 5.72x10 <sup>3</sup>	23°S 5	Unidentified diatoms	2.29x10 <sup>3</sup>	<i>Protoperidinium</i> spp	1.14x10 <sup>3</sup>
23°S 10	<i>Pseudo-nitzschia</i> seriata-gr	82.48x10 <sup>3</sup>	Naked dinoflagellates Unidentified dinoflagellates	17.18x10 <sup>3</sup> 13.74x10 <sup>3</sup>	23°S 10	<i>Pseudo-nitzschia</i> delicatissima-gr <i>Navicula</i> spp	3.43x10 <sup>3</sup> 2.29x10 <sup>3</sup>	Unidentified dinoflagellates	1.14x10 <sup>3</sup>
23°S 20	<i>Pseudo-nitzschia</i> seriata-gr	12.48x10 <sup>4</sup>	Unidentified dinoflagellates	6.87x10 <sup>3</sup>	23°S 20	<i>Chaetoceros curvisetus</i>	73.32x10 <sup>3</sup>	<i>Dinophysis fortii</i> <i>Protoperidinium</i> spp	1.14x10 <sup>3</sup> 1.14x10 <sup>3</sup>
23°S 30	<i>Pseudo-nitzschia</i> seriata-gr	12.71x10 <sup>4</sup>	Unidentified dinoflagellates <i>Ceratium</i> spp	8.02x10 <sup>3</sup> 3.37x10 <sup>3</sup>	23°S 30	<i>Chaetoceros constrictus</i>	6.87x10 <sup>3</sup>	<i>Scrippsiella trochoidea</i>	4.58x10 <sup>3</sup>
23°S 40	<i>Pseudo-nitzschia</i> seriata-gr	3.83x10 <sup>6</sup>	Naked dinoflagellates <i>Scrippsiella trochoidea</i>	4.58x10 <sup>3</sup> 3.43x10 <sup>3</sup>	23°S 40	<i>Chaetoceros curvisetus</i>	1.14x10 <sup>3</sup>	Unidentified dinoflagellates	2.29x10 <sup>3</sup>
23°S 50	<i>Rhizosolenia robusta</i> <i>Cylindrotheca closterium</i>	1.05x10 <sup>3</sup> 1.14x10 <sup>3</sup>	Unidentified dinoflagellates	5.72x10 <sup>3</sup>	23°S 50	<i>Chaetoceros convolutus</i>	14.89x10 <sup>3</sup>	None	

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23°S	Centric diatoms	1.14x10 <sup>3</sup>							
60	Centric diatoms	8.02x10 <sup>3</sup>	<i>Scrippsiella trochoidea</i>	13.74x10 <sup>3</sup>	23°S	<i>Pseudo-nitzschia delicatissima-gr</i>	32.07x10 <sup>3</sup>	<i>Gyrodinium</i> spp	2.29x10 <sup>3</sup>
	<i>Pseudo-nitzschia seriata-gr</i>	5.72x10 <sup>3</sup>	<i>Gyrodinium</i> spp	5.72x10 <sup>3</sup>	60	<i>Chaetoceros atlanticus</i>	22.91x10 <sup>3</sup>		
23°S						<i>Pseudo-nitzschia seriata-gr</i>	20.62x10 <sup>3</sup>		
70	<i>Thalassiosira</i> sp	12.94x10 <sup>4</sup>	Naked dinoflagellates	5.72x10 <sup>3</sup>	23°S	<i>Pseudo-nitzschia delicatissima-gr</i>	67.59x10 <sup>3</sup>	Unidentified dinoflagellates	3.43x10 <sup>3</sup>
					70			<i>Protoperidinium oblongum</i>	1.14x10 <sup>3</sup>

## Figure legends

**Figure 1.** Monthly composites of MODIS Aqua Sea Surface Temperature for (a) May 2014 and (c) September 2014, and chlorophyll *a* concentration for (b) May 2014 and (d) September 2014. Black dots and squares indicate positions of sampling stations on the 20°S and 23°S transects and the ZZ stations respectively. White areas indicate missing data due to cloud cover or fog. Abbreviations are WB-Walvis Bay, SW-Swakopmund, CC-Cape Cross, TC-Toscanini, TB-Terrace Bay. The images provide a larger “aerial view” geographic and hydrographic context for the two cruise periods.

**Figure 2.** Daily Eckman transport (dark grey) for 6-18 May 2014 at (a) 20°S and (b) 23°S and for 5-16 September 2014 at (c) 20°S and (d) 23°S. Light grey indicates the cruise periods for 9-15 May and 8-13 September 2014.

**Figure 3.** Temperature profiles on the 20°S transect for (a) May 2014 and (c) September 2014, and on the 23°S transect for (b) May 2014 and (d) September 2014. Horizontal black lines indicate the depth of the upper mixed layer ( $Z_m$ ). Vertical dotted lines indicate the depth of CTD profiles.

**Figure 4.** Salinity profiles on the 20°S transect for (a) May 2014 and (c) September 2014, and on the 23°S transect for (b) May 2014 and (d) September 2014. Horizontal black lines indicate the depth of the upper mixed layer ( $Z_m$ ). Vertical dotted lines indicate the depth of CTD profiles.

**Figure 5.** Temperature profiles on the ZZ inshore transect for (a) May 2014 and (c) September 2014, and on the ZZ offshore transect for (b) May 2014 and (d) September 2014. Horizontal black lines indicate the depth of the upper mixed layer ( $Z_m$ ). Vertical dotted lines indicate the depth of CTD profiles.

**Figure 6.** Surface pattern on the 20°S transect during May and September 2014 for (a, d) temperature and nutrients, (b, e) TChla, and (c, f) the proportion of each phytoplankton group contributing to TChla.

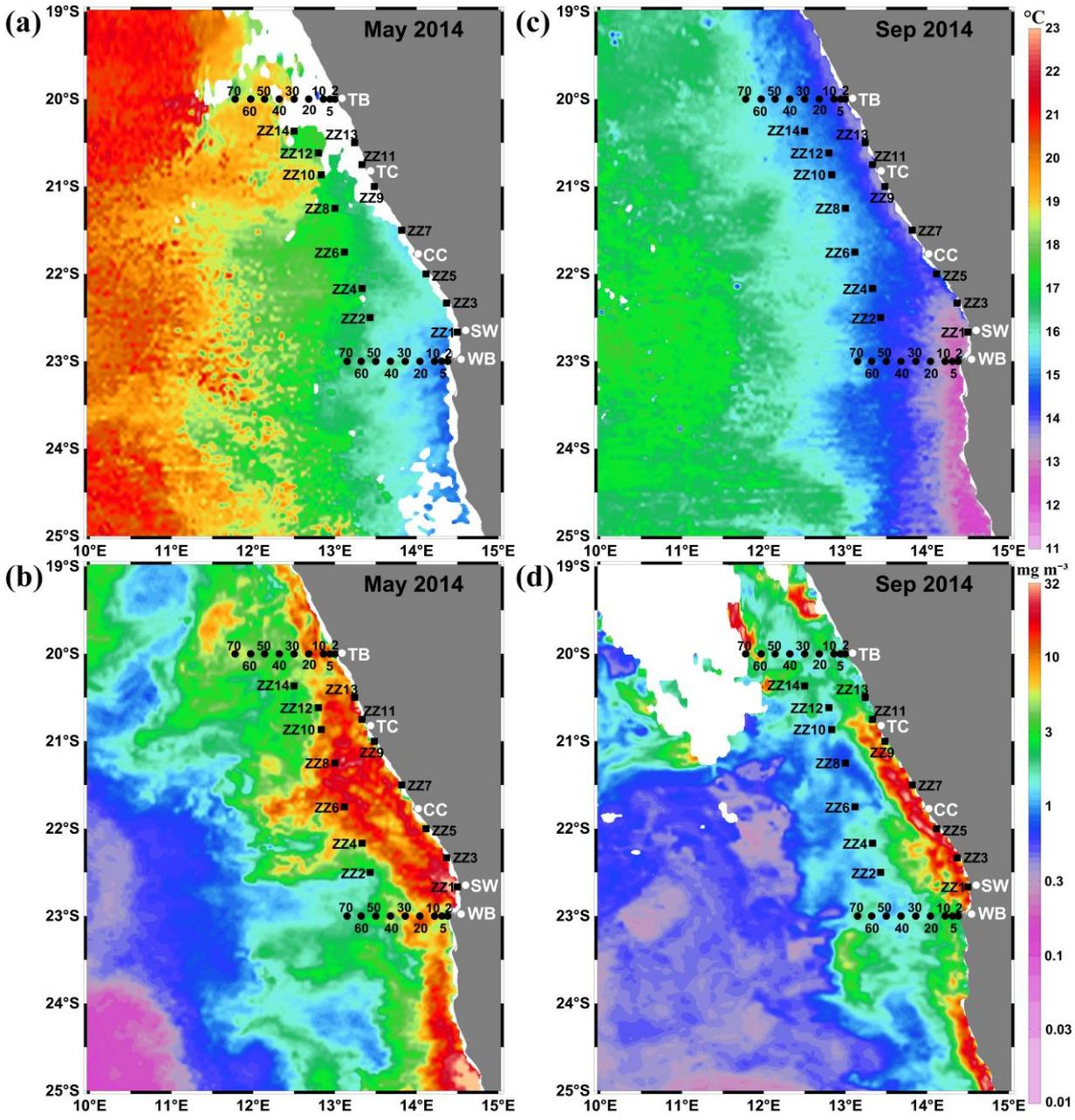
**Figure 7.** Surface pattern on the 23°S transect during May and September 2014 for (a, d) temperature and nutrients, (b, e) TChla, and (c, f) the proportion of each phytoplankton group contributing to TChla.

**Figure 8.** Surface pattern at the ZZ inshore stations during May and September 2014 for (a, d) temperature, (b, e) TChla, and (c, f) the proportion of each phytoplankton group contributing to TChla.

**Figure 9.** Surface pattern at the ZZ offshore stations during May and September 2014 for (a, d) temperature, (b, e) TChla, and (c, f) the proportion of each phytoplankton group contributing to TChla.

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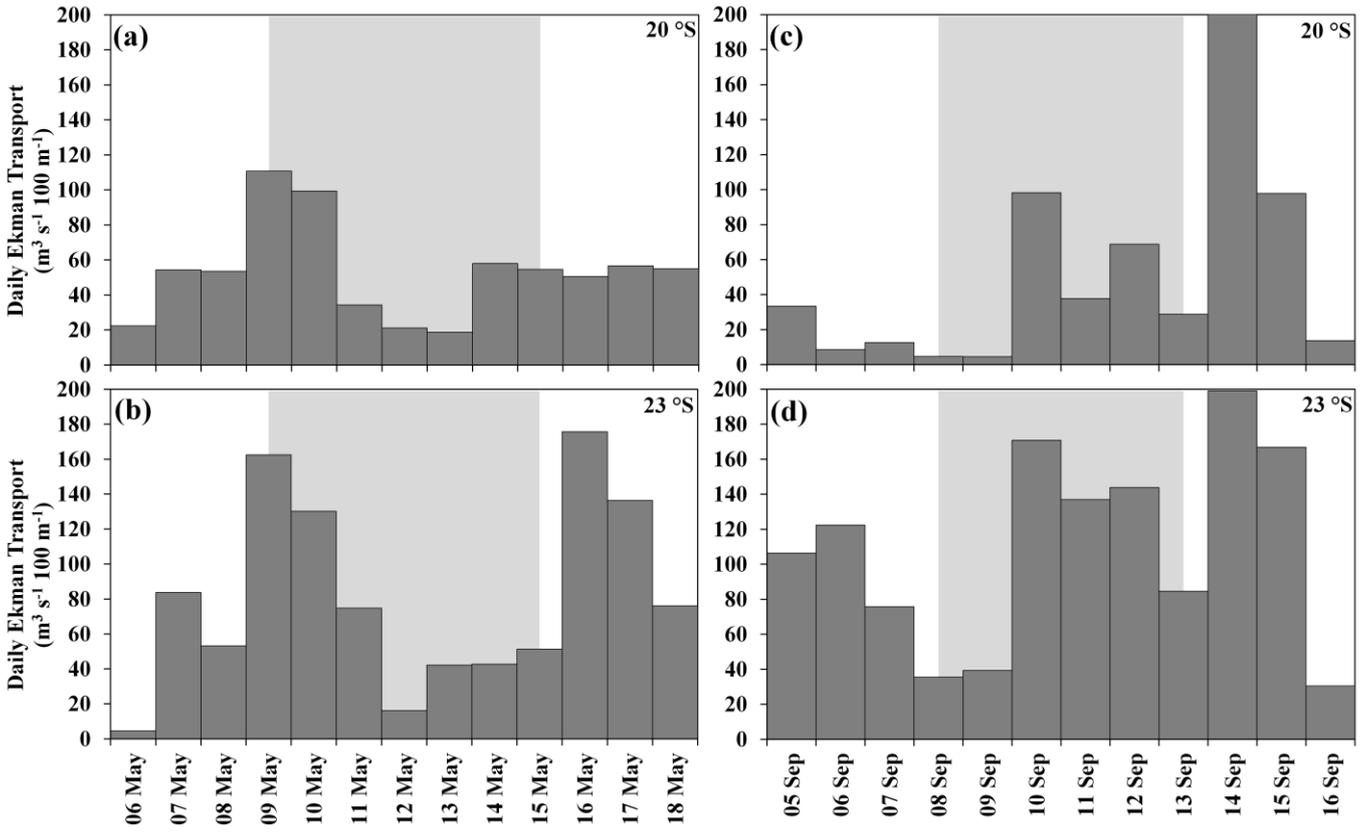
Fig. 1



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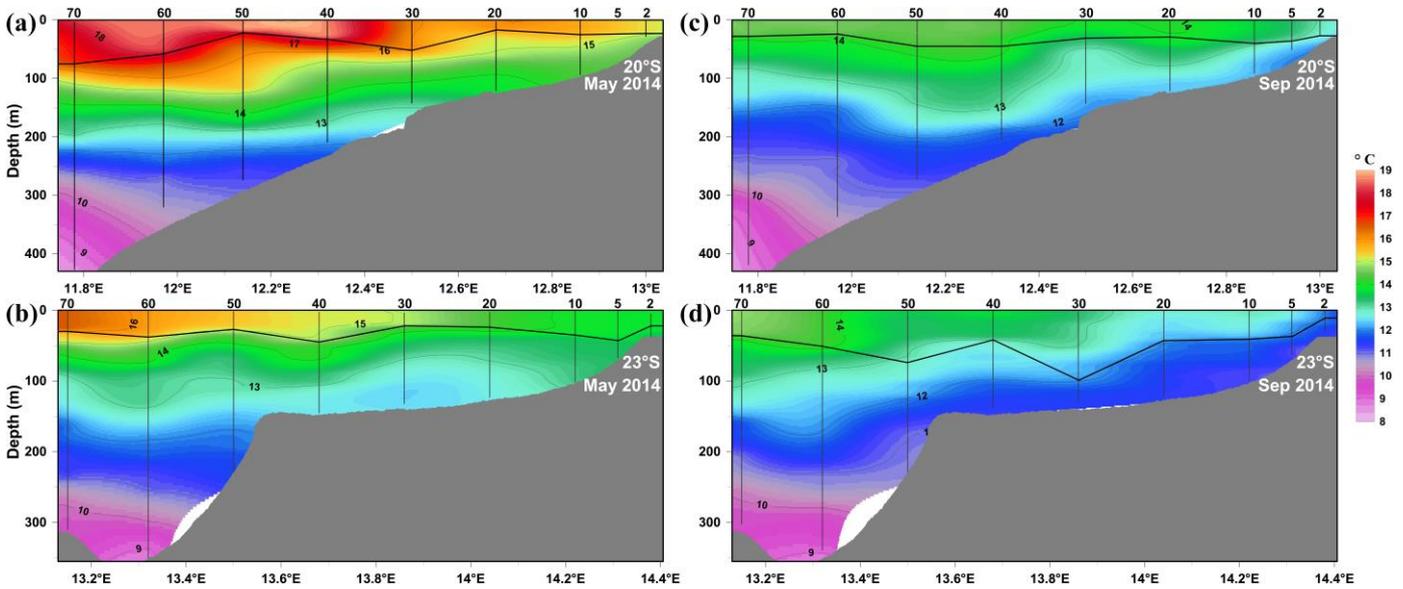
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Fig. 2



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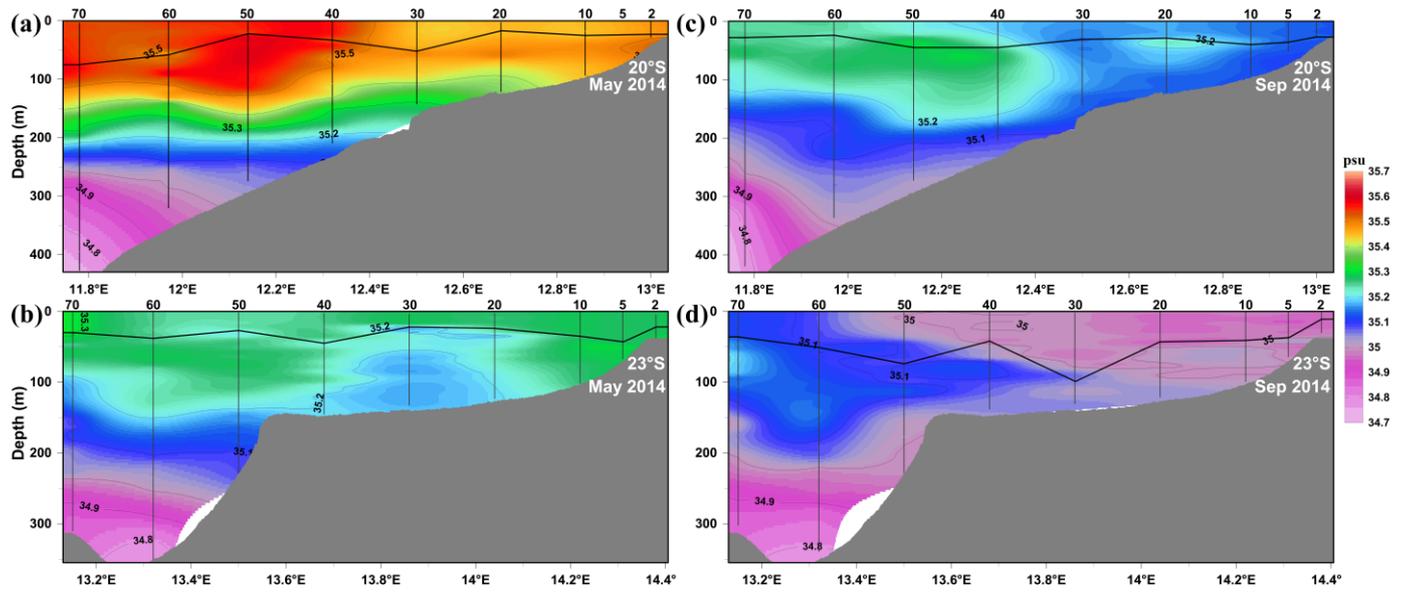
Fig. 3



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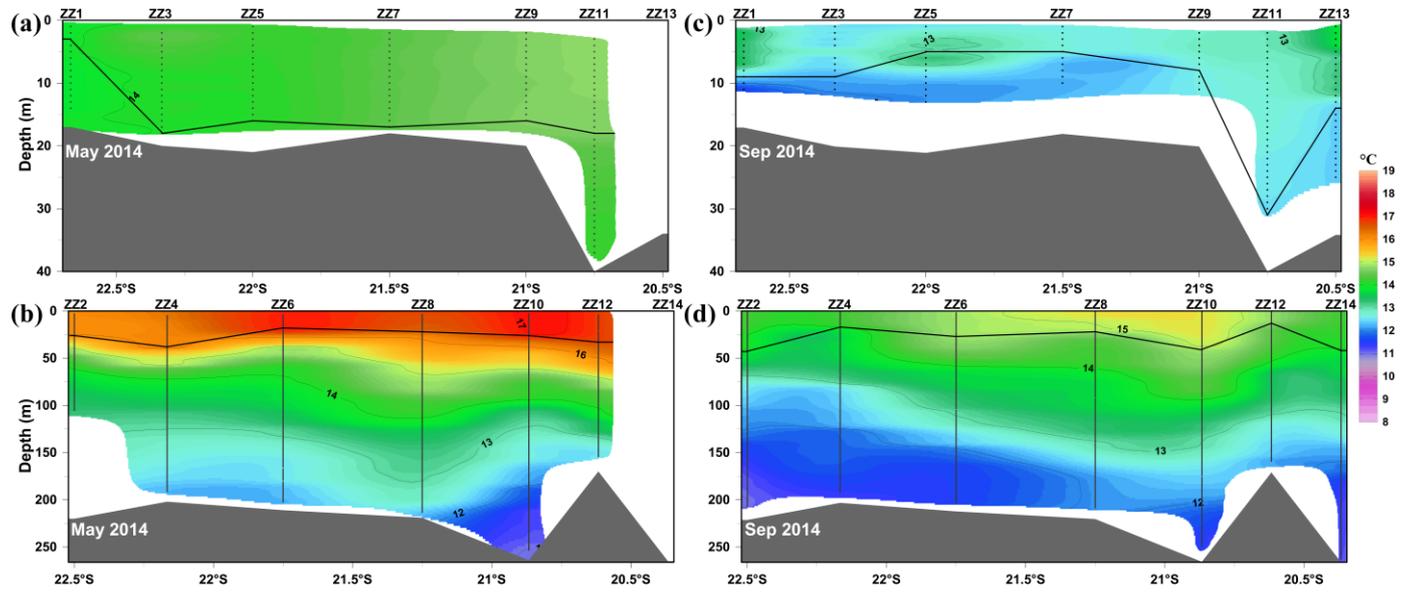
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Fig. 4



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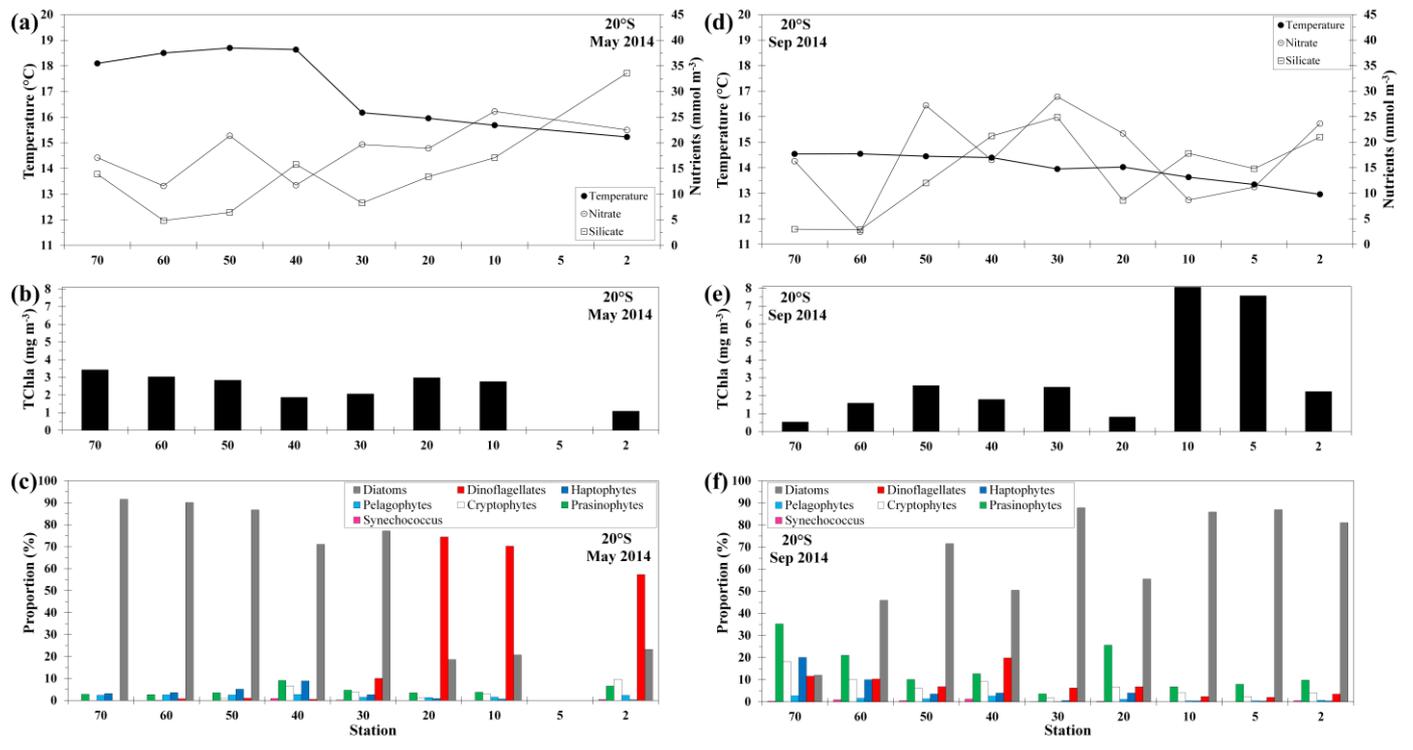
Fig. 5



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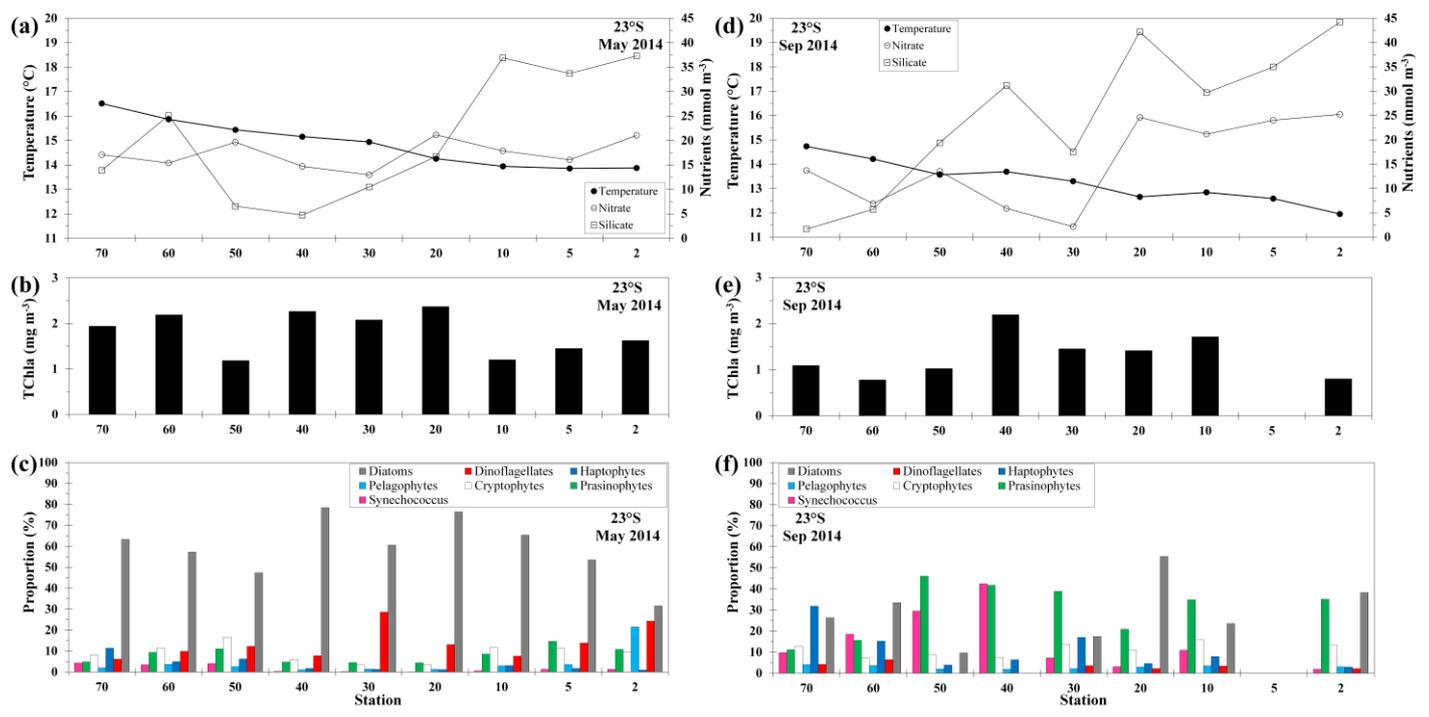
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Fig. 6



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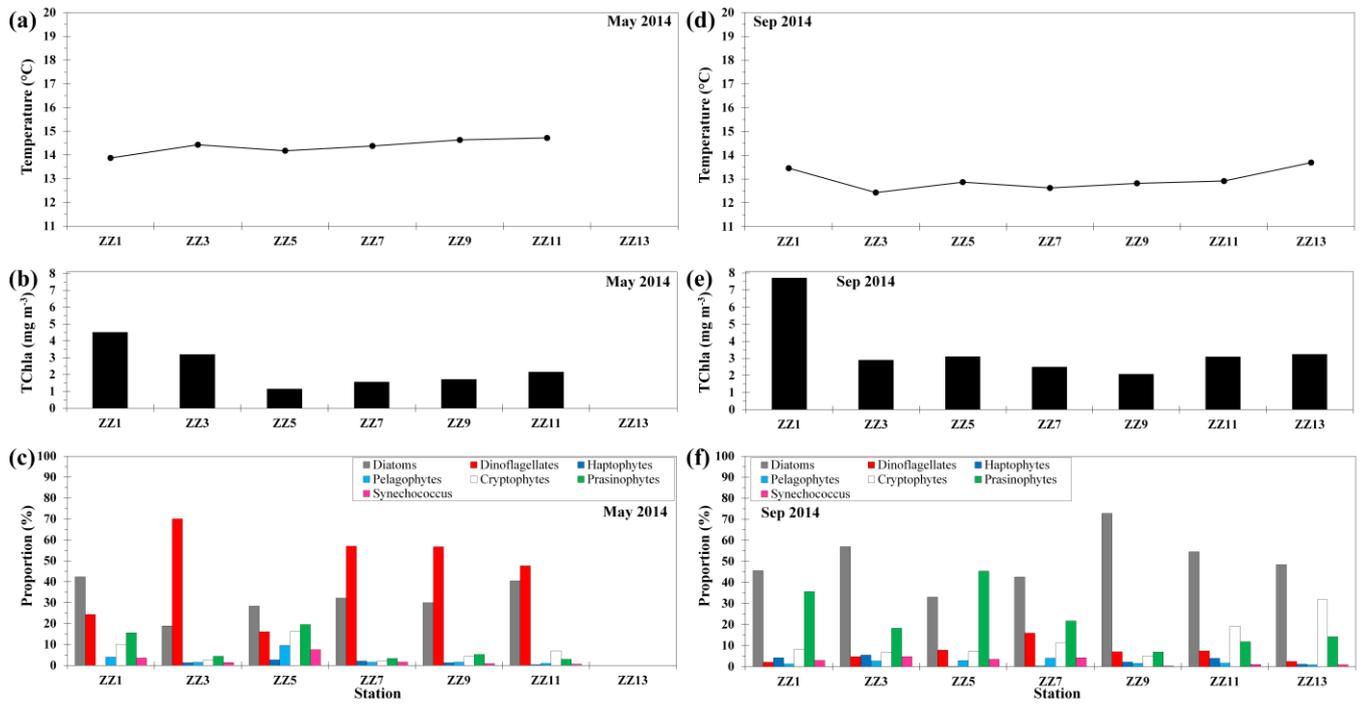
Fig. 7



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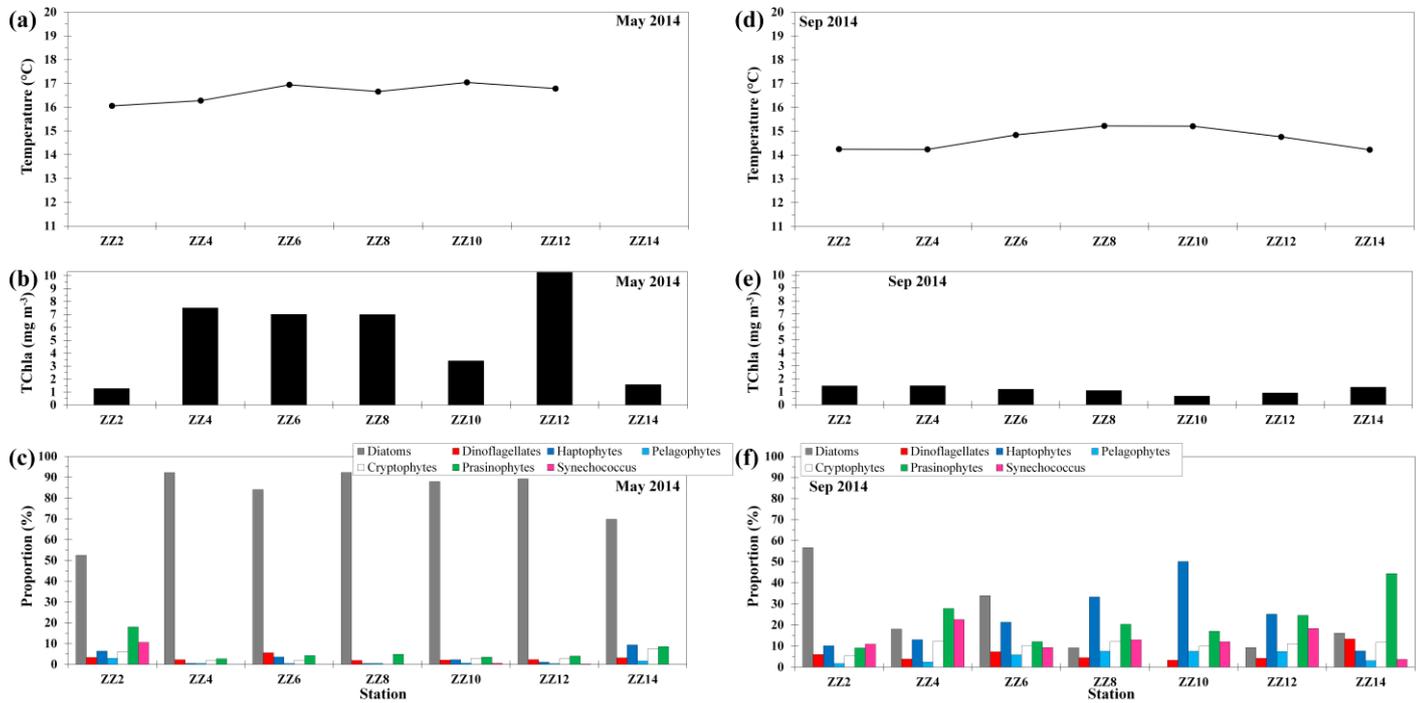
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Fig. 8



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Fig. 9



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