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Distribution and drivers of phytoplankton biomass along the Saya de Malha Bank in the Western Indian Ocean

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ABSTRACT

The Saya de Malha bank found in the Western Indian Ocean is known as a key biodiversity area with high productivity. In-situ data, however, is characterised by paucity, therefore the Indian Ocean 2022 mission of the Monaco Explorations provided an opportunity to assess the productivity and investigate the major drivers of the phytoplankton community across this bank. The main findings on phytoplankton indicated a well-mixed water column across the bank, with some spatial differences observed in total chlorophyll-a, and the relative abundance of the pico-, nano- and microplankton. Based on the total chlorophyll-a, higher pelagic productivity was found on the shelf in the north-eastern section of the bank, decreasing towards the south. Size distribution of phytoplankton biomass indicated that the communities of the bank were dominated by pico-phytoplankton (~46 %), and that highest relative abundance of this group was encountered in the surface waters. Conversely, the micro-phytoplankton had low relative abundance in the surface water (~13 % at <60 m), increasing towards deeper waters (~36 % at >60 m). Comparison of the phytoplankton biomass with Acoustic Doppler Current Profiler (ADCP) data obtained during this expedition shows a strong alignment between maximum biomass and dominant current velocities at 30 m depth across the bank, and therefore can be used to inform the likely export patterns of biomass towards the rest of the Western Indian Ocean and the contribution of the Saya de Malha bank as a carbon sink and a carbon exporter to the rest of the pelagic trophic web in the region.

1. Introduction

The Mascarene Plateau, situated between Mauritius and Seychelles, is a submerged volcanic plateau characterised by four banks ranging from 20 to 350 m in depth and separated by deep ridges and channels (>2000 m, New et al., 2005), and extends for 230 km and 290 km along its west-east and north-south axes, respectively (Betzler et al., 2021). It is a unique feature in the Southern Indian Ocean associated with high productivity in what is otherwise considered oligotrophic waters. The steep slopes of these banks are associated with upwelling of deep, cold, nutrient rich waters (Hilbertz et al., 2002) that drive higher productivity in this region. Furthermore, the Mascarene Plateau forms a barrier for the westwards moving South Equatorial Current (SEC), resulting in upwelling along the eastern edge of the plateau, and elevated nutrient

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concentrations, higher chlorophyll biomass and secondary production (New et al., 2005, 2013; Bhagooli and Kaullysing, 2019). With these changes in circulation, it is plausible that biological productivity may also be influenced. Indeed, in the subtropical South China Sea, Li et al. (2018) and Shih et al. (2020) found similar patterns of biological enrichment due to internal waves and bathymetry that sustained high primary productivity and phytoplankton biomass. It was also noted by Burnett et al. (2001) that the Saya de Malha bank is particularly rich in primary productivity mainly through extensive seagrass meadows that cover approximately 80–90 % of the shallow surfaces of the bank due to steep slopes facilitating an influx of colder nutrient-rich water from the Southern Ocean via eddy formations and upwelling.

Ocean colour data from 1998 to 2010 shows strong seasonal (monsoonal) changes in chlorophyll-a concentrations along the plateaus, indicating biological enrichment which may drive megafauna such as whales visiting these waters for breeding and feeding (Branch et al., 2007; Bergstad et al., 2021). According to Dennett et al. (1999) and Garrison et al. (2000), there is a vast amount of evidence to support carbon export from ocean systems via food web structures, most facilitated through the primary productivity of phytoplankton. Preliminary observational data in 2020 and 2021 by Florida International University and the University of Seychelles have recorded over 20 species of cetacean (in 29 days) along the eastern boundary of the Seychelles Plateau that included Bryde's whales (*Balaenoptera edeni*), Blue whales (*B. musculus*), Sei whales (*B. borealis*), pygmy Killer whales (*Feresa attenuata*), and Sperm whales (*Physeter macrocephalus*), together with short-fined pilot whales and 6 species of dolphin (some pods of >400 individuals). Tagging experiments provided evidence of movements of humpback whales from Reunion Island towards the western edge of the Southern Mascarene shelf and Nazareth plateau (Dulau et al., 2017). The carbon export, however, is often regulated by particle size fluxes (i.e., phytoplankton size ranges; Suess, 1980) and community structure (i.e., functional groups; Garrison et al., 2000) together with bathymetry and/or depth (Tremblay et al., 1997).

For the Saya de Malha bank, past chlorophyll concentrations do appear to remain similar (~0.16 μg l^{-1}) throughout seasons (Vianello, 2015), with the exception of the 2008 ASCLME cruise when the lowest concentrations were recorded amongst the banks (<0.07 μg l^{-1}) due to downwelling at that time (October 2008). It must, however, be noted that data in this region is limited with incomplete understanding of physical (i.e., currents, heat transfer), chemical (pH, dissolved oxygen) and biological (i.e., phytoplankton, neuston, zooplankton & coral reef interactions) processes dominating the ecology of the Mascarene Plateau (ASCLME, 2008). Past surveys of the Saya de Malha bank include mainly hydrographic surveys (1838: British Royal Navy, 1960–1989: Russia fishing expeditions, 2002: RRS Charles Darwin, New et al., 2005; ASCLME, 2018: Nansen), limited coral mapping (1997, 2002 by Global Coral Reef Alliance), benthic mapping (2018: Nansen, Ramah et al., 2021), zooplankton investigation (2000–2003: UK Royal Geographic Society), preliminary micro-phytoplankton studies (May 2018: Nansen, Soondur et al., 2021), chemical (May 2018: Nansen, Audit-Manna et al., 2021) and biological oceanography (2008: ASCLME), seismic and physical oceanography (2019: RV Sonne Cruise SO270), and cetacean observations (2021: Greenpeace).

Despite these past surveys, data on the region is limited, especially when compared to other major ocean basins such as the Atlantic and Pacific (Demopoulos et al., 2003). In 2022, the Monaco Explorations mission of the Indian Ocean focused on the Saya de Malha bank within the Mascarene Plateau to assess the benthic biodiversity of this important and key biodiversity area. The expedition furthermore included basic oceanographic surveys (temperature, pH, dissolved oxygen, salinity, density, nutrients) and the collection of phytoplankton biomass and size fractionation (i.e., pico- nano- or micro-plankton). Understanding these components of the open ocean is important as phytoplankton form the basis of the pelagic food web, and considering the uniqueness of the Saya de Malha bank, will assist in understanding the physical, chemical and biological drivers for this region high in biodiversity and productivity.

2. Methodology

2.1. Study site

The expedition was conducted from 30 October to November 21, 2022 (inter-monsoonal period) departing from Victoria, Seychelles towards Port Louis, Mauritius onboard the South African polar research vessel, R/V Agulhas II. Based on bathymetry data from the May 2018 Nansen cruise across the Saya de Malha bank, sites were selected for CTD (conductivity, temperature and depth, Sea-Bird 911+V2 system) deployment to represent deep water (>1000 m), shelf/ridge (steep sloped) and shallow water/bank (<60 m) areas along the north-south and east-west axes of the bank (Fig. 1). Due to the large size of the area (~40 000 km^2) and limited time (2 weeks), full coverage of the bank was not possible and consequently five areas were selected during the preparatory phase based on the diversity of the sediments that were described by previous cruises (i.e. Boxes 1 to 5).

A hull-mounted Acoustic Doppler Current Profiler (ADCP, RD Instruments) was operated continuously along the survey transit at a frequency of 75 kHz with an 8m vertical resolution and maximum operational depth of 800m.

2.2. Phytoplankton biomass

Phytoplankton biomass was accessed based on the total chlorophyll-a content of seawater samples collected from the upper 200 m of water column using 12 L Niskin bottles attached to a 24-holder CTD-rosette. Samples were taken based on the fluorescence maximum (F_{max}) depth measured by the CTD fluorescence sensor, and generally included a surface (<5 m), 40 m, 60 m, 80 m, 100 m, and 150 m/200 m depths. From all corresponding Niskin bottles, 1 L of water was collected and filtered through Fisherbrand MF300 glass fibre filters (25 mm diameter, 0.7 μm pore) under gentle vacuum. Filters were immediately placed in 6 mL of 90 % Acetone for chlorophyll-a extraction and stored at +4 °C for 24 h. The fluorescence was then read on a Turner-Designs Trilogy Laboratory fluorometer, calibrated prior for the non-acidification measurement of chlorophyll-a. For each batch, both the solid standard and a blank containing only 90 % Acetone were measured prior to measuring of samples.

For size fractionated chlorophyll-a, 250 mL seawater was sequentially gravity filtered through 20 μm, 2 μm and 0.2 μm 47 mm Nuclepore filters, and all filters placed in 6 mL of 90 % Acetone for extraction.

Total chlorophyll-a was calculated following the equation of Welschmeyer (1994);

$$\text{Chl-a } (mg.m^{-3}) = DF \text{ x R-reading x } (FR_s - FR_b) \text{ x } (Vol_a - Vol_s)$$

Where DF = Dilution factor; R-reading = R-adjusted reading based on calibrated solid standard and batch solid standard reading; FR_s = Fluorometer reading of sample; FR_b = Fluorometer reading of blank; Vol_a = Volume of acetone used for extraction (mL); and Vol_s = Volume of sample filtered (mL).

The total Chl-a concentration was used to assess the calibration of the fluorescence sensor of the CTD while the size fractionated Chl-a was used as an index of the proportion of micro-, nano- and picoplankton.

Nutrient samples were collected at the same depths during CTD deployment, and pasteurized on-board at 80 °C for 2–3 h and stored at room temperature in the dark until analysed at the Chemical Laboratories of the IRD in Brest following the method of Aminot and Kerouel (2000) and the use of an AAIII auto-analyser.

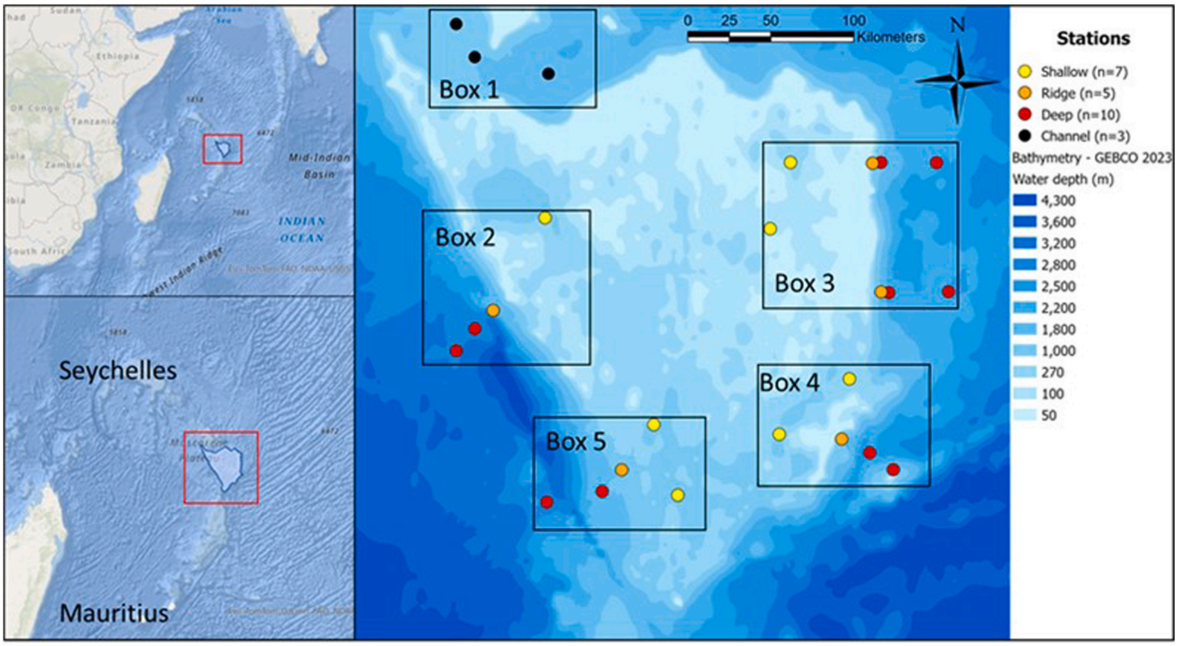

Fig. 1. Study area map indicating the 25 CTD deployments during the 2022 Monaco Expedition (Esri, 2023 ArcGIS Pro 7 GEBCO Compilation Group, 2023 Bathymetry data).

2.3. Statistical analyses

Pairwise student t-tests and Pearson Product Moment Correlation analyses were performed on the chlorophyll-a data to determine; 1) significant differences with depth, 2) significant differences between day and night samples, 3) site positional differences in biomass and dominant size fractions, and 4) any correlations between total chlorophyll-a and dominant size fractions. Furthermore, one-way ANOVAs (Permanovas using Primer 7) were performed on the CTD data together with phytoplankton biomass and size-fractionated data to determine relationships between relative abundance and physico-chemical drivers (i.e., salinity, temperature, dissolved oxygen, density, nutrients). All nutrient data were log (V+1) transformed prior to normalising in order to conduct all analyses. Phytoplankton biomass and functional group abundance data were visualized using ArcGIS Pro 7 and applying kriging to model biomass distribution across the bank.

Table 1

Average environmental (CTD) and nutrient concentrations measured along the Saya de Malha bank (mean ± standard deviation; *p < 0.05 & lower than other sites; **p < 0.05 & higher than other sites).

CTD stations	Temp. (°C)	EC (mS.cm^{-1})	Salinity (PSU)	DO (mg.l^{-1})
Channel	21.2 ± 5.3*	49.7 ± 5.6*	35.3 ± 0.2	3.35 ± 0.9
Deep	23.3 ± 4.2	51.8 ± 4.5	35.3 ± 0.2	3.51 ± 0.2
Ridge	23.7 ± 3.6	52.5 ± 3.9	35.3 ± 0.2	3.54 ± 1.0
Shallow	24.7 ± 3.5	53.2 ± 3.8	35.3 ± 0.2	3.73 ± 1.0
Nutrients	**NO_2^- (µmol. l^{-1})**	**TOxN (µmol. l^{-1})**	**SRP (µmol. l^{-1})**	**Si (µmol. l^{-1})**
Channel	0.16 ± 0.2	10.68 ± 8.6**	0.81 ± 0.5**	9.7 ± 6.9**
Deep	0.21 ± 0.3	7.93 ± 8.9	0.67 ± 0.6	7.9 ± 6.7
Ridge	0.19 ± 0.2	7.02 ± 8.0	0.60 ± 0.5	7.2 ± 5.7
Shallow	0.14 ± 0.2	5.5 ± 8.2	0.52 ± 0.5	6.2 ± 6.1

3. Results & discussion

A total of 25 CTD deployments were successfully executed ranging in water depth from 60 m to 1993 m, and included 7 shallow stations, 5 stations on the ridge, 10 deep stations and 3 stations within the northern channel between Saya de Malha and Richie banks. Average measurements obtained from the CTD deployments across the channel, shallow, ridge and deep stations indicate that temperature and conductivity (EC) were significantly low at the channel stations (Student t-test, $p < 0.05$) and increased towards the shallow stations, while salinity remained constant across all sites. Nutrient concentrations (total oxidized nitrogen - TOxN, soluble reactive phosphorus - SRP, and silicate – Si) were significantly higher (Student t-test, $p < 0.05$) in the channel. Although not significant, shallow sites showed on average slightly elevated temperatures and dissolved oxygen concentrations, while nutrient levels were generally lower than sites located along the ridge or deeper sections (Table 1).

3.1. Currents

Based on θ-S analyses, there is a clear separation of water masses along the Saya de Malha bank with less saline waters encountered on the eastern compared to the western bank (Fig. 2), as well as between the northern and southern boundary channels of the bank. Overall, the pycnocline/thermocline ranged between 80 and 100 m across the bank. ADCP current data collected underway indicate that the westward flowing South Equatorial Current (SEC) was well established at 30 m depth, with current velocities of up to 30 cm s^{-1} encountered over the bank, and of up to 63 cm s^{-1} along the slopes/ridges (Fig. 3). This data conforms to previous surveys and highlights the different water masses encountered at the Saya de Malha bank, i.e., intrusion of Arabian Sea High Salinity Water (ASHSW) and Antarctic Intermediate Water (AAIW, Beal et al., 2000; Tool and Warren, 1993) in the deep waters surrounding the bank, and surface waters dominated by the SEC carrying fresh Tropical Surface Water (TSW) and Indonesian Throughflow Water (ITW) to the bank (Vianello, 2015). Furthermore, Goes et al. (2005) highlighted the strong equatorial westerlies that dominate in the inter-monsoonal period (October–November) in the Southern Indian Ocean, which can be seen in Fig. 3, while New et al. (2007) reported SEC velocities of 30–70 cm s^{-1} for the bank.

3.2. Nutrients

Results of nutrient analyses indicate clear depth profiles whereby

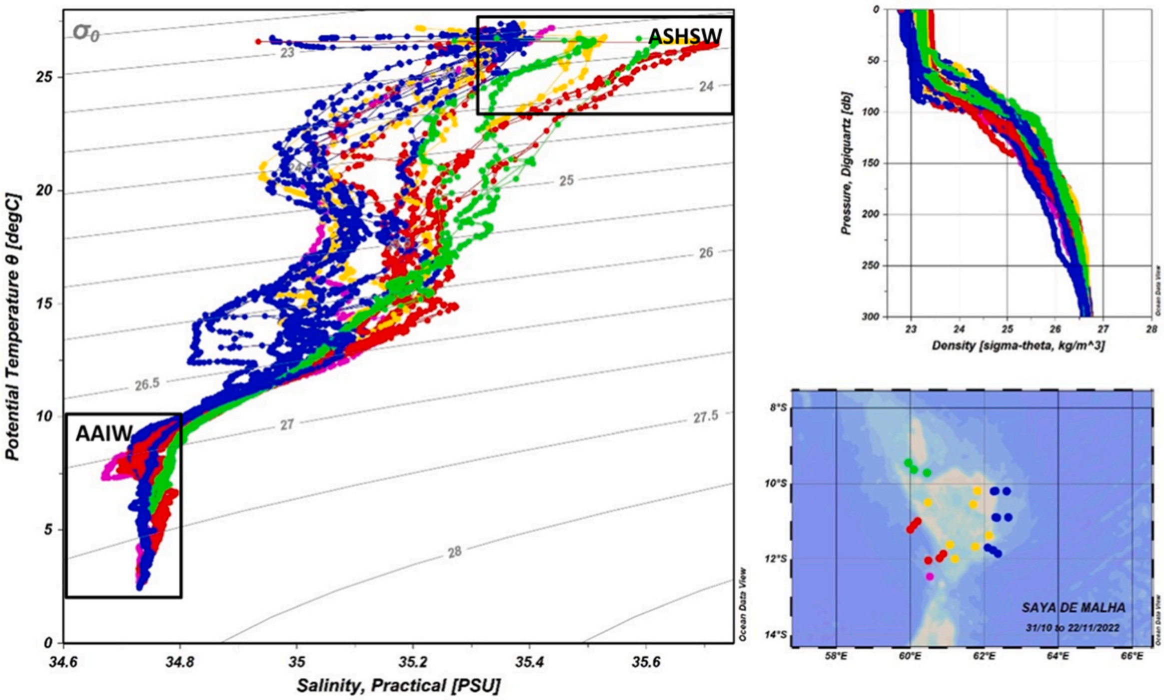

Fig. 2. T-S diagram of all CTD stations along the Saya de Malha bank indicating various water masses (blue: eastern bank; red: western bank; green: northern channel; yellow: Saya de Malha bank; pink: southern channel). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

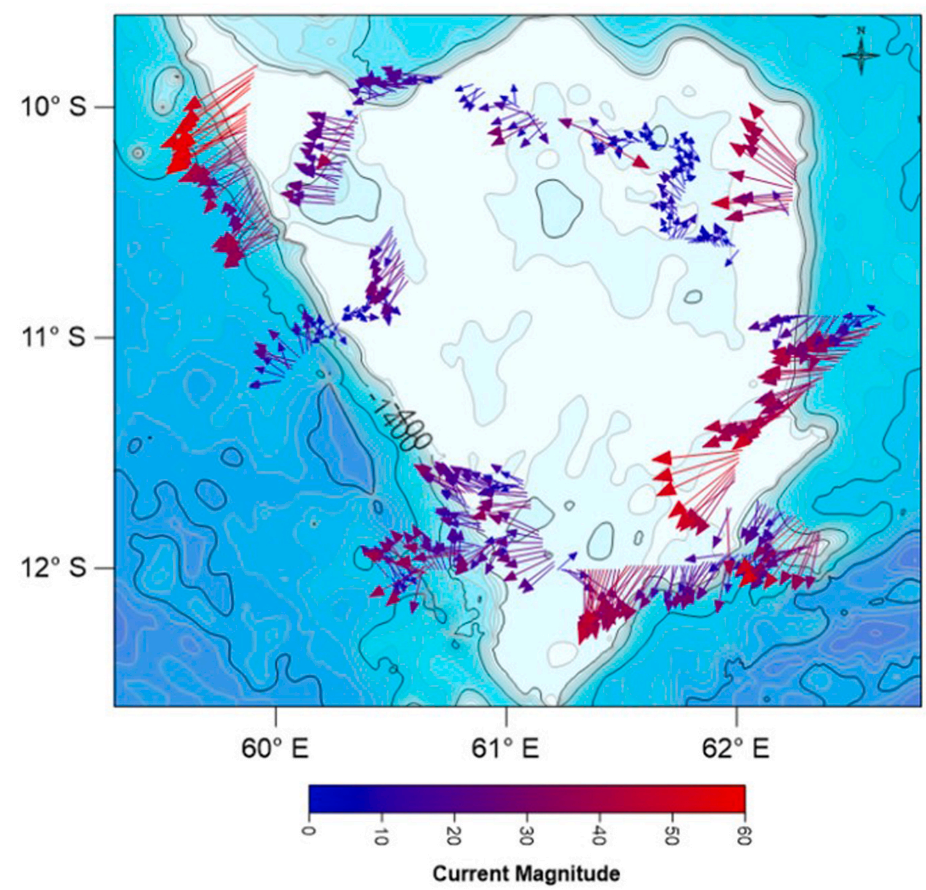

Fig. 3. Current velocity (cm.s^{-1}) and direction at 30 m depth measured by ADCP over the Saya de Malha bank (courtesy P. Coopen and Y. Oozeeraully, CSZMAE, Mauritius).

total oxidized nitrogen (TOxN), SRP and Si levels increased with depth, while concentrations in the surface water above the thermocline and F_{max} were significantly lower (Fig. 4). This conforms with the water masses for the Saya de Malha bank (Fig. 2) as deeper Arabian Sea High Salinity Water (ASHSW) are generally rich in nutrients (Vianello, 2015), and Sub-Tropical Surface Water (STSW) are generally nutrient poor. Similar patterns of vertical nutrient profiles are also reported by New et al. (2005) for the Mascarene Plateau, and by Betzler et al. (2021), especially in the area of the Saya de Malha bank (13°S). Average concentrations recorded were 37.65 μmol l^{-1}, 2.68 μmol l^{-1} and 114.1 μmol l^{-1} for TOxN, SRP and Si, respectively at depths exceeding 1000 m, and similar to previous surveys by New et al. (2005), Betzler et al. (2021) and Audit-Manna et al. (2021). The highest nitrite concentration, however, were encountered between 90 and 100 m (1.2 μmol l^{-1}), with significantly lower levels recorded at greater depth. As nitrite is an intermediate in the nitrogen cycle, its formation is facilitated by nitrite-oxidizing chemoautotrophs whose activity is dependent on dissolved oxygen levels and biological competition with photosynthetic autotrophs. Consequently, this group of microorganisms are generally excluded in the photic zone by phytoplankton but thrive below the photic zone where light limits phytoplankton productivity (Zakem et al., 2018). Although some spatial variability in nutrient concentrations could be observed across the Saya de Malha bank, these were found to be non-significant. Correlation analyses (Table 2) furthermore indicate strong relationships between nutrient levels (TOxN, SRP and Si) with depth, but negative correlations with temperature, conductivity and dissolved oxygen levels ($R > -0.7$).

3.3. Phytoplankton biomass & size distribution

Results of the chlorophyll-a extracted onboard indicate a maximum phytoplankton biomass between 60 and 80 m, corresponding to F_{max} recordings from the CTD (Fig. 5) and the position of thermocline/pycnocline across the bank (Fig. 2). The highest biomass was recorded in the shallow shelf areas, especially in the north-eastern section of the bank (Box 3) with a maximum concentration of 0.55 mg m^{-3} measured (Table 3). These results are similar to Audit-Manna et al. (2021) whom, recorded phytoplankton biomass (chlorophyll-a) at shallower site (<60 m) of the Saya de Malha bank at concentrations of 0.5 mg m^{-3} at 50 m, and for deeper sites (~1000 m) of 0.4 mg m^{-3}. In contrast, our results are much higher than the average chlorophyll-a biomass reported by Vianello (2015) for 1998–2010, where maximum biomass on the Saya de Malha bank only reached 0.18 mg m^{-3} during the same inter-monsoonal period. It should be noted that Vianello (2015) used remotely sensed ocean colour and the Globcolour Hermes (2014) database as his source for phytoplankton biomass data that may not truly reflect accurate *in-situ* biomass levels, and which generally only represents surface chlorophyll-a levels. Considering only surface chlorophyll-a, then this study compares well with the values reported by Vianello (2015), i.e., median of 0.18 ± 0.07 mg m^{-3}.

Correlation analyses between phytoplankton biomass (chlorophyll-a) and environmental drivers above and below the mixed layer depth (i.e., Fmax, Table 4) indicated that chlorophyll-a increased towards the MLD across the Bank with the exception of Box 1(Channel) where a weak, insignificant positive correlation was encountered ($r = 0.36$, $p = 0.3$). This may indicate a well-mixed water column within the Channel due to stronger and more turbulent bottom currents as observed from ACDP data (Fig. 3). Phytoplankton chlorophyll-a was also found to increased significantly towards the "nitracline" (Fig. 4) across Box 1, 2 and 4, and could indicate nutrient input from deeper water sustaining phytoplankton productivity in the photic zone. Especially for Box 4, situated on the south-eastern edge of the Bank, and which is exposed to the strong currents bringing nutrient-rich deep water from the Southern Ocean, this may indicate localized upwelling events. For Box 3, however, no significant correlations were found between phytoplankton chlorophyll-a and nutrients. This is most likely due to high uptake rates by phytoplankton and the incorporation of nutrient in biomass as evident by the high total chlorophyll-a concentrations recorded for this region of the Bank (Fig. 7). Box 5 (south-western edge) showed similar results with no significant correlations between chlorophyll-a and nutrient concentrations above the MLD. Again, higher uptake rates and incorporation into biomass could explain this observation. Interestingly,

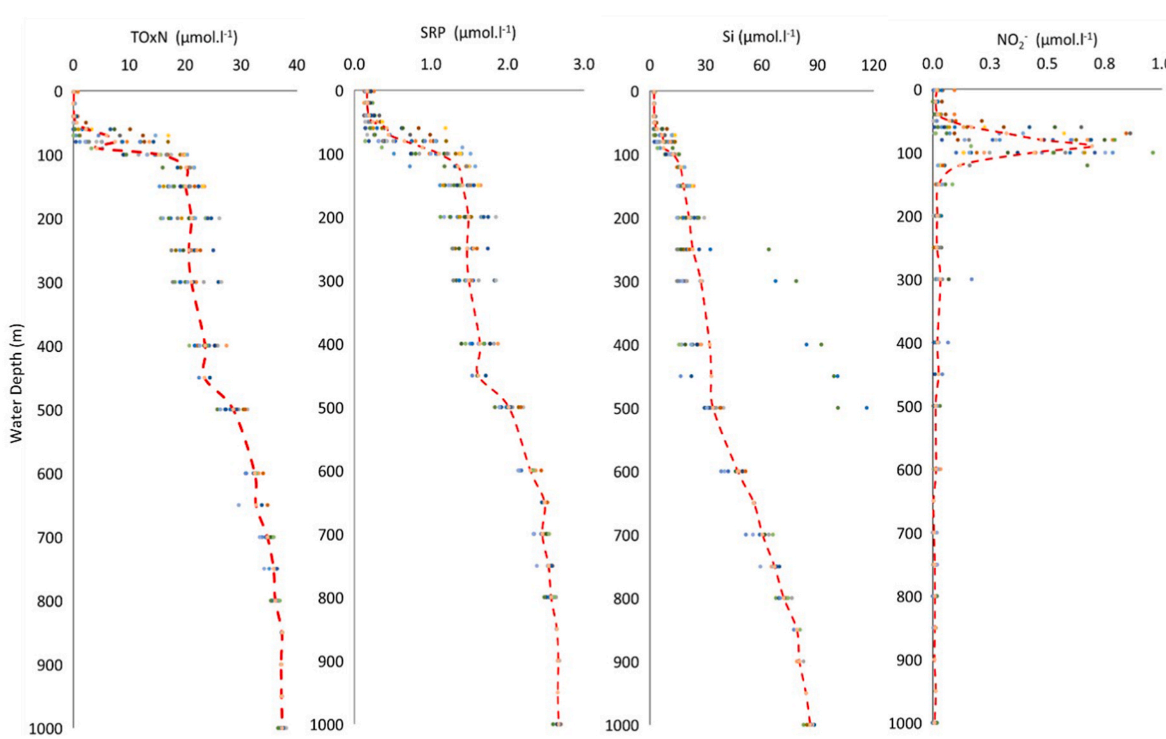

Fig. 4. Concentration of Total Oxidized Nitrogen (TOxN), Soluble Reactive Phosphate (SRP), Silicate (Si) and Nitrite (NO_2^-) along the Saya de Malha bank (Red line = overall average values). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Pearson Product Moment Correlation Matrix of overall environmental and phytoplankton biomass data for Saya de Malha during the 2022 Monaco Expedition (TOxN = total oxidized nitrogen; **BOLD** = correlations >0.6 and <-0.6).

	Station	Depth	Location	Temperature	E. Conductivity	Salinity	D. Oxygen	Nitrites	TOxN	SRP	Silicate
Depth	−0.06										
Location	−0.06	−0.10									
Temperature	0.12	**−0.91**	0.15								
E. Conductivity	0.09	**−0.91**	0.16	**1.00**							
Salinity	−0.42	**−0.60**	0.24	**0.68**	**0.72**						
D. Oxygen	0.03	**−0.67**	0.09	**0.87**	**0.88**	**0.72**					
Nitrites	0.00	0.17	0.04	−0.12	−0.14	−0.25	−0.25				
TOxN	−0.04	**0.84**	−0.12	**−0.95**	**−0.95**	**−0.74**	**−0.94**	0.29			
SRP	−0.07	**0.85**	−0.11	**−0.95**	**−0.95**	**−0.72**	**−0.93**	0.29	**1.00**		
Silicate	−0.07	**0.85**	−0.11	**−0.96**	**−0.96**	**−0.71**	**−0.92**	0.19	**0.99**	**0.99**	
Total Chl-a	0.10	−0.30	0.15	0.47	0.46	0.26	0.42	0.34	−0.37	−0.36	−0.44

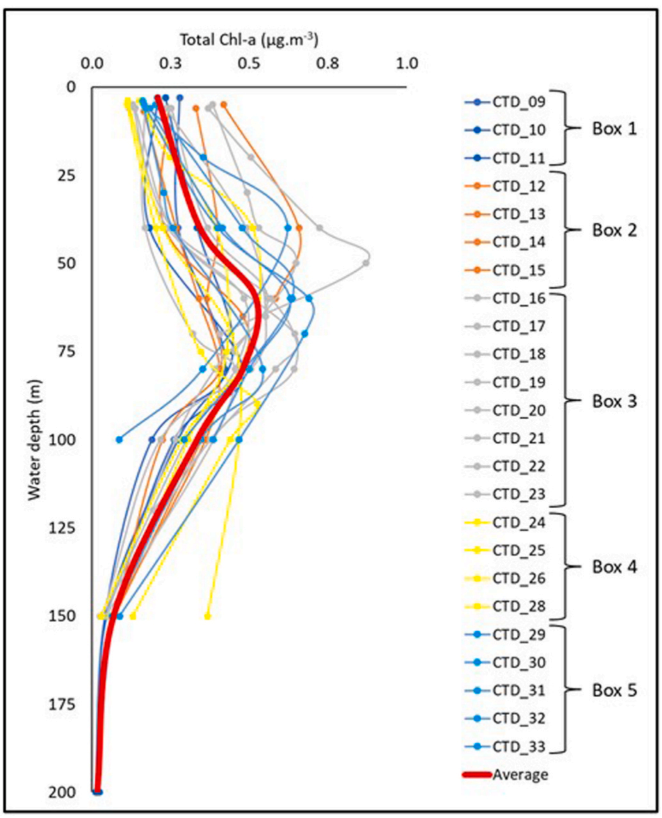

Fig. 5. Phytoplankton biomass (chl-a) measured along the Saya de Malha bank indicating vertical profile and maximum biomass.

nutrient levels below the MLD were found to significantly correlate with lower phytoplankton chlorophyll-a and may indicate the export of phytoplankton as particular organic matter (POC) to the deeper waters where light may limit productivity (Xing et al., 2020; Cornec et al., 2021).

Size distribution of phytoplankton biomass indicated that the communities of the Saya de Malha bank were dominated by the very small pico-plankton (~46 %), and that highest relative abundance was encountered in the surface waters and decreasing with depth(Table 3). The dominance of pico-plankton in tropical oligotrophic waters are well documented (Burkill et al., 1993; Chen, 2000; Richardson and Jackson, 2007; Maranón et al., 2001; 2012; Morán et al., 2010; Chen et al., 2021), with vertical segregation and accumulation in subsurface water attributed to environmental control factors such as higher water temperatures and photosynthetic radiation as well as nitrogen availability (Boyd et al., 2010; Chen et al., 2021). Tripathy et al. (2020) found similar time-series results for the South-Western Tropical Indian Ocean where strong

Table 3
Average total chlorophyll-a (mg.m^{-3}) and phytoplankton size distribution (% relative abundance) for the various sampling sites and habitat depths along the Saya de Malha bank (mean ± SD, **BOLD** = $p < 0.05$).

Area	Depth	Chl-a (mg. m^{-3})	<0.2 μm %	2 μm %	>20 μm %	n
Box 1	Channel	0.21 ± 0.15	47 ± 18	36 ± 12	17 ± 11	18
Box 2	Deep	0.29 ± 0.14	64 ± 15	29 ± 13	7 ± 5	12
	Ridge	0.30 ± 0.13	65 ± 11	26 ± 13	9 ± 11	6
	Shallow	**0.55 ± 0.12**	61 ± 16	**35 ± 15**	**4 ± 2**	3
Box 3	Deep	0.30 ± 0.19	43 ± 17	38 ± 12	19 ± 11	24
	Ridge	0.34 ± 0.19	41 ± 24	30 ± 16	29 ± 14	12
	Shallow	**0.54 ± 0.16**	50 ± 16	**42 ± 18**	**9 ± 9**	10
Box 4	Deep	0.26 ± 0.15	59 ± 16	27 ± 17	14 ± 8	12
	Ridge	0.29 ± 0.17	52 ± 11	39 ± 7	9 ± 7	6
	Shallow	0.27 ± 0.16	54 ± 20	31 ± 17	15 ± 12	12
Box 5	Deep	0.37 ± 0.2	47 ± 16	29 ± 10	24 ± 17	5
	Ridge	0.41 ± 0.25	52 ± 20	24 ± 15	23 ± 18	5
	Shallow	0.30 ± 0.19	45 ± 20	**31 ± 16**	24 ± 23	15

thermocline development during monsoonal periods resulted in limited vertical mixing and nutrient supply to the photic zone, and the shift of the phytoplankton communities towards the much smaller pico-plankton. -On the other hand, the larger micro-plankton had low relative abundance in the surface water (~13 %), increasing towards the deeper waters and toward the southern edge of the bank (~36 %; Table 3). This can be attributed due to the sinking of larger, ungrazed and generally heavier cells during the normal diel cycle encountered for especially diatoms and dinoflagellates that make up the bulk of micro-plankton in oceanic waters (Lampitt, 1985; Garrison et al., 2000). In addition, mixing related to the presence of internal wave in the deep layer in the south of the Saya de Malha bank (Coopen et al., 2021; New et al., 2013) might contribute to the increase of micro-plankton with depth. Xing et al. (2020) describes the process of "POC injection" whereby surface waters are subducted below the MLD by processes such as wind mixing and eddy formation, and POC are transported to deeper waters. Dennett et al. (1999) also reported that nano- and micro-plankton vertical distribution in the Arabian Sea was affected by the subsurface Oxygen Minimum Layer (OML), however, in this study the Oxygen Minimum Zone was generally found below 100 m and at ~75–100 μmol kg^{-1} with only a slight negative correlation between chlorophyll-a biomass and dissolved oxygen (R = −0.30, Table 3).

Although the phytoplankton results indicate a rather uniform water column across the Saya de Malha bank, some slight spatial differences could be observed in total chlorophyll-a, and the relative abundance of the pico-, nano- and micro-plankton along the west-east and north-south axes of the bank (Fig. 7). Interestingly, nano-plankton relative abundance at 80 m depth was found to correlate with average total chlorophyll-a distribution across the bank (Fig. 6 a and c). For the total chlorophyll-a, there appears to be higher pelagic productivity on the

Table 4
Pearson Product Moment correlations (r) between phytoplankton chlorophyll-a biomass and environmental variables for each Box site above and below the mixed layer depth (MLD) (**BOLD** = $p < 0.05$).

Chl - a vs:	Box 1		Box 2		Box 3		Box 4		Box 5	
	Above MLD	Below MDL	Above MLD	Below MDL	Above MLD	Below MDL	Above MLD	Below MDL	Above MLD	Below MDL
Depth	0,36	**−0,9**	**0,73**	**−0,84**	**0,4**	**−0,94**	**0,87**	**−0,65**	**0,79**	**−0,91**
Temperature	−0,51	**0,98**	−0,47	**0,96**	−0,12	**0,98**	**−0,59**	**0,91**	**−0,49**	**0,98**
E. Conductivity	−0,51	**0,97**	−0,51	**0,96**	−0,13	**0,98**	**−0,58**	**0,92**	**−0,47**	**0,97**
Salinity	−0,49	**0,78**	**−0,67**	**0,94**	−0,11	0,001	−0,34	0,44	−0,14	−0,14
D. Oxygen	−0,29	**0,55**	0,33	**0,98**	0,14	0,12	−0,32	0,5	**0,59**	**0,82**
NO2-	0,62	**0,9**	**0,6**	**0,97**	0,25	**0,79**	**0,6**	**0,72**	0,17	**0,89**
TOxN	**0,67**	**−0,96**	**0,58**	**−0,89**	0,18	−0,43	**0,56**	**−0,83**	0,19	**−0,82**
SRP	**0,71**	**−0,96**	**0,63**	**−0,89**	0,21	−0,45	**0,57**	**−0,84**	0,29	**−0,83**
Si	0,62	**−0,98**	**0,57**	**−0,91**	0,15	**−0,74**	**0,57**	**−0,88**	0,19	**−0,89**

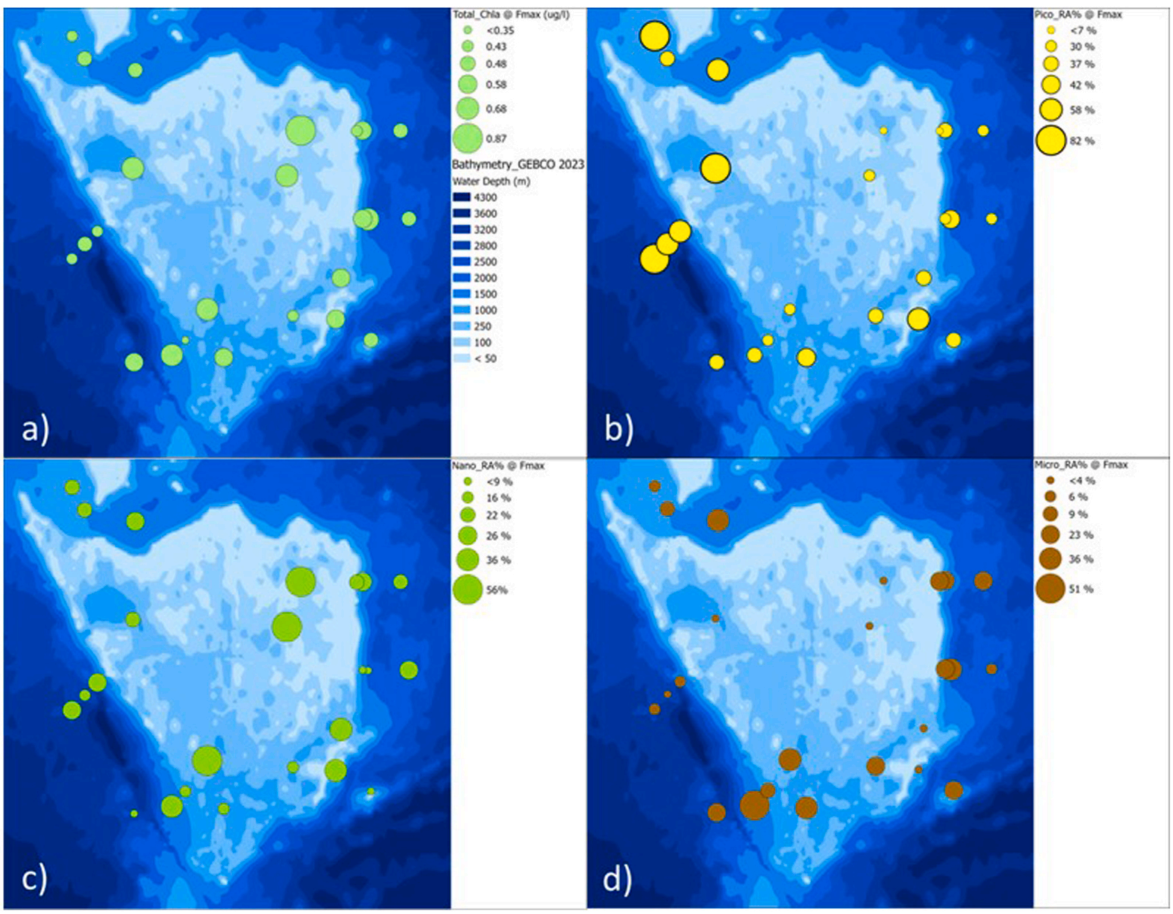

Fig. 6. Phytoplankton biomass distribution for a) average chlorophyll-a concentrations at 80 m, and size distribution across the Saya de Malha bank at 80 m depth for b) pico-plankton, c) nano-plankton, and d) micro-plankton relative abundance (%) (*Note various scale values for relative abundance between functional groups*).

shelf (shallow areas) in the northern section of the bank, decreasing towards the southern section, and is comparable with a similar pattern of biomass distribution (chlorophyll-a) as the 2008 ASCLME cruise along the Mascarene Plateau with a slight difference in maximum chlorophyll-a concentrations found though. This higher productivity could be related to the intrusion of nutrient rich ASHSW and the optimal cells size (surface area: volume ratio) of the plankton facilitating rapid nutrient uptake and growth rates. Comparing the phytoplankton biomass with ADCP and density (Fig. 7, Annex) data obtained during this expedition, also shows a strong pattern of maximum biomass distribution aligned with less dense water bodies on the eastern edge (Box 4) and boundaries of the bank, and dominant current velocities at 30 m depth across the bank, and therefore can be used to inform the likely export patterns of biomass towards the rest of the Western Indian Ocean and the contribution of the Saya de Malha bank to the rest of the pelagic trophic web in the region. Indeed, Vianello (2015) highlighted that phytoplankton biomass adjacent to the Saya de Malha bank showed great variability over time (and monsoonal season) related to the strength of these westerly currents and the south-north migration of the SEC exporting biomass and carbon from the bank. Furthermore, this study provides preliminary findings for the export of phytoplankton biomass (as POC) to the deep waters around the Saya de Malha where light may limit productivity. These exports (deposits) may potentially also provide nutrient-rich waters during seasonal upwelling events driven by monsoonal shifts in major ocean currents to the Bank and surrounding ocean.

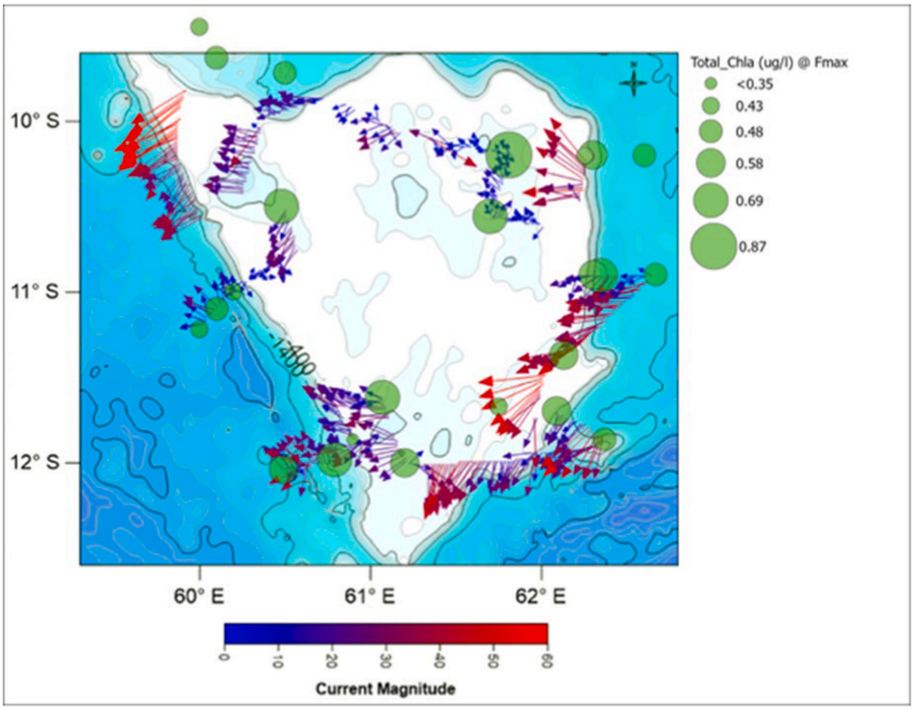

Fig. 7. Average phytoplankton biomass (chlorophyll-a) at 80 m depth superimposed on the ADCP vectors illustrating the alignment of biomass transport via SEC westerlies across the Saya de Malha.

4. Conclusions

The Saya de Malha bank is a key area for primary productivity in the Southern Indian Ocean that is vitally important for pelagic food webs in tropical oligotrophic waters and in maintaining the high biodiversity of this ocean region. This unique bank is subject to major ocean circulation patterns and its productivity is greatly influenced by the westward flow and north-south migration of the SEC that bring nutrient-rich bottom water to the surface along the eastern ridge of the bank. These currents across the bank impact the distribution of phytoplankton size classes, with cascading impacts to the food web and the export of biomass (carbon) to the rest of the Western Indian Ocean. The productivity of pico-plankton, the dominant size group found in this study, can be linked to inorganic nutrient supply and is comparable to various other studies globally. Furthermore, the dominance of larger sized plankton within the bottom waters may indicate the export of C-biomass and the recycling of nutrients to deeper water, thereby contributing to deep water productivity in what would otherwise be nutrient poor habitats. With further research required to investigate the top-down controls on phytoplankton for the Saya de Malha bank, important aspects of climate change impacts can be addressed for this region and the valuable role it plays in the Southern Indian Ocean.

CRediT authorship contribution statement

Nuette Gordon: Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Margaux Noyon:** Supervision, Resources, Methodology, Investigation. **Deepeeka Kaullysing:** Writing – review & editing. **Ranjeet Bhagooli:** Writing – review & editing. **Sundy Ramah:** Writing – review & editing. **Jean-Francois Ternon:** Writing – review & editing, Visualization, Supervision, Formal analysis, Data curation. **Bianca Marzocchi:** Writing – review & editing, Investigation. **Francis Marsac:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Nuette Gordon reports article publishing charges, equipment, drugs, or supplies, and travel were provided by Monaco Explorations. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Annex

Alignment of Phytoplankton Biomass and ADCP current profiles for Saya de Malha.

Data availability

The authors do not have permission to share data.

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