

Adaptations of phytoplankton in the Indian Ocean sector of the Southern Ocean during austral summer of 1998–2014

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Abstract This study investigates the effects of light and temperature on the surface water diatoms and chlorophytes, phytoplankton in the Indian Ocean sector of the Southern Ocean (SO) during the austral summer of 1998–2014. Significant longitudinal variations in hydrographic and biological parameters were observed at the Sub tropical front (STF), Sub Antarctic front (SAF) and Polar front (PF) along 56°E–58°E. The concentrations of total surface chlorophyll *a* (*Chl a*), diatoms, and chlorophytes measured by the National Aeronautics Space Agency (NASA) estimated by the Sea-Viewing Wide Field-of-View Sensors (SeaWiFS), the Moderate Resolution Imaging Spectro Radiometer (MODIS), and the NASA Ocean Biological Model (NOBM) were used in the study. Variations in the concentration of total *Chl a* was remarkable amongst the fronts during the study period. The contribution of diatoms to the total concentration of surface *Chl a* increased towards south from the STF to the PF while it decreased in the case of chlorophytes. The maximum photosynthetically active radiation (PAR) was observed at the STF and it progressively decreased to the PF through the SAF. At the PF region the contribution of diatoms to the total *Chl a* biomass was $\geq 80\%$. On the other hand, the chlorophytes showed a contrary distribution pattern with $\geq 70\%$ of the total *Chl a* biomass recorded at the STF which gradually decreased towards the PF, mainly attributed to the temperate adaptation. This clearly reveals that the trend of diatoms increased at the STF and decreased at the SAF and the PF. Further, the trend of chlorophytes was increased at the STF, SAF and PF with a shift in the community in the frontal system of the Indian Ocean sector of the SO.

Keywords chlorophyll *a*, diatoms, chlorophytes, SST, PAR, Southern Ocean

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1 Introduction

Biogeochemical processes in the Southern Ocean (SO) play a significant role in regulating the global climate (Takahashi et al., 2012; Suhas et al., 2015). Phytoplankton composition plays a major role in biogeochemical cycles in the ocean. The rate of carbon fixation and quantum of export are strongly dependent on the phytoplankton community. The contribution of various phytoplankton communities in the total production is still poorly understood in the Indian Ocean sector of SO. Therefore, it is imperative to estimate the spatial and temporal variabilities of phytoplankton production so as to understand the oceanic biogeochemical cycle and its response to climatic change. The data collected from satellite observations (Hirata et al., 2009) suggest that the photosynthetic rates of micro-phytoplankton were higher than that of nano-phytoplankton in several regions. Similarly, when the spatial extent was considered at the boundary of the SO, the production of nano-phytoplankton was comparable and/or even larger than that of the micro-phytoplankton. In addition to this, climate variability was shown to be linked with the phytoplankton compositions and their shifting in some regions (Dandonneau et al., 2004; Martinez et al., 2009; Masotti et al., 2011; Rousseaux and Gregg, 2012) of the SO. The changes, like in the physico-chemical parameters of water masses, are likely to exert an effect on chlorophyll *a* (*Chl a*) biomass primary production as well as the quantum of secondary and tertiary productions. The seasonal and interannual variations change the composition of phytoplankton and their contribution to the total production. The phytoplankton blooms in the SO towards the PF were typically dominated by larger diatoms (Smetacek et al., 1997; Brown and Landry, 2001). In the SO the smaller phytoplankton species experience strong grazing pressure by micro-zooplankton while large diatoms in the SO are grazed mainly by some of the larger micro-zooplanktons. However, larger diatoms are often not

subjected to strong grazing pressures due to their sizes (Gall et al., 2001; Selph et al., 2001; Zeldis, 2001).

Temperature plays a major role on the spatial distribution of diatoms in oceans thus classifying them into different groups such as tropical, temperate, and polar species (Eppley, 1972; Smyda, 1980). The diatoms also experience the magnitude of light and dark events during their life cycle (Smetacek, 1985). Dark adaptation might be an important factor, which controls the distribution and seasonal occurrence of the various species. It has been observed that several polar diatom species can survive during the darkness in the vegetative state for at least 4 to 9 months without any mortality, and live at least 3 months without changes in cell physiology (Peters and Thomas, 1996). The cells adapt to the darkness, maintaining the photosynthetic apparatus by low carbon consumption during the dark conditions (Anderson, 1976).

The seasonal and spatial distributions of microalgae are controlled by one of the important factors, i.e., dark adaptations (Peters, 1996), and this has been proven by the incubation experiment method for temperate diatoms which survived for 21–35 days. However, the polar species survived up to 9 months in the dark condition (Peters and Thomas, 1996). This happened due to the physiological mechanism during the dark period wherein compounds such as glucan in diatoms and starch in chlorophytes, which accumulate in polar micro-phytoplankton, were utilized during the period of darkness, besides the uptake of dissolved organic materials, to meet their energy requirements and life extensions (Morgan-Kiss et al., 2006). However, in comparison to diatoms, the temperate chlorophytes in the SO show gene-enrichment in amino acids that mediate the transport of various molecules and promote enhanced uptake of organic nutrients (Blanc et al., 2012). This results in metabolic flexibility in both diatoms and chlorophytes, whereas the diatoms' genomes reveal the ability to flourish within the intense and highly variable environmental conditions typical of the SO and polar region (Blanc et al., 2012). In reality, chlorophytes are capable of switching between autotrophic and heterotrophic growths, and the highest growth occurs in the mixotrophic growth condition in the presence of light and glucose carbon cycle. Similarly, several dinoflagellate groups could also shift from heterotrophic to mixotrophic sea ice communities during the winter period (Bachy et al., 2011). However, more research is needed to understand the metabolic activities for dark adaptation of phytoplankton communities, even at species levels that shift from temperate to polar region and vice versa during the austral summer and winter periods of extended darkness.

Light availability and utilization in the SO and polar regions are highly variable, therefore the microalgae at polar regions avoids photo damage during the periods of high light and prefers to adapt to the low-light condition (Mock and Gradinger, 1999). Similarly, the sea ice diatoms are a dense package of pigments with their binding

proteins that facilitate high photosynthetic efficiencies under very low-light conditions, while the carbohydrate and alternate energy sources utilization help to counteract any energy scarcity. This mechanism helps the polar algae to adapt themselves and maintain their ability for state transitions to balance PSI (photosystem-I) and PSII (photosystem-II), and sustain optimal photosynthetic activity under the extreme light conditions (Morgan-Kiss et al., 2008). Phytoplankton communities and variability have been observed in the vicinity of the major SO fronts (Banse and English, 1997; Moore et al., 1999; Moore and Abbott, 2000). A number of *in-situ* observations in the meridional transects show elevated phytoplankton biomass at the PF relative to the surrounding waters (Allanson et al., 1981; Bathmann et al., 1997; Mengelt et al., 2001). While the elevated chlorophyll concentrations have often been observed at the PF, little is known about the temporal or spatial distributions of these frontal-associated blooms. The response of frontal ecosystem to climate is difficult to assess due to lack of large scale *in-situ* biological monitoring programs (Alvain et al., 2013). Here we have analyzed remotely sensed estimates of sea surface temperature, PAR, surface chlorophyll concentrations, diatoms, and chlorophytes to map out the spatial variability of frontal regions associated blooms which have not been studied earlier over longer periods in the Indian Ocean sector of the SO. In the present study we have not considered the nutrients (nitrates, phosphate, and silicates) to understand their influence on the surface density of diatoms and chlorophytes in the SO and polar regions because it has been observed that these waters are high-nutrient low-chlorophyll regions (HNLC), and the productivity is solely controlled by photosynthetic physiology (Boyd, 2002). Therefore, the present study would provide a first step information of its kind of adaptation of phytoplankton such as diatoms and chlorophytes along their shifts in various frontal regions of the Indian Ocean sector of the SO.

2 Material and methods

An extensive study was carried out to identify the different frontal regions of the Indian Ocean sector of the SO using satellite and model analysed observations (Orsi et al., 1995; Belkin and Gordon, 1996; Holliday and Read, 1998). Positional discrepancies have been observed in the Indian Ocean sector of the SO due to the different datasets and methodology used for identification purposes. In this paper, we have identified three frontal regions, viz, the subtropical front (STF: 39°S–43°S), the sub-Antarctic front (SAF: 45°S–48°S), and the polar front (PF: 52°S–56°S) along 56°E–58°E in the Indian Ocean sector of the SO (Fig. 1). The frontal ranges are selected based on the sea surface temperature (SST) that restrains during each austral summer of the study period (1998–2014).

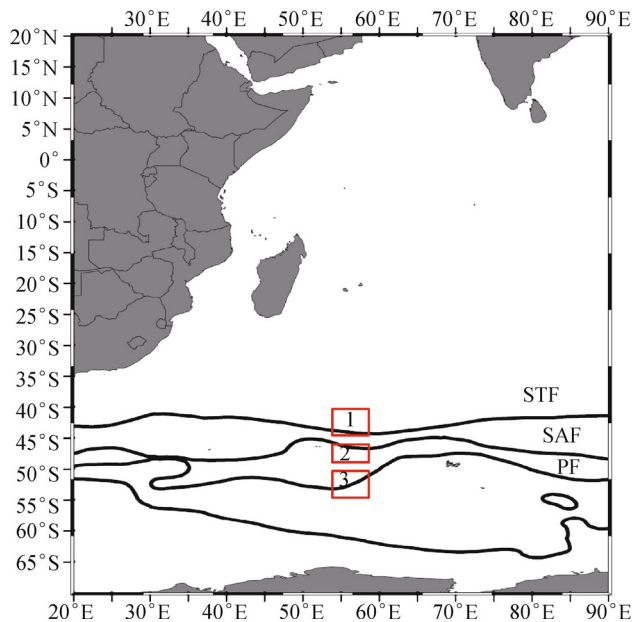


Fig. 1 The boxes 1, 2, and 3 indicate the observation area of the frontal regions (1 represents STF, 2 represents SAF, and 3 represents PF) of the Indian Ocean sector of the SO during austral summer (1998–2014).

The satellite datasets such as *Chl a*, SST, and PAR were collected from the National Aeronautics and Space Administration (NASA) data archive for the period 1998–2014. We analyzed the SeaWiFS monthly *Chl a* and PAR product (9 km×9 km resolution) during the austral summer (December–February) 1998–2002 and MODIS monthly *Chl a* and PAR product (9 km×9 km resolution) during 2003–2014, which were processed by the Ocean Biology Processing Group (OBPG) at Goddard Space Flight Center. The National Oceanic Atmospheric Administration Advanced Very High Resolution Radiometer (NOAA-AVHRR), and the SST (spatial resolution: 4 km) were acquired from NASA's Jet Propulsion Laboratory (JPL).

The monthly products of diatoms and chlorophytes during the austral summer 1998–2007 were collected from the NASA Ocean Biogeochemical Model (NOBM). The model data were based on 14 vertical layers in quasi-isopycnal coordinates, driven by wind stress, sea surface temperature, shortwave radiation, and the ocean general circulation model (OGCM), and have been extensively validated with *in-situ* based nutrients and chlorophyll concentrations (Gregg et al., 2003). The model data for diatoms and chlorophytes were available only for the period 1998–2007. Therefore a linear regression relationship was established between satellite measured *Chl a* and NOBM model based diatoms during the austral summer, 1998–2007 for each frontal region as follows:

$$y = 0.6591x - 0.1403(\text{STF}), \quad (1)$$

$$y = 1.2085x - 0.0728(\text{SAF}), \quad (2)$$

$$y = 1.3286x - 0.0918(\text{PF}). \quad (3)$$

Similarly the linear regression relationship between satellite measured *Chl a* and NOBM model based chlorophytes during the austral summer 1998–2007 for each frontal region was established as given below:

$$y = 0.8061x - 0.0199(\text{STF}), \quad (4)$$

$$y = -0.1103x + 0.034(\text{SAF}), \quad (5)$$

$$y = -3E-07x + 8E-08(\text{PF}). \quad (6)$$

The relationship obtained from the linear equation was applied for further analysis of diatoms and chlorophytes for the extended periods during the austral summer 2008–2014. In the present study, only diatoms and chlorophytes were measured in various frontal regions of the SO due to their maximum concentration compared to other communities. This study was intended only for the austral summer of each year for the long period of study so as to derive the consistent datasets used from the location to avoid the cloud coverage (if any). The cloud free and summer significant data were used straightaway for the estimation of diatom and chlorophyte concentrations for further periods.

3 Results

The significant relationship was observed between satellite measured *Chl a* and NOBM model based diatoms in Eqs. (1), (2), and (3), and *Chl a* and NOBM model based chlorophytes in Eqs. (4), (5), and (6) (Fig. 2). The linear relationship between them gradually increased from STF ($r = 0.7$) to SAF ($r = 0.95$) and PF ($r = 0.87$), indicating that the contribution of diatoms to total *Chl a* was elevated southward of the frontal regions. The relationship between *Chl a* and NOBM model chlorophytes showed an inverse trend, decreasing from STF ($r = 0.80$) to SAF ($r = 0.45$) and PF ($r = 0.46$), and indicating that the chlorophytes contribution to total *Chl a* was low (Figs. 2 and 3). The concentrations of chlorophytes and diatom communities in different frontal regions are shown in Fig. 4. PAR and SST values are shown in Fig. 5. Chlorophytes concentrations showed a decreasing trend from STF to PF (Figs. 4 and 6), as in the case of SST. During the study period (1998–2014), the chlorophytes concentrations were found to have a positive trend at the PF and SAF, and a negligible trend in the STF region (Fig. 4). The maximum concentration of chlorophytes was observed at STF ($0.3 \text{ mg} \cdot \text{m}^{-3}$), whereas very low concentrations were found at SAF and PF (Fig. 4). The abundance of chlorophytes was observed mainly between the temperature ranges of 16°C to 18°C (Figs. 4

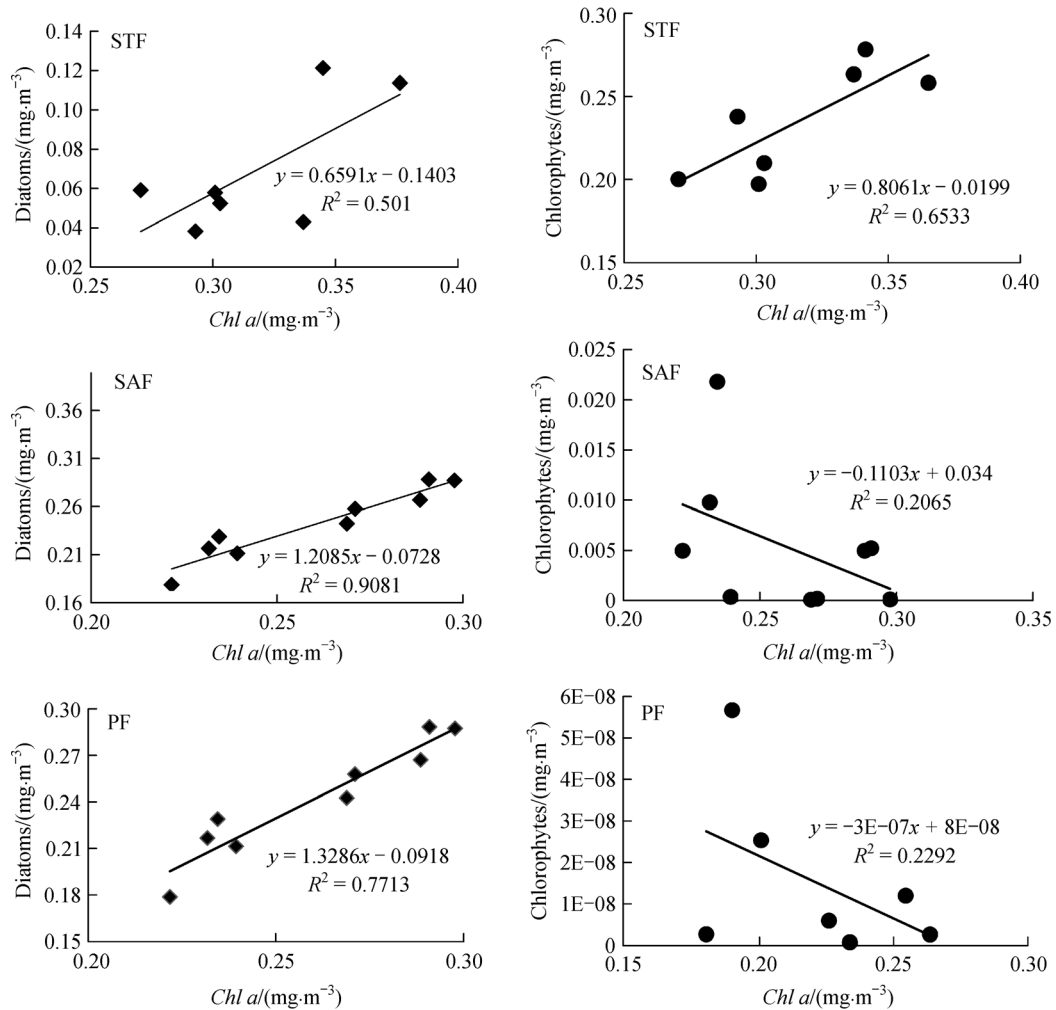


Fig. 2 Scatter plot shows the regression relationship between *Chl a*, diatoms, and chlorophytes during austral summer (1998–2007).

and 5), hence the STF zone serves as suitable for the growth of chlorophytes.

Diatoms showed an increasing trend at STF, but a decreasing trend at SAF and PF (Fig. 4) during the study period. The *Chl a* concentration of diatoms was almost two-fold at SAF and PF as that of STF. However, the diatom concentration increased from STF to PF, indicating the abundance of diatoms which were evident between the temperatures 2°C and 9°C, and gradually declined with the increase of temperature (Figs. 4 and 5). This signifies the diatom biomass increases towards PF and was more adapted to cold, i.e., cold adaptation. On the other hand, the growth of chlorophytes was seen between 7°C and 18°C, and consequently chlorophytes were adapted more to the STF and SAF than PF. The mean SST showed a gradual negative trend at STF and a positive trend at SAF and PF during the study period (Fig. 5). The chlorophytes and diatoms concentrations were decreased with a decline of temperature, and hence the total *Chl a* concentrations were decreased during 2002–2014 (Figs. 4 and 5). The maximum concentration of chlorophytes and total *Chl a*

coincides with the respective temperature of the region (Figs. 4 and 7). However, at the PF, the chlorophytes concentration declined with a decrease in temperature, and it was increasing with an elevated temperature at SAF and STF, but limited to the temperature $\leq 18^\circ\text{C}$. The concentrations of diatoms elevated towards PF, and accordingly the total *Chl a* concentration enhanced significantly towards PF with a temperature of 2°C (Fig. 7(c3)). However, the trend reversed at the STF where the temperature was above 16°C (Fig. 7(a1)). The total *Chl a* concentration showed a decrease of the phytoplankton biomass during the last 16 years. The diatom biomass increased from the STF to PF indicates the ideal situation for cold adapted diatoms at PF (Fig. 7). The total *Chl a* concentration was significantly decreased from STF ($(0.33 \pm 0.04) \text{ mg} \cdot \text{m}^{-3}$) to PF ($(0.197 \pm 0.039) \text{ mg} \cdot \text{m}^{-3}$) through SAF ($(0.24 \pm 0.036) \text{ mg} \cdot \text{m}^{-3}$). The results revealed that the diatoms were dominant over the chlorophytes in abundance during the 16 year time period, with a contrary trend from STF to PF. The photosynthetic active radiation (PAR) showed a marked variation along the frontal

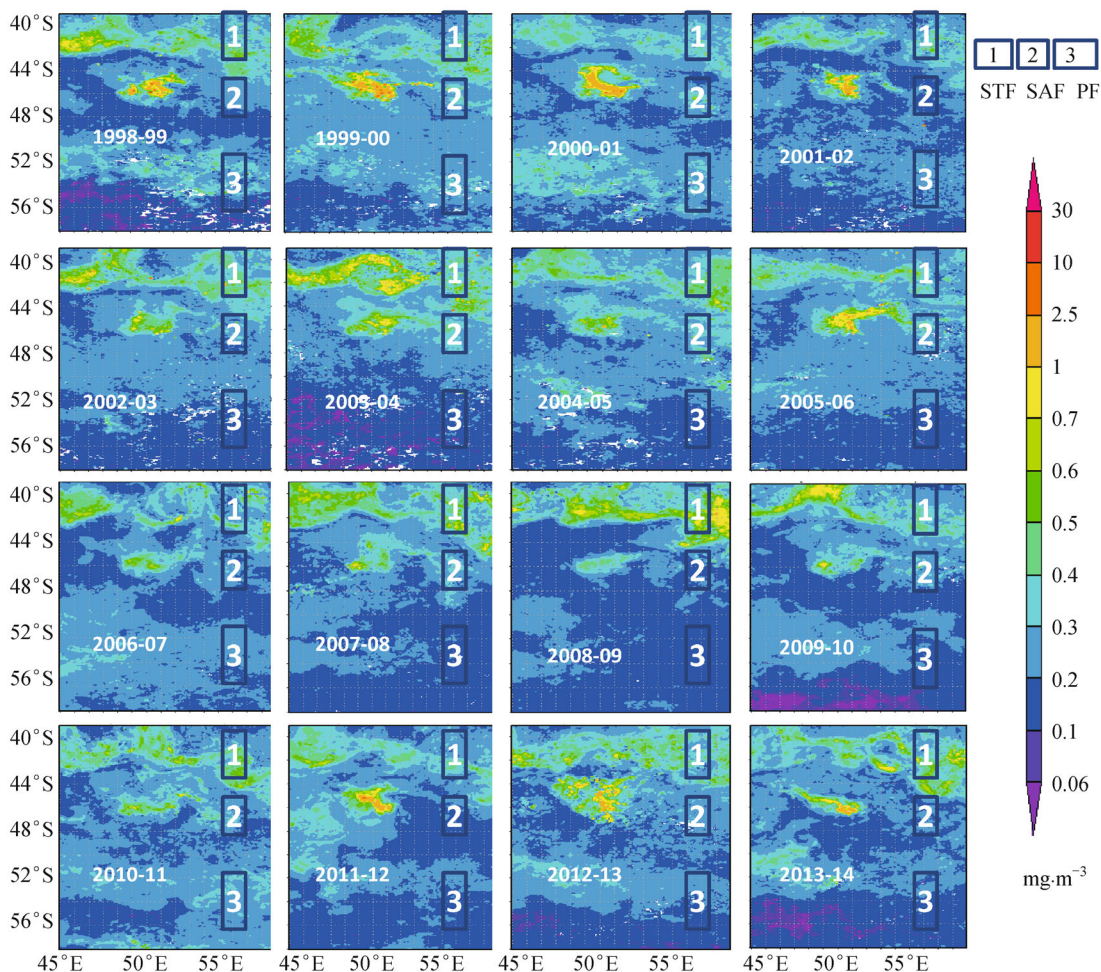


Fig. 3 The *Chl a* distribution of SeaWiFS and MODIS during austral summer (1998–2014) in surface water of the SO. The rectangular boxes as 1, 2, and 3 represent study locations at STF, SAF, and PF respectively.

regions. The maximum PAR was observed at STF whereas the minimum was observed at PF (Figs. 5(d)–5(f)). The total *Chl a* concentration showed a declining trend coinciding with a negative trend of PAR during the study period.

4 Discussion

Studies on the effect of temperature on diatoms and chlorophytes ecotypic variation are very few in the Indian Ocean sector of the SO. Like other algae, the diatoms and chlorophytes showed great variations under the influence of temperature that varies from tropical to polar regions (Bolton, 1983). In the present study, the biomass of diatoms and chlorophytes were observed to be of opposite trend in different frontal regions due to the temperature adaptations. The concentration of chlorophytes and total *Chl a* decreased from the STF to the PF while it showed a

reversed trend for diatoms. This indicates that the diatoms have a better cold adaptation mechanism as compared to the chlorophytes. Wiencke and Fischer (1990) have observed that the rate of photosynthesis remains similar in Antarctic microalgae from temperature 0°C to higher temperature, which certainly reflects the significant adaptation to cold temperature. Such adaptations have also been observed by the growth measurement of phaeophyta algae elsewhere at 0°C which were of similar magnitude to those of temperate species at higher temperatures (Bolten and Lüning, 1982). In the Antarctic diatoms, the molecular adaptation for regulation of RuBP carboxylase has a minimum Micheaelis constant (K_m) for cold adapted species at 4.5°C and 20°C for temperate species in a tropical environment. This result agrees with the present diatoms abundance at STF and PF where the observed upper temperature was 18°C and the lower temperature was 2°C, respectively. However, the sizes and species of similar groups may have different survival rates

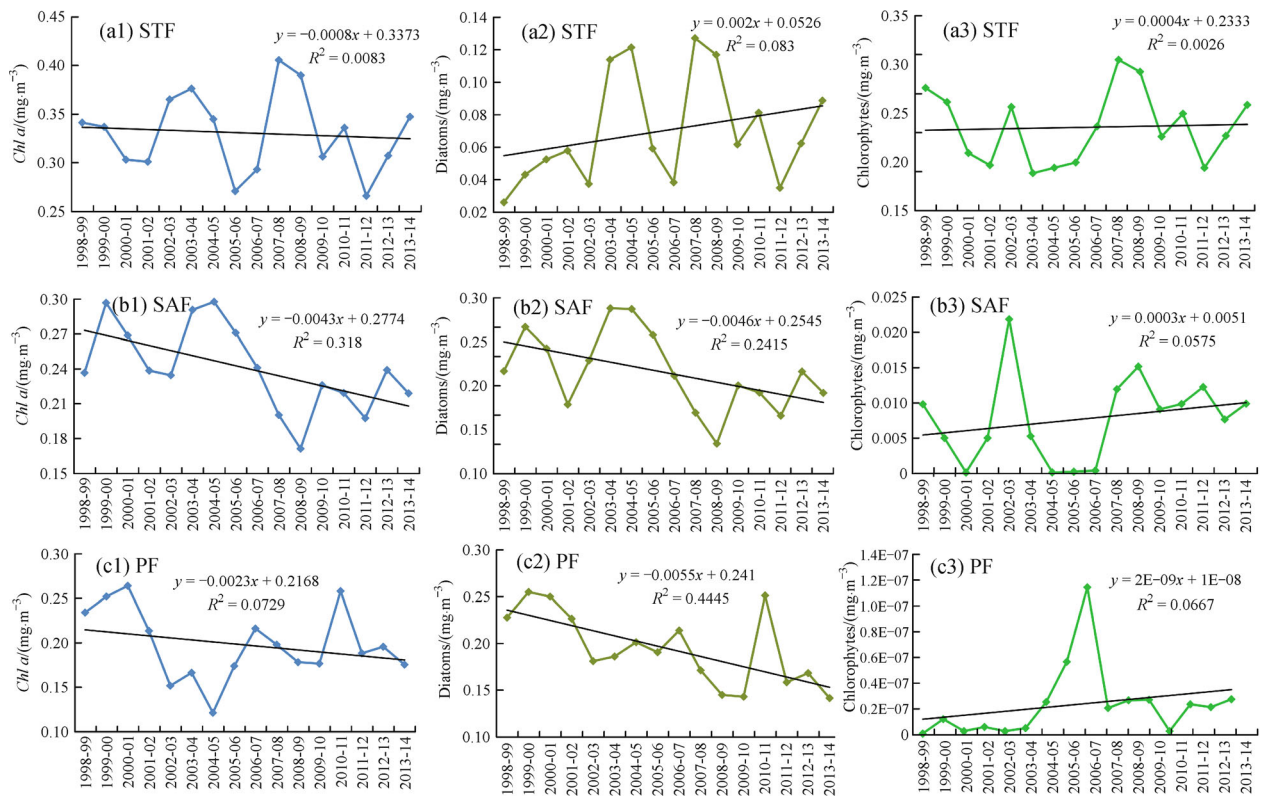


Fig. 4 Frontal variability and trends of *Chl a*, diatoms, and chlorophytes at the surface water of the Indian Ocean sector of the SO during austral summer (1998–2014).

at the STF and PF regions. The higher abundance of chlorophytes at STF could be linked to the preferential temperature for their growth since, adaptations of chlorophytes were elevated for optimal growth when the temperature reaches 15°C (Bischoff and Wiencke, 1995), and in the present study the temperature of the STF ranges between 16°C to 18°C (Fig. 5). Hence, it is in agreement with the observations made by Bischoff and Wiencke (1995). In other words, the poor cold adaptations mechanism of chlorophytes is the reason for its lower abundance at PF (Fig. 7(c2)) and it increased progressively when the temperature rose between 7°C and 10°C as seen in (Fig. 7(b2)). Probably this could be one of the reasons for shifting of chlorophytes from PF to SAF and STF.

The effect of light could be another factor for a lower abundance of chlorophytes that decreases from STF to PF. The present observation on PAR indicates the decreasing trend from STF to PF (Fig. 5) and light limitation can restrict the utilization of the nutrient available in the surface water (de Baar et al., 2005). However, under the lower light intensities, the diatoms' growth and survival enhances the light harvesting pigments. In addition to this, it has been described that the Oceanic diatoms have much lower concentrations of iron rich photosynthetic apparatus (Strzepek and Harrison, 2004). This leads to the interplay of light and iron by diatoms as the co-limits for the growth.

This result is consistent with the study at the PF (Figs. 4 and 5) in the Indian Ocean sector of the SO.

The diatoms trend does not follow the trend of *Chl a* and PAR from STF to PF. But the chlorophytes follow the trend of *Chl a* and PAR that decreases from STF to PF (Fig. 6). This indicates that chlorophytes decreased with the decrease of PAR from STF to PF with falling of 6 units and 10 units $E \cdot m^{-2} \cdot d^{-1}$ from STF to SAF and PF respectively. In addition, the results confirm that chlorophytes adaptation was with warmer temperature and diatoms adaptation was with colder temperature. However, it is not always true that the diatoms of micro plankton can adapt to low temperature at any polar region. As it has been observed that under the low temperature requirements the micro algae growth and survival is well in the Southern Hemisphere, particularly in sub-tidal endemic Antarctic and cold adapted species. In contrast, in the Arctic region the adaptations to low temperature are much less pronounced in endemic Arctic algae (Wiencke and tom Dieck, 1989). The reason for cold adaptation depends on the geological time span of exposure to low temperature and that adaptation regulates the growth and survival (Wiencke et al., 1994). In the study site, the results reflect the adaptations of chlorophytes and diatoms over the 16 years time period with respect to various temperatures. The same has been studied on polar algae, which describes as a

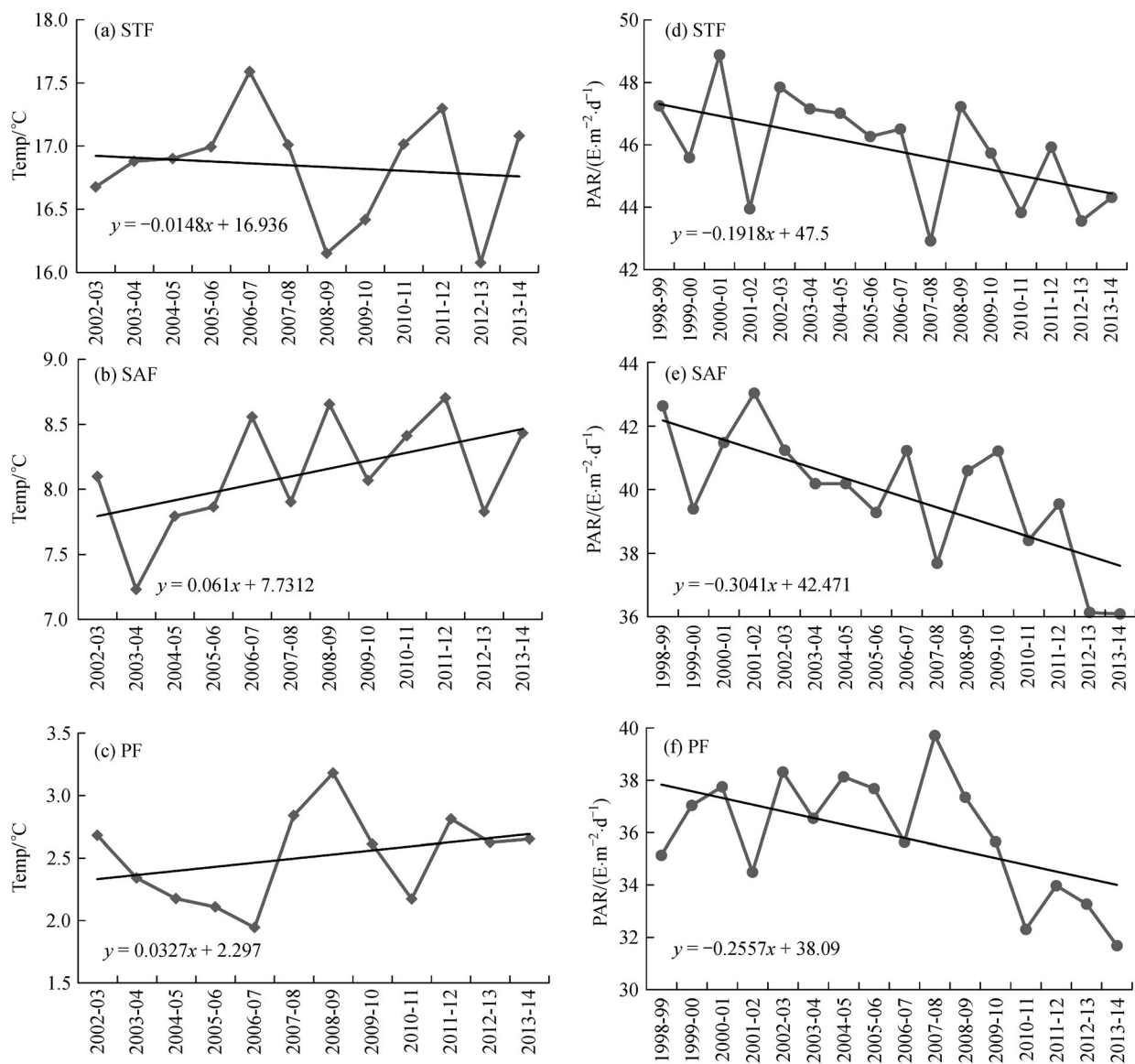


Fig. 5 The variability and trend of SST and PAR at different frontal regions (a,d) STF, (b,e) SAF, and (c,f) PF during austral summer (1998–2014).

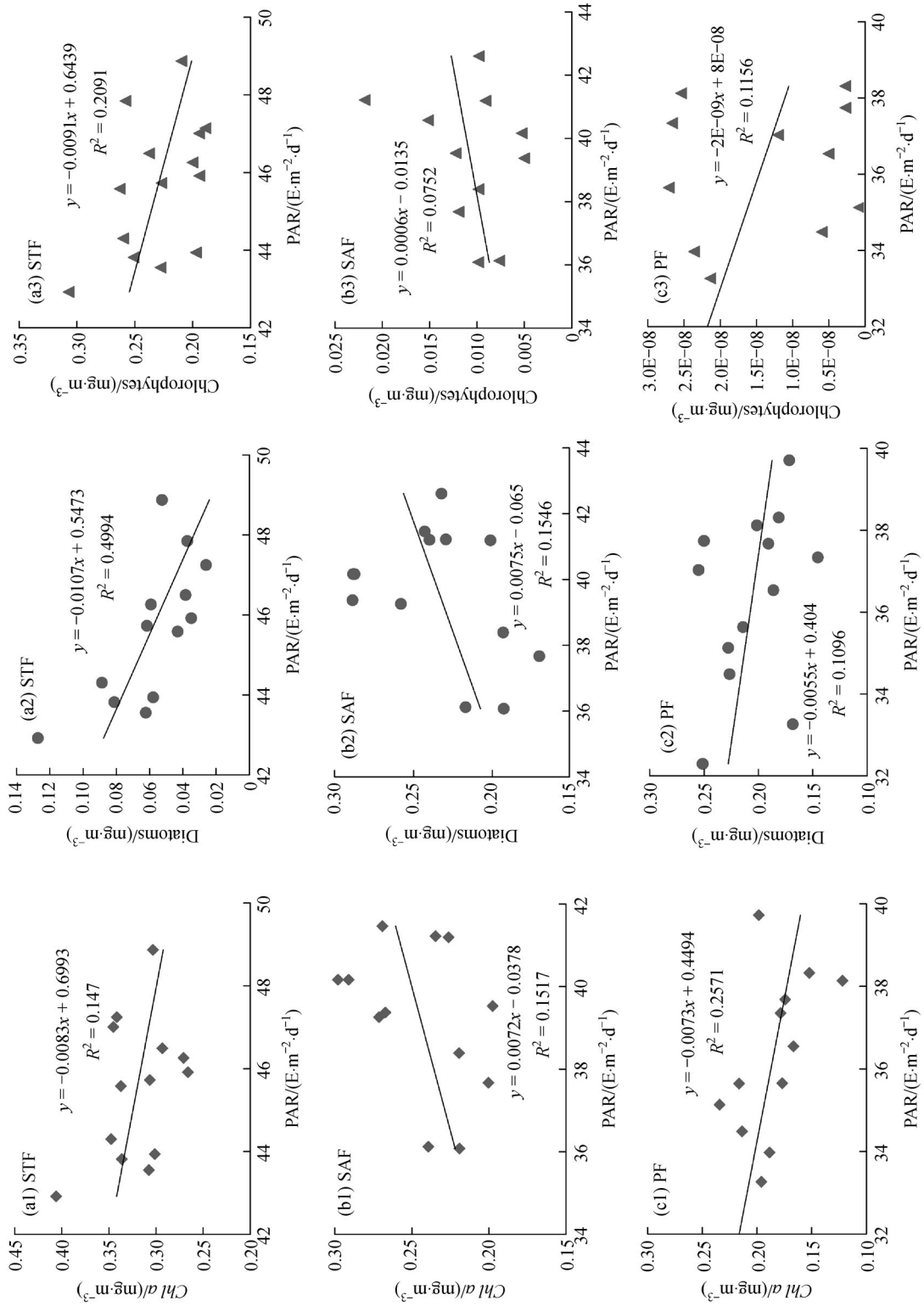


Fig. 6 Linear relationship between PAR, *Chl a*, diatoms, and chlorophytes during austral summer (1998-2014) at the STF (a1-a3), SAF (b1-b3), and PF (c1-c3).

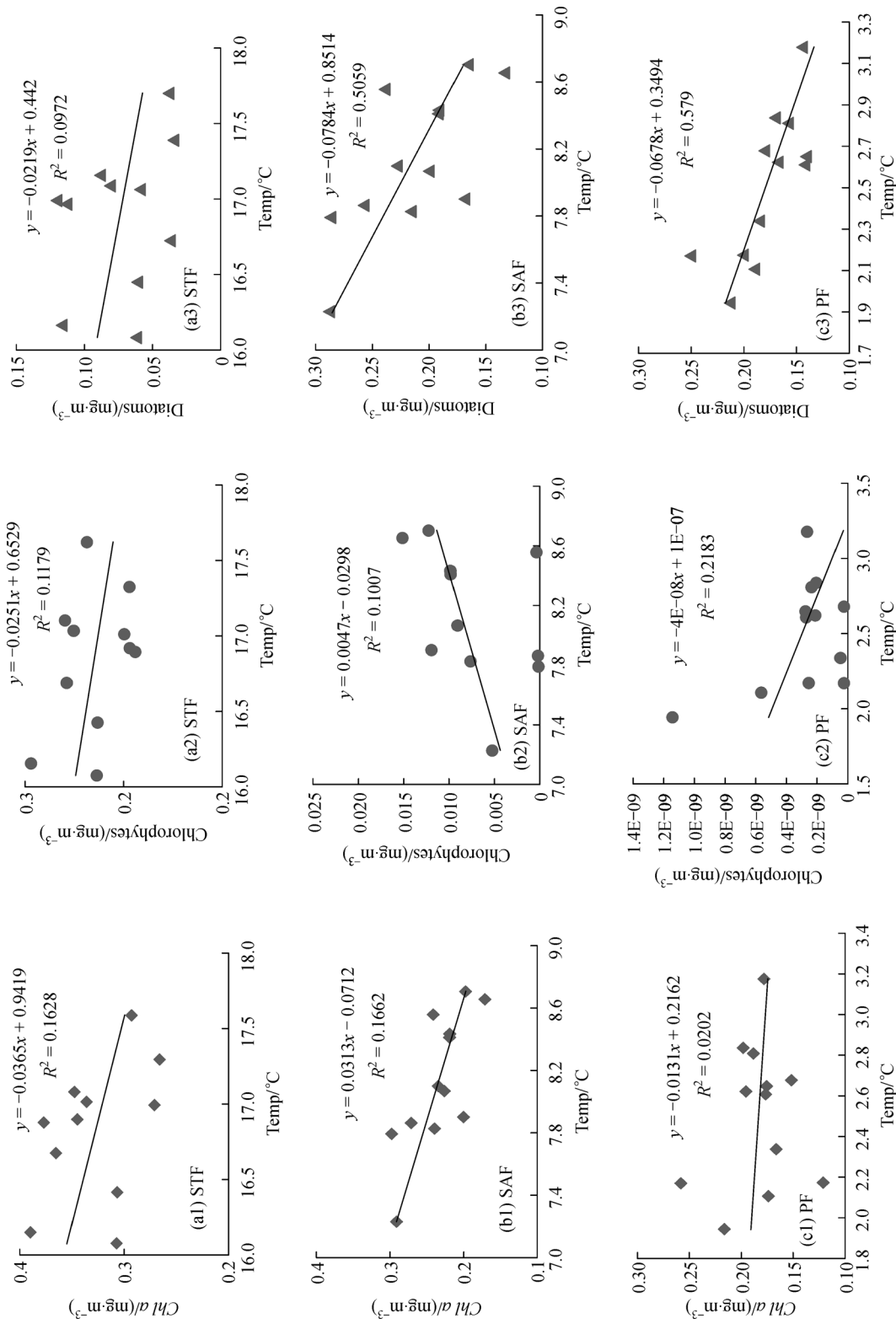


Fig. 7 Linear relationship between temperature, *Chl a*, diatoms, and chlorophytes during austral summer (1998–2014) at the STF (a1–a3), SAF (b1–b3), and PF (c1–c3).

high plasticity in regards to the adaptation of communities and inorganic carbon uptake (Neven et al., 2011) in the Indian sector of the SO.

5 Conclusions

The diatoms community in the SO was adapted to a wide range of temperature at various frontal regions, the maximum being at the PF of the SO, indicating the mechanism of cold adaptation. On the other hand, the chlorophytes' growth was restricted at the PF due to lack of cold adapted species. Hence, their trend in abundance decreased with the lowering of temperature while diatoms showed increased trend with lowering temperature from moderate to low magnitudes. Light was found to be another influential parameter for the growth of both chlorophytes and diatoms; however, it was more influential on the chlorophytes. However, the species specific community adaptation mechanism under various light and temperature conditions needs to be further studied by conducting laboratory experiments so as to understand the frontal specific biogeochemistry of the Indian Ocean sector of the SO. In addition, it will be necessary to investigate whether the trends of biological variability observed in satellite datasets and modeling output are a direct consequence of climate change or just a manifestation of the natural oscillation of the climate system (Jena et al., 2013).

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