

New insights into the primary production and the structure of the phytoplankton community in the South Indian Ocean using size fractionation experiments

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Abstract. As part of the South Indian Ocean CARBOn fluxes from the surface to the mesopelagic twilight zone (SOCARB) project, the phytoplankton biomass and net primary production (NPP), along with the biomass of phytoplankton chemotaxonomic groups, were assessed ~~in contrasting biogeochemical areas of the South Indian and Southern Oceans in late austral summer 2023~~ **during late austral summer 2023 in contrasting biogeochemical areas: the oligotrophic subtropical waters of the South Indian Ocean, High Nutrient Low Chlorophyll (HNLC) waters, and the highly productive waters in the vicinity of Kerguelen Islands in the Southern Ocean.** A size fractionation approach was performed to characterize the size structure of primary production and phytoplankton chemotaxonomic groups biomass in three size classes: picophytoplankton (< 3 µm), nanophytoplankton (3–20 µm), and microphytoplankton (> 20 µm). Across the study area, NPP was dominated by microphytoplankton (56% ± 21%) while total chlorophyll *a* (TChl*a*) was sustained by nano- (40% ± 11%) and microphytoplankton (37% ± 18%), notably by nanophytoplankton haptophytes and microphytoplankton diatoms. Our results highlighted the spatial variability of NPP and TChl*a* size structures, mainly driven by temperature, ~~salinity~~ and macronutrients (N, P). In the Subtropical and Subantarctic zones, NPP ~~and TChl*a* were~~ **was dominated by nano- and microphytoplankton while TChl*a* was** sustained by pico- and nanophytoplankton with a diversified community (cyanobacteria, haptophytes, chlorophytes, pelagophytes). Conversely in the Polar Frontal and Antarctic zones, NPP and TChl*a* were dominated by nano- and microphytoplankton with a less diversified community (diatoms, haptophytes). **The coupling of pigment-based chemotaxonomy with size fractionation reveals new insights into the size-specific distribution of phytoplankton chemotaxonomic groups, challenging traditional functional type approaches on the bulk fraction and highlighting the presence of key groups such as diatoms and haptophytes across all three size classes.** Our results also underline the intra-zonal variability of NPP and TChl*a* through bottom-up processes, such as cyclonic eddy in the Subtropical zone or Si-depleted water mass intrusion in the Polar Frontal zone. Focusing on the links between NPP and TChl*a*

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size structure across the study area, NPP was mainly driven by the biomass of nano- and microphytoplankton, more specifically
35 by the biomass of nano- and microphytoplankton diatoms, haptophytes and dinoflagellates. This study paves the way for a
better understanding of phytoplankton productivity and community size structure, which could contribute to a more detailed
knowledge on their role in the biological carbon pump.

1 Introduction

One of the main challenges in marine biogeochemistry is to understand the impact of factors controlling the efficiency
40 of the soft tissue pump, or so-called “biological carbon pump” (BCP). Among these factors, the intensity of net primary
production (NPP) and the structure of phytoplankton communities are known to play key roles in biogeochemical fluxes
involved in the BCP and depend on the chemico-physical conditions of the ocean. More specifically, the taxonomic composition
and the size structure of phytoplankton communities can affect significantly the intensity and fate of NPP by controlling the
photosynthetic CO₂ uptake efficiency (*e.g.* Cermeño et al., 2005), the transfer of NPP through either microbial trophic pathway
45 or higher trophic levels (*e.g.* Marañón, 2009) and the carbon export and sequestration in the deep ocean (*e.g.* Guidi et al.,
2009). **For instance, phytoplankton communities dominated by large cells are expected to contribute greatly to organic
carbon export through their faster sinking velocity rates and more efficient transfer towards higher trophic levels
compared to phytoplankton communities dominated by smaller cells (Legendre and Le Fèvre 1989; Wassmann 1998).
Also, particulate organic carbon export may be enhanced when phytoplankton communities are dominated by**
50 **biomineralizing organisms, as mineral ballast increases particle sinking rates (Armstrong et al., 2001; Klaas and
Archer, 2002).** Therefore, considering phytoplankton as a single generic variable is ~~irrelevant~~ **insufficient** for fully
understanding the BCP. To tackle this issue, a common approach is to assess phytoplankton in size classes, either through size
fractionation experiments to quantify size structure and its associated fluxes such as NPP (*e.g.* Froneman et al., 2001; Marañón
et al., 2001) or from phytoplankton functional type approaches used to estimate phytoplankton size structure from bulk
55 measurements (*e.g.* Uitz et al., 2006; Hirata et al., 2011).

The South Indian Ocean (~~SIO~~), including the Indian sector of the Southern Ocean, is a unique oceanic region with
contrasting biogeochemical features. Since the first monitoring measurements of air-sea CO₂ fluxes in this region carried out
by Metzl et al. (1995), the Southern Ocean, south of the Subtropical Front (STF), is known to be a net CO₂ sink (Takahashi et
al., 2009; Hauck et al., 2023). It is characterized by High Nutrient Low Chlorophyll (HNLC) conditions, with low
60 phytoplankton biomass (< 0.5 mg m⁻³) despite high macronutrients concentrations (NO_x (NO₃⁻ + NO₂⁻) **and** dissolved
inorganic phosphorus (DIP)). This paradox is explained by limitations of the phytoplankton growth by micronutrients,
especially iron (Fe) (Martin, 1990; Martin et al., 1990) or manganese (Mn) (Browning et al., 2021; Hawco et al., 2022) and by
secondary limiting factors such as light, water column stability and grazing pressure (Moore and Abbott, 2000). Furthermore,
the Southern Ocean is characterized by the Antarctic Circumpolar Current (ACC), a massive eastward flowing current driven
65 by westerly winds, that divides the region into several hydrographic zones defined by specific water masses and fronts (Nowlin

and Klinck, 1986). The Antarctic Zone (AZ), south of the Polar Front (PF), exhibits typical HNLC conditions (Minas and Minas, 1992). The Polar Frontal Zone (PFZ), between the PF and the Subantarctic Front (SAF), and the Subantarctic Zone (SAZ), between the SAF and the STF, display high NO_x and DIP concentrations but low dissolved silicon (DSi) concentrations (usually < 5 μmol L⁻¹), **in contrast to HNLC waters of the AZ (usually > 20 μmol.L⁻¹)**, resulting in High Nutrient Low Silicon Low Chlorophyll (HN-LSi-LC) conditions (Nelson et al., 2001; Sarmiento et al., 2004). The STF delineates the boundary between the Southern Ocean and the Subtropical Zone (STZ) of the **SIO South Indian Ocean**, which is characterized by Low Nutrient Low Chlorophyll (LNLC) conditions (McClain et al., 2004) and acts as a CO₂ source during austral summer (Sarma et al., 2023).

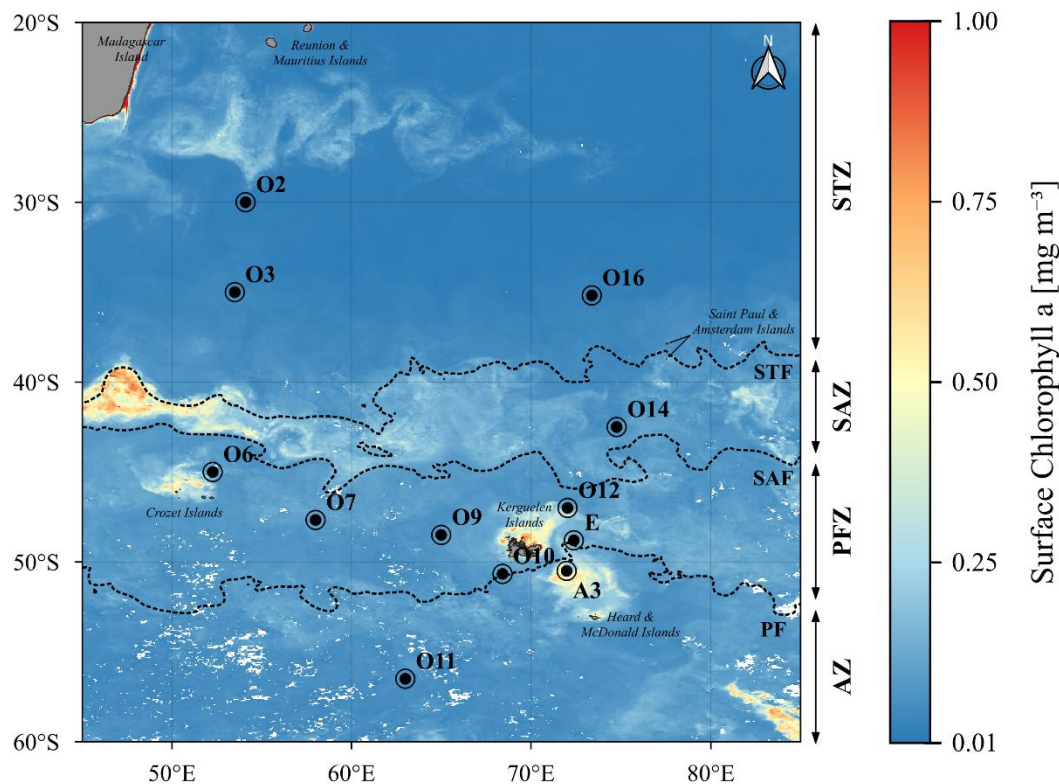
While the contrasting physical and biogeochemical regimes in the **SIO South Indian Ocean** exert a strong bottom-up control on phytoplankton biomass, composition and productivity (Hörstmann et al., 2021; Hayward et al., 2024), most of this knowledge is restricted to the ~~upper~~ surface layer. By contrast, much less is known about these phytoplankton characteristics ~~within~~ **throughout** the euphotic layer, especially as these features were mostly determined from bulk measurements. Moreover, previous field studies conducted in the **SIO South Indian Ocean** investigating phytoplankton composition and size structure within the euphotic layer have primarily focused on high productivity regions – *i.e.* areas in the vicinity of subantarctic islands – where enhanced surface NPP results from natural Fe fertilization (Blain et al., 2007; Pollard et al., 2009; Holmes et al., 2020) such as Crozet Islands (Seeyave et al., 2007), Kerguelen Islands (Uitz et al., 2009; Irion et al., 2020), **and** Heard and McDonald Islands (Wojtasiewicz et al., 2019). By contrast, the vast low productivity regions ~~of the~~ **SIO** with LNLC, HN-LSi-LC and HNLC conditions have received considerably less attention, despite covering the majority of the **SIO South Indian Ocean**. While some studies have provided relevant insights into phytoplankton biomass and composition in the upper water column using pigment chemotaxonomy tools (Schlüter et al., 2011; Mendes et al., 2015; Latasa et al., 2023), data remain scarce, particularly concerning NPP (Leblanc et al., 2002; Jasmine et al., 2009; Gandhi et al., 2012).

The SOCARB (South Indian Ocean CARBon fluxes from the surface to the mesopelagic twilight zone) cruise took place during the late austral summer of 2023. SOCARB aims to provide key metrics to characterize the BCP components and the associated fluxes of organic carbon, from the euphotic layer to the base of the mesopelagic zone in the **SIO South Indian Ocean**. SOCARB was implemented as part of the long-term monitoring program OISO (Océan Indien Service d'Observations), involved since 1998 in the long-term monitoring of oceanic CO₂ parameters in the **SIO South Indian Ocean** (Metzl and Lo Monaco, 1998; <https://doi.org/10.18142/228>). This opportunity allowed us to investigate phytoplankton NPP, biomass and community size structure, along with their respective size structures across contrasting biogeochemical regions of the **SIO South Indian Ocean**. The first objective was to describe the size structure (pico-, nano- and microphytoplankton) of (i) the net primary production, (ii) the phytoplankton biomass (total chlorophyll *a*) and (iii) the biomass of phytoplankton chemotaxonomic groups. The second objective was to assess their vertical and spatial variability in relation to the environmental conditions. The third objective was to determine whether NPP is determined by the size structure of the phytoplankton biomass and/or by the size structure of the biomass of specific phytoplankton chemotaxonomic groups.

2 Materials and Methods

100 2.1 Cruise transect – Sampling Strategy

Our study was part of the MD240 / OISO33-SOCARB cruise (Lo Monaco et al., 2023) on board the R/V *Marion Dufresne II*, conducted in the South Indian and Southern Oceans during austral summer, from January 23rd to February 28th,



2023. SOCARB experiments were conducted at twelve stations in contrasting biogeochemical regions (Fig. 1), including the oligotrophic subtropical gyre of the **SIØ South Indian Ocean** characterised by LNLC conditions, open ocean regions exhibiting HNLC or HN-LSi-LC characteristics, and bloom areas near Subantarctic islands such as the Crozet Islands and Kerguelen Plateau, both renowned for being naturally iron-fertilized regions (Blain et al., 2007; Pollard et al., 2009).

Figure 1: Map of the OISO33-SOCARB study area showing the location of the stations from this study, overlying the satellite-derived surface chlorophyll *a* concentration averaged over February 2023 (MODIS L3 product). The dotted lines indicate the positions of the main fronts determined from satellite-derived surface temperature averaged over February 2023 (CMEMS L4 product): STF, Subtropical Front (18 °C); SAF, Subantarctic Front (13 °C); PF, Polar Front (4.5 °C).

Seawater was collected using a CTD (Sea-Bird SBE 911 Plus) mounted on a rosette equipped with 24 Niskin bottles (12 L, General Oceanics, Inc.). Samples for phytoplankton primary production and pigments were collected at six depths, between the surface (~ 10 m) and 200 m maximum. Sampling depths were determined from the fluorescence downcast profiles

115 during the CTD measurements acquisition, to best describe the fluorescence profile and its gradients, such as subsurface chlorophyll maximum (SCM) (**Appendix A**).

2.2 Size fractionated primary production

All materials were acid-washed (HCl Suprapur 32%) following trace metal clean procedures (Cutter et al., 2017), and polycarbonate bottles were rinsed three times before sampling with the collected seawater. For NPP, 2.3 L of unfiltered
120 seawater was collected for the total fraction and 5.5 L for the size fractions. Prefiltration was performed using 20 and 3 μm filter cartridge (Sartorius) under pressurised filtration units. For each prefiltration, bottles were rinsed three times with the seawater filtrates, and 2.3 L of respectively $< 20 \mu\text{m}$ and $< 3 \mu\text{m}$ seawater filtrates were collected. This size fractionation approach enabled us to determine the contributions of the three phytoplankton size classes: picophytoplankton ($< 3 \mu\text{m}$), nanophytoplankton ($3\text{--}20 \mu\text{m}$), and microphytoplankton ($> 20 \mu\text{m}$) (Sieburth et al., 1978; Vaultot et al., 2008). NPP rates were
125 determined using the ^{13}C tracer addition method (Hama et al., 1983; Ridame et al., 2022) in the total, $< 20 \mu\text{m}$ and $< 3 \mu\text{m}$ fractions. After prefiltration, 1 mL of $\text{NaH}^{13}\text{CO}_3$ (99%; Eurisotop) was added to the bottles to obtain a final ^{13}C enrichment of $\sim 10\%$. Each bottle was ~~shaken vigorously~~ **thoroughly homogenized** before incubation for 24 h in on-deck containers with circulating seawater. To simulate an irradiance level as close as possible to the sampled depth, blue filters with several sets of blue neutral density filters were used (LEE Filters: 75, 54.4, 36, 19.3, 10.4, 5.6, 2.7 and 1% attenuation). After 24 h incubation,
130 2.3 L was vacuum filtered ($< 200 \text{ mbar}$) onto pre-combusted ($450 \text{ }^\circ\text{C}$) 25 mm GF/F filters (WhatmanTM glass microfiber) and stored at $-20 \text{ }^\circ\text{C}$. Filters were dried at $40 \text{ }^\circ\text{C}$ for 48 h before analysis at the Alysés analytical platform (IRD-SU, Bondy, France). In addition, 2.3 L of surface and SCM seawaters were immediately filtered after collection onto pre-combusted GF/F filters to determine natural concentration and isotopic signature of particulate organic carbon (POC). POC and ^{13}C isotopic ratio were quantified using an online continuous flow elemental analyser (EA, Thermo Fisher Scientific Inc. Flash 2000 HT) coupled
135 with an isotopic ratio mass spectrometer (IRMS, Thermo Fisher Scientific Inc. Delta V Advantage via a ConFlow IV interface). For each sample, POC was higher than the experimental detection limit of $0.42 \mu\text{mol C}$, defined as three times the standard deviation of the blanks. The mean natural ^{13}C signature was $1.081 \pm 0.002 \text{ atom}\%$ ($n = 24$), with no significant differences between surface and SCM values (Student test: $t = -0.1491$, $p = 0.88$). The atom% excess of the dissolved inorganic carbon (DIC) was calculated by using DIC concentrations measured at the SNAPO- CO_2 analytical platform (LOCEAN-IPSL, Paris,
140 France, Metzl et al., 2025). **Volumetric NPP is expressed as a flux in $\text{mgC m}^{-3} \text{ d}^{-1}$.**

2.3 Size fractionated phytoplankton pigments

The size fractionation filtration procedure was the same as described for the NPP (see section 2.2). For pigments, 2.3 L of unfiltered seawater was directly filtered onto GF/F filters for the total fraction, and 3.5 L of $< 20 \mu\text{m}$ and $< 3 \mu\text{m}$ seawater filtrates were filtered onto GF/F filters. The filters were placed in cryotubes, flash-frozen in liquid nitrogen and stored at -80
145 $^\circ\text{C}$ until analysis at the SAPIGH analytical platform (IMEV, Villefranche-sur-Mer, France). Filters were extracted during 2 hours in 3 mL HPLC-grade methanol (100%) containing an internal standard (Vitamin E acetate, Sigma), sonicated once and

then clarified by vacuum filtration through GF/F filters. Extracts analysis was carried out within 24 h after extraction using an Agilent Technologies Inc. 1200 series HPLC system. The general procedure for HPLC pigment analysis, identification and quantification is described in Ras et al. (2008). **Volumetric pigment concentrations are expressed as stocks in mg m⁻³**. This method allows the detection of 26 separate pigments with low detection limits (≤ 0.0002 mg m⁻³). Pigments include chlorophyll *a* (Chl*a*) and divinyl-chlorophyll *a* (DVChl*a*), whose sum of the concentrations is referred to as total chlorophyll *a* (TChl*a*), an indicator of the phytoplankton biomass. Pigments also include various accessory pigments, some of which can be used as biomarkers of phytoplankton taxonomic groups (Higgins et al., 2011). In this study, the following eleven accessory pigments were further used to study the TChl*a* biomass of the phytoplankton chemotaxonomic groups: fucoxanthin (Fuco), peridinin (Peri), 19'-hexanoyloxyfucoxanthin (Hex-fuco), 19'-butanoyloxyfucoxanthin (But-fuco), alloxanthin (Allo), chlorophyll *b* (Chl*b*), zeaxanthin (Zea), neoxanthin (Neo), ~~prasinolaxanthin (Pras)~~ **lutein (Lut)**, violaxanthin (Viola), and DVChl*a*.

2.4 Biomass of the phytoplankton chemotaxonomic groups

To estimate the Chl*a* biomass of different phytoplankton chemotaxonomic groups from pigment concentrations measured in the sizes classes, we used the open-source R package `phytclass` (v.2.0.0; <https://cran.r-project.org/package=phytclass>), following the procedure described in Hayward et al. (2023). Compared to the commonly used CHEMTAX algorithm (Mackey et al., 1996), the `phytclass` algorithm improves the accuracy of the phytoplankton group biomass estimates, and removes the need for initial assumptions about their pigment:Chl*a* ratios (Hayward et al., 2023). Briefly, datasets were first clustered based on their pigment:Chl*a* ratios, then loaded into `phytclass` set with an iteration of 500, a step of 0.009 and 7 phytoplankton chemotaxonomic groups: diatoms, haptophytes, cryptophytes, dinoflagellates, chlorophytes, pelagophytes and *Synechococcus*. After `phytclass` analyses, an 8th taxonomic group, *Prochlorococcus*, was added by using DVChl*a*, which was summed with Chl*a* to obtain the TChl*a* biomass of phytoplankton community. The attribution of the pigments to the phytoplankton chemotaxonomic groups is presented in Table 1.

Table 1: Phytoplankton chemotaxonomic groups and associated pigments computed with `phytclass` in this study.

Phytoplankton group	Pigments used for <code>phytclass</code> in this study
Diatom	Chl <i>a</i> ; Fuco
Haptophytes	Chl <i>a</i> ; But-fuco; Fuco; Hex-fuco
Cryptophytes	Chl <i>a</i> ; Allo
Dinoflagellates	Chl <i>a</i> ; Peri
Chlorophytes	Chl <i>a</i> ; Chl <i>b</i> ; Lut; Neo; Viola; Zea
Pelagophytes	Chl <i>a</i> ; But-fuco; Fuco
<i>Synechococcus</i>	Chl <i>a</i> ; Zea
<i>Prochlorococcus</i>	DVChl <i>a</i>

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2.5 Ancillary supporting data

The depth of the surface mixed layer (Z_{SML}), defined as the depth at which the density anomaly (σ , kg m^{-3}) differed by 0.03 kg m^{-3} from the 10 m σ value (de Boyer Montégut et al., 2004), was determined from the CTD downcast profiles. The depth of the euphotic layer (Z_{EL}) was determined from the downcast profiles of photosynthetically active radiation (PAR, 400-175 700 nm, Biospherical Instruments Inc. QCP 2350) and from the surface reference measurements (Biospherical Instruments Inc. QCR 2200). Here, we defined two Z_{EL} : $Z_{\text{EL}1\%}$ corresponding to the depth at which PAR is reduced to 1% of its surface value (Morel and Berthon, 1989), and $Z_{\text{EL}0.01\%}$ representing the depth at which PAR is reduced to 0.01% of its surface value. $Z_{\text{EL}0.01\%}$ was subsequently used for the integration of biogeochemical parameters (see section 2.6 and text S1).

Macronutrients samples were collected at fixed depths, and bottles were rinsed three times before sampling with the 180 collected seawater. 30 mL of seawater were filtered through $0.4 \mu\text{m}$ filters and poisoned with $100 \mu\text{L}$ saturated HgCl_2 to stop biological activity, and stored at $4 \text{ }^\circ\text{C}$ until analysis at the IMAGO analytical platform (IRD, Plouzané, France). NO_x , DIP and DSi were analysed by colorimetry using a segmented flow analyser (SEAL Analytical Inc. AA500) following the protocol from Aminot and K  rouel (2007). The detection limits were $0.1 \mu\text{M}$ for NO_x , $0.05 \mu\text{M}$ for DIP and $0.03 \mu\text{M}$ for DSi. Accuracy was checked with certified reference material for nutrients in seawater (KANSO Technos Co.) within 1.4% for NO_x and DIP 185 and 1.7% for DSi.

2.6 Computations, statistical analyses and numerical tools

In this study, the size structure of primary production and pigments – including the biomass with TChl*a* – was determined from the bulk and size-fractionated measurements ($< 3 \mu\text{m}$ and $< 20 \mu\text{m}$). Picophytoplankton ($< 3 \mu\text{m}$) NPP and pigments were obtained directly from the $< 3 \mu\text{m}$ fraction. Nanophytoplankton ($3\text{--}20 \mu\text{m}$) NPP and pigments were obtained 190 by subtracting the $< 20 \mu\text{m}$ fraction from the $< 3 \mu\text{m}$ fraction. Microphytoplankton ($> 20 \mu\text{m}$) NPP and pigments were obtained by subtracting the total fraction from the $< 20 \mu\text{m}$ fraction. To best represent the data within the productive layer, biogeochemical parameters in this study were integrated from the surface (0 m) down to the $Z_{\text{EL}0.01\%}$, as previous studies have reported significant primary production below the $Z_{\text{EL}1\%}$ (e.g. Cavagna et al., 2015). The detailed explanation for the choice of the $Z_{\text{EL}0.01\%}$ is presented in the Supplement (Text S1 and S2; Tables S1 and S2; Fig. S1). Values at 0 m were extrapolated from 195 those at the first sampled depth ($\sim 10 \text{ m}$). **Integrated NPP are expressed thereafter in $\text{mgC m}^{-2} \text{ d}^{-1}$, while integrated pigment concentrations and integrated biomass of phytoplankton chemotaxonomic groups are expressed in mg m^{-2} .**

For each size-fractionated parameter (e.g. NPP, TChl*a*, phytoplankton chemotaxonomic group biomass), the relative contributions of each size class averaged across the study area were compared using a one-way ANOVA followed by a post-hoc Tukey test. When normality and homoscedasticity assumptions were not respected, a Kruskal-Wallis test was applied 200 followed by a post-hoc Dunn test. Spearman's rank correlations were performed to assess statistical relationships between biogeochemical parameters based on the volumetric data, as not all volumetric datasets met the normality and homoscedasticity assumptions. Principal component analysis (PCA) was performed on the volumetric dataset ($n = 72$) to **explore the**

relationships between environmental parameters (explanatory variables) **and net primary production as well as** phytoplankton chemotaxonomic groups **biomass** (supplementary descriptors). **The initial** explanatory variables were **sea surface temperature (SST) potential temperature, sea surface salinity (SSS), σ , dissolved oxygen, PAR, DIC, NO_x, DIP, DSi, Z_{SML} and Z_{EL0.01%}. Prior to the analysis, explanatory variables and supplementary descriptors were standardized (vegan::deconstand() function). Furthermore, collinearity among of explanatory variables was checked using the variance inflation factors (VIFs): explanatory variables with the highest VIFs (SST, SSS, dissolved oxygen, DIP) were removed until all remaining variables had VIF scores < 10, assessed using a Spearman correlogram (Fig. S2). Potential temperature was strongly correlated with σ ($\rho = -0.98$), dissolved oxygen ($\rho = -0.92$) and DIC ($\rho = -0.92$); among these variables, potential temperature was retained, as it is a key driver of water mass structure and biological activity. NO_x and DIP were also highly correlated ($\rho = 0.98$), and only NO_x was retained. After this selection, potential temperature and salinity displayed a variance inflation factor (VIF) > 20 (vegan::vif.cca() function); salinity was discarded in favour of temperature. Final explanatory variables were potential temperature, PAR, NO_x, DSi, Z_{SML} and Z_{EL0.01%}. All variables displayed VIF values < 10, exceptfor NO_x (14).**

All statistical analyses were conducted in the programming environment R 4.4.2 (R Core Team 2024). The package tidyverse (v2.0.0; Wickham et al., 2019) was used for data manipulation; oce (v1.8.3; Kelley & Richards 2024) for trapezoidal integration computations; stats (v4.4.2; R Core Team 2024), ~~and~~ rstatix (v0.7.2; Kassambara 2023) **and corrplot (v0.95; Wei and Simko 2024)** for statistical analyses; **FactoMineR (v2.12; Lê et al. 2008) and vegan (v2.6.10; Oksanen et al. 2025) for multivariate analyses.**

3 Results

3.1 Hydrographic and biogeochemical features of the study area

The OISO33-SOCARB transect crossed the three main hydrographic fronts (STF, SAF and PF) which divided the study area into four hydrographic zones (Fig. 1). Located near the PF, stations O10 and E were attributed to the AZ, as the temperature minimum at 200 m reached 2 °C for O10 and was < 2 °C for E (Belkin and Gordon, 1996). A detailed analysis of the fronts position is presented in the Supplement (Text S3).

The study area can be further subdivided into distinct biogeochemical regions, with contrasting surface TChl_a and nutrient concentrations in the **surface mixed layer (SML)** (Table 2). In the STZ, stations O2, O3 and O16 exhibited LNLC conditions, with very low surface TChl_a. The NO_x/DIP ratios in the SML were notably lower than the Redfield ratio of 16/1 (Redfield, 1958), indicating **a relative deficiency of NO_x with respect to DIP for phytoplankton nutritional requirements, and thus suggesting** a potential NO_x limitation of the phytoplankton activity (**Geisen et al., 2022**). Station O11 in the AZ featured HNLC conditions, with low surface TChl_a despite high macronutrient concentrations. The NO_x/DIP and DSi/NO_x ratios in the SML were close to ~~their optimal values~~ **the Redfield and Brzezinski ratios** (Si/N for diatoms = 1.12 ± 0.33, Brzezinski 1985), **indicating that NO_x, DIP and DSi were not limiting, and thus** suggesting a potential micronutrient

235 limitation (Geisen et al., 2022). Stations O6, O7, O9 in the PFZ and O10 in the AZ shared similar features with O11 (AZ) but exhibited lower surface DSi concentrations, leading to suboptimal DSi/NO_x ratios notably lower than the Brzezinski ratio. These stations exhibited HN-LSi-LC conditions, indicating a potential (co-)limitation by Si (Pondaven et al., 2000). Station O14 stood out from the latter HN-LSi-LC stations, exhibiting lower NO_x, DIP and DSi concentrations in the SML along with a NO_x/DIP and DSi/NO_x ratios below the suboptimal values Redfield and Brzezinski ratios. Stations O12, E and 240 A3, located in the naturally Fe-fertilized Kerguelen bloom (Blain et al., 2008; Qu  rou   et al., 2015), exhibited the highest surface TChl_a and a suboptimal DSi/NO_x ratio in the SML lower than the Brzezinski ratio, indicating a potential (co-)limitation by Si (Geisen et al., 2022). These stations were grouped into a region hereafter referred to as ‘‘Kerguelen bloom’’ (KER), which differed from the offshore stations in the PFZ (O6, O7, O9) and AZ (O11, O10) (Table 2).

245 **Table 2: Metadata, hydrological and biogeochemical features for the SOCARB stations. Stations were grouped according to their hydrographic zone and biogeochemical region. Region assignment was based on surface TChl_a, nutrient concentrations and molar ratios (mean ± SD) in surface mixed layer (SML).**

METADATA			HYDROLOGY			SURFACE VALUES			SURFACE MIXED LAYER VALUES (MEAN ± SD)						
St.	Zone	Region	Lat. [�S]	Lon. [�E]	Z _{SML} [m]	Z _{EL1%} [m]	Z _{EL0.01%} [m]	SST [�C]	SSS [psu]	TChl _a [mg m ⁻³]	NO _x [μ mol L ⁻¹]	DIP [μ mol L ⁻¹]	DSi [μ mol L ⁻¹]	NO _x /DIP [mol/mol]	DSi/NO _x [mol/mol]
O2	STZ	LNLC	30.00	54.10	24	93	185	25.0	35.71	0.078	0.17	0.04	2.19	3.6	13.6
O3	STZ	LNLC	35.00	53.50	14	118	236	20.4	35.53	0.10	0.33	0.11	2.37	3.1	7.3
O16	STZ	LNLC	35.18	73.37	40	90	181	21.3	35.42	0.07	0.11 ± 0.02	0.18 ± 0.02	1.63 ± 0.02	0.6 ± 0.1	15.3 ± 3.9
O14	SAZ	HN-LSi-LC	42.50	74.75	49	87	174	14.5	34.90	0.21	3.72	0.42	1.25	8.9	0.3
O6	PFZ	HN-LSi-LC	45.00	52.27	27	84	168	9.5	33.68	0.15	21.0	1.40	3.77	15.0	0.2
O7	PFZ	HN-LSi-LC	47.67	58.00	30	82	164	8.6	33.73	0.19	19.9	1.38	2.78	14.5	0.1
O9	PFZ	HN-LSi-LC	48.50	65.00	30	83	166	6.1	33.78	0.20	24.9 ± 0.45	1.63 ± 0.03	6.07	15.3 ± 0.1	0.2
O12	PFZ	KER (PFZ)	47.00	72.02	85	46	93	7.5	33.70	0.7459	20.1 ± 1.41	1.42 ± 0.10	1.92 ± 0.57	14.1 ± 0.1	0.1 ± 0.0
E	AZ	KER (AZ)	48.80	72.37	82	63	125	4.4	33.89	0.40	25.5 ± 0.30	1.71 ± 0.05	5.72 ± 0.85	15.0 ± 0.5	0.2 ± 0.0
A3	AZ	KER (AZ)	50.50	71.97	108	48	97	4.3	33.91	0.67	25.4 ± 0.94	1.81 ± 0.05	4.16 ± 0.35	14.0 ± 0.2	0.2 ± 0.0
O10	AZ	HN-LSi-LC	50.67	68.42	84	69	137	4.7	33.83	0.30	26.6 ± 0.54	1.75 ± 0.04	8.56 ± 0.41	15.2 ± 0.1	0.3 ± 0.0
O11	AZ	HNLC	56.50	63.00	90	101	203	1.9	33.85	0.17	29.6 ± 0.23	2.04 ± 0.09	27.7	14.6 ± 0.4	0.9

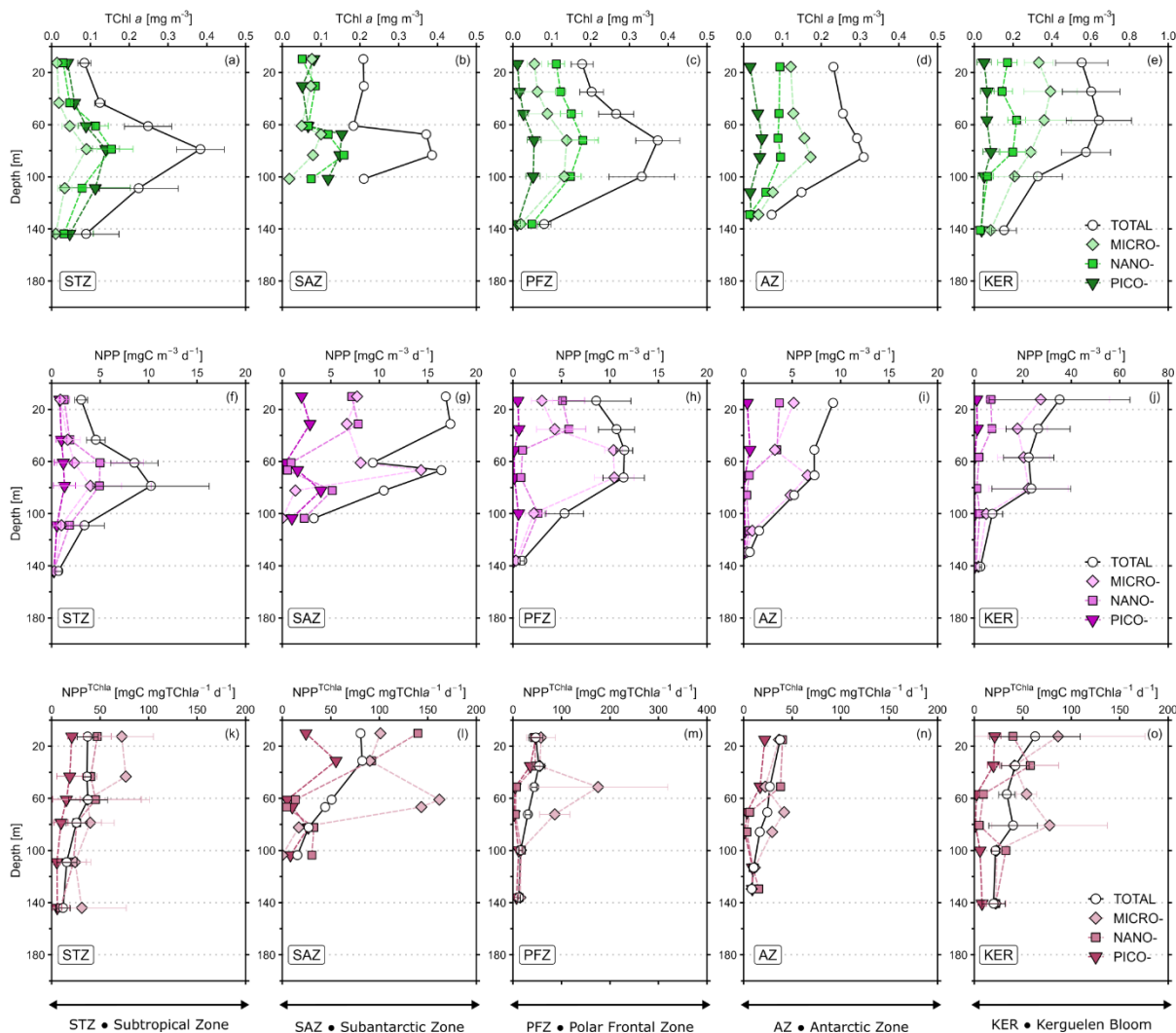
250 **STZ, Subtropical Zone; SAZ, Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone; KER, Kerguelen bloom; SST, Sea Surface Temperature; SSS, Sea Surface Salinity; TChl_a, total chlorophyll *a*; NO_x = NO₃⁻ + NO₂⁻; DIP, dissolved inorganic phosphorus; DSi, dissolved silicon.**

3.2 Synoptic view of the distribution of phytoplankton biomass and primary production

3.2.1 Vertical distribution of TChl_a and NPP

255 The mean TChl_a profiles of the total fraction (TChl_aTOTAL) and the size classes (TChl_aPICO, TChl_aNANO, TChl_aMICRO) are presented in Fig. 2a-c for each hydrological zone at five stations, representative of each biogeochemical region (O2 for STZ, O14 for SAZ, O9 for PFZ, O11 for AZ, O12 for KER), and also displayed in Fig. A1 (Appendix A) for all stations. Across all zones stations, the depth of SCM (Z_{SCM}) of TChl_aTOTAL occurred between 60 and 100 m and was usually below

the Z_{SML} , except for O12 in the KER region where the SCM was located at 45 m and above the Z_{SML} . For all zones at most stations, the Z_{SCM} depth was similar for the total fraction and the size classes, except in the KER region where the Z_{SCM} for $TChla_{MICRO}$ peaked around 40 m while the Z_{SCM} of $TChla_{NANO}$ was deeper (between 60 and 80 m). However, some stations exhibited notable differences. For instance, at O16 (STZ) and O6 (PFZ), the SCM of $TChla_{PICO}$ was deeper than that of $TChla_{TOTAL}$ (Fig. A1). Despite vertical variations in $TChla$, the $TChla$ size structure – *i.e.* the relative contributions of each size class to $TChla_{TOTAL}$ – remained unchanged with depth for all zones (not shown), stations, except for O11 with $TChla$ dominated by nano at the surface and by microphytoplankton at the SCM.



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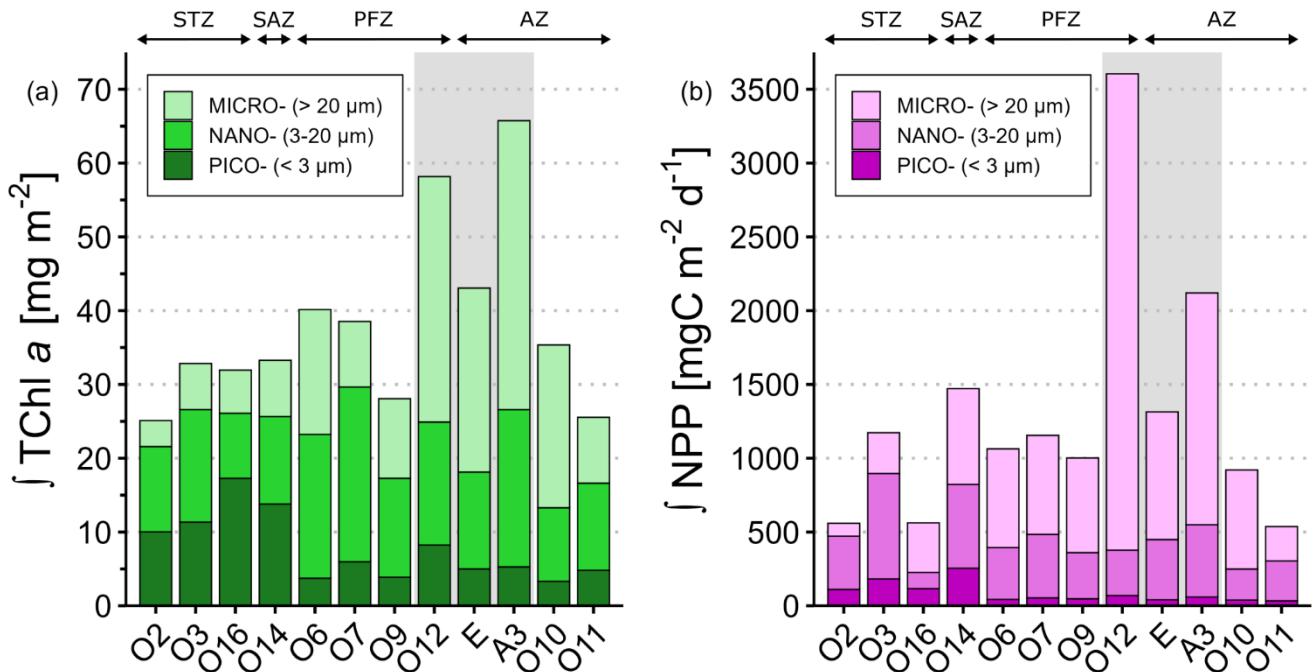
Figure 2: Mean vertical profiles of (a-e) total chlorophyll a ($TChla$), (f-j) net primary production, (k-o) $TChla$ -normalised primary production (NPP^{TChla}) for the five hydrographic zones in the study area: Subtropical zone (STZ: a, f, k, $n=3$), Subantarctic zone (SAZ: b, g, l, $n=1$), Polar Frontal zone (PFZ: c, h, m, $n=3$), Antarctic zone (AZ: d, i, n, $n=2$) and Kerguelen bloom (KER: e, j, o, $n=3$). Values are mean \pm SD (or mean value only when $n < 3$), at five stations located in each hydrographic zone: O2 in the Subtropical zone

270 (a, f, k), O14 in the Subantarctic zone (b, g, l), O9 in the Polar Frontal zone (e, h, m), O11 in the Antarctic zone (d, i, n) and O12 in the Kerguelen bloom (e, j, o). Mind the scale differences in **Note the differences in scale for KER at O12 for TChla and NPP, and in PFZ for NPP^{TChla}**. All the profiles for every station are presented in Appendix A: Fig. A1 for TChla, Fig. A2 for NPP and Fig. A3 for pp^{TChla}.

As for TChla, the **mean** NPP profiles of the total fraction (NPP_{TOTAL}) and the size classes (NPP_{PICO}, NPP_{NANO}, NPP_{MICRO}) are presented in Fig. 2f-j **for each zone at five stations** and displayed in Fig. A2 (Appendix A) for all stations. Here, the subsurface NPP maximums were not as marked as the SCM. Moreover, the subsurface NPP maximums coincided with SCM **at O2 and O3** in the STZ **and PFZ**. Contrary to TChla, the NPP size structure – *i.e.* the relative contributions of each size class to NPP_{TOTAL} – was heterogeneous with depth (**not shown**). In the STZ, surface NPP was evenly distributed in each size class, while subsurface NPP maximum was dominated by one size class. It is noteworthy that **in the STZ**, subsurface NPP maximums at O2 and O3 were mainly dominated by nanophytoplankton while that **at O6** was surprisingly dominated by microphytoplankton (**Fig. A2**). In the SAZ, PFZ and AZ, surface NPP was mainly supported by nano- and microphytoplankton, while subsurface NPP maximum was dominated by microphytoplankton. In the KER region, NPP **in the size classes** was mainly dominated by microphytoplankton. By normalizing NPP to TChla, **we calculated NPP^{TChla}** (in mgC mgTChla⁻¹ d⁻¹) which can reflect photosynthesis efficiency under given environmental conditions (*e.g.* light/nutrient availability; Cermeño et al., 2005). NPP^{TChla}_{TOTAL} was maximal **in the first 50 m SML** at all **zones stations** – except at O3 and O6 where it peaked below the SML – and decreased with depth (Fig. 2k-o; Fig. A3 **in Appendix A**). Interestingly when considering the size classes, NPP^{TChla}_{MICRO} often peaked **at depth across all zones and coincided with minima in NPP^{TChla}_{NANO} and NPP^{TChla}_{PICO}, except in the STZ. below the SML for several stations in the STZ (O16), the SAZ (O14), the PFZ (O6, O7, O9) and the AZ (O11), while NPP^{TChla}_{NANO} and NPP^{TChla}_{PICO} were minimal.**

290 3.2.2 Spatial distribution of TChla and NPP

Integrated TChla_{TOTAL} over the Z_{EL0.01%} ranged from 25.1 mg m⁻² at O2 (**STZ**) to 65.7 mg m⁻² at A3 (**KER**) (Fig. 3a). Stations in the KER region displayed the highest TChla_{TOTAL} (55.7 ± 11.6 mg m⁻²), while the remaining stations exhibited lower TChla_{TOTAL} (32.3 ± 5.3 mg m⁻²). Across the study area, nano- and microphytoplankton contributed the most to TChla_{TOTAL} and represented respectively 40% ± 11% and 37% ± 18% of TChla_{TOTAL} (Table S3). It is noteworthy that the picophytoplankton relative contribution to TChla_{TOTAL} (23% ± 16%) was significantly lower than those of nano- and microphytoplankton (*p* < 0.05). In the STZ and SAZ, integrated TChla_{TOTAL} was similar and dominated by both pico- and nanophytoplankton, which contributed to 42% ± 8% and 39% ± 9% respectively. In the offshore PFZ and AZ, integrated TChla_{TOTAL} was similar and dominated by the biomass of nano- (46% ± 12%) and microphytoplankton (40% ± 14%). In the KER region, microphytoplankton biomass contributed the most to integrated TChla_{TOTAL} (58% ± 1%). Furthermore, the integrated TChla size structure also varied within specific hydrographic zones. For instance, in the PFZ, integrated TChla at O7 was dominated by nanophytoplankton (61%) while the main contributors at O6 and O9 were nano- (48%) and micro- (40%) (Table S3).



305 **Figure 3: Spatial distribution of the phytoplankton size classes for (a) integrated total chlorophyll *a* (\int TChl*a*) and (b) integrated net primary production (\int NPP) over the $Z_{EL0.01\%}$. The relative contributions values for \int TChl*a* and \int NPP are detailed in Supplement Table S3. Stations were grouped according to their hydrographic zone and biogeochemical region. The grey box covers the stations located in the Kerguelen region. STZ, Subtropical Zone; SAZ, Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone.**

The lowest integrated NPP_{TOTAL} over the $Z_{EL0.01\%}$ were observed at O11 (AZ), O16 and O2 (STZ) ($553 \pm 14 \text{ mgC m}^{-2} \text{ d}^{-1}$), while the highest values were recorded at A3 ($2120 \text{ mgC m}^{-2} \text{ d}^{-1}$) and O12 ($3605 \text{ mgC m}^{-2} \text{ d}^{-1}$) in KER (Fig. 3b). Such differences highlighted the greater variability of NPP_{TOTAL} during SOCARB compared to $TChl a_{TOTAL}$, with a factor of 6.7 for NPP_{TOTAL} versus 2.7 for $TChl a_{TOTAL}$. In particular in the STZ, integrated NPP_{TOTAL} at O3 was twice higher than at O2 and O16 (Fig. 3b). Across the study area, microphytoplankton was the main contributor to NPP_{TOTAL} ($56\% \pm 21\%$), followed by nano- (310 $35\% \pm 17\%$) and picophytoplankton ($9\% \pm 7\%$) (Table S3). The relative contributions of each size class to NPP_{TOTAL} were significantly different from each other ($p < 0.05$). The NPP size structure remained homogeneous within the PFZ, AZ and 315 KER region, where microphytoplankton contributed the most to integrated NPP_{TOTAL} ($66\% \pm 13\%$), except at O11 where nano- and microphytoplankton accounted respectively for 50% and 43%. The STZ was the sole zone with notable heterogeneity: while nanophytoplankton dominated at the western stations O2 and O3 (mean contribution of 63%), microphytoplankton was the main contributor to integrated NPP_{TOTAL} at the eastern station O16 (60%).

320 Across the global study area, correlations between the total fraction and each size class were significant for both TChl*a* and NPP (Table 3). $TChl a_{TOTAL}$ exhibited the strongest correlations with $TChl a_{MICRO}$ ($\rho = 0.87$) and $TChl a_{NANO}$ ($\rho = 0.80$), while NPP_{TOTAL} was most strongly correlated with NPP_{MICRO} ($\rho = 0.86$). When comparing the hydrographic zones, both

TChla and NPP correlations revealed a clear spatial variability. In the STZ, the total fraction displayed the highest correlations with pico- and nanophytoplankton, while in the PFZ, AZ and KER region it correlated most strongly with nano- and microphytoplankton. NPP_{TOTAL} was significantly correlated with TChla for each size class over the global study area, with the strongest correlations found with TChla_{NANO} ($\rho = 0.76$) and TChla_{MICRO} ($\rho = 0.70$). When comparing the hydrographic zones, TChla_{PICO} had a significant impact on NPP_{TOTAL} only in the STZ, while TChla_{NANO} and TChla_{MICRO} had a significant impact on NPP_{TOTAL} in each hydrographic zone. The SAZ was the sole exception, as no significative correlations were found between NPP_{TOTAL} and TChla in any size class, likely due to the small number of samples.

Table 3: Spearman's rank correlation coefficients of volumetric TChla and NPP for the different size classes (total, pico-, nano- and micro-) in the global study area and within the different zones. Significant results are presented in bold font.

Area	Global	STZ	SAZ	PFZ	AZ	KER
Stations	study area	O2; O3; O16	O14	O6; O7; O9	O10; O11	O12; A3; E
	n = 72	n = 18	n = 6	n = 18	n = 12	n = 18
TChla _{TOTAL} vs. TChla _{PICO}	0.49 ***	0.94 ***	0.70	0.76 ***	0.52	0.41
TChla _{TOTAL} vs. TChla _{NANO}	0.80 ***	0.92 ***	0.93 **	0.82 ***	0.66 *	0.85 ***
TChla _{TOTAL} vs. TChla _{MICRO}	0.87 ***	0.77 ***	0.61	0.87 ***	0.93 ***	0.95 ***
NPP _{TOTAL} vs. NPP _{PICO}	0.32 **	0.56 *	0.60	0.20	0.48	0.35
NPP _{TOTAL} vs. NPP _{NANO}	0.58 ***	0.61 **	0.60	0.29	0.68 *	0.50 *
NPP _{TOTAL} vs. NPP _{MICRO}	0.86 ***	0.45	0.31	0.89 ***	0.92 ***	0.97 ***
NPP _{TOTAL} vs. TChla _{PICO}	0.30 *	0.57 *	-0.31	0.33	0.31	0.43
NPP _{TOTAL} vs. TChla _{NANO}	0.76 ***	0.82 ***	0.03	0.53 *	0.69 *	0.77 ***
NPP _{TOTAL} vs. TChla _{MICRO}	0.70 ***	0.79 ***	0.49	0.47 *	0.80 **	0.82 ***

Significance level: * for < 0.05; ** for < 0.01; * for < 0.001. STZ, Subtropical Zone; SAZ, Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone; KER, Kerguelen region.**

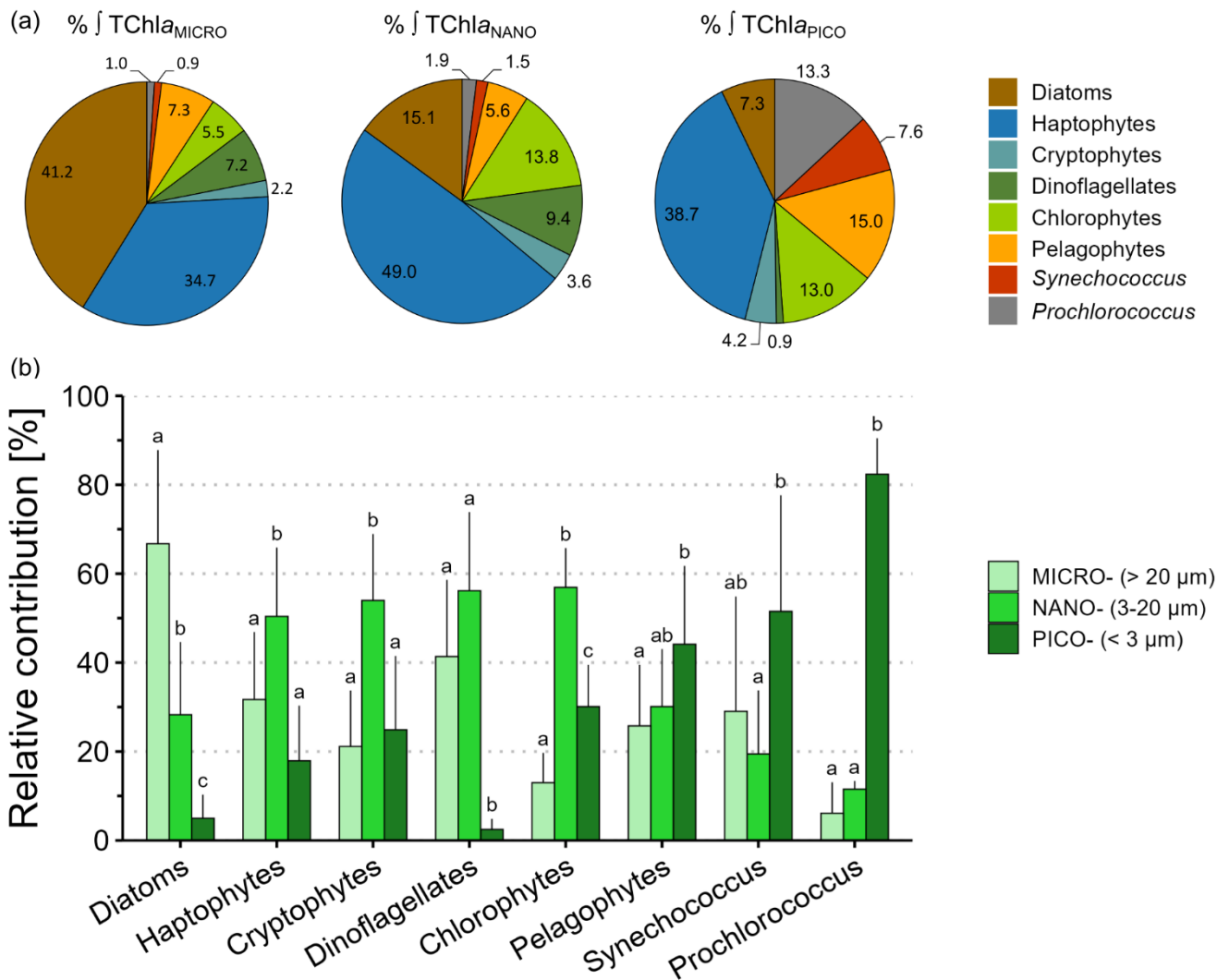
3.3 In-depth description of the distribution of the phytoplankton community

The concentrations and relative contributions of the 8 main accessory pigments (Fuco, Peri, Hex-fuco, But-fuco, Allo, Chlb, Zea and DVChla) integrated over the $Z_{EL0.01\%}$ for the total fraction and the size classes are presented in the Supplement (Table S4; Fig. S3).

3.3.1 Insights into the biomass and size structure of phytoplankton chemotaxonomic groups across the study area

Over the study area, the main contributors to integrated TChla_{TOTAL} were microphytoplankton diatoms ($20\% \pm 18\%$) followed by nanophytoplankton haptophytes ($19\% \pm 7\%$) and microphytoplankton haptophytes ($14\% \pm 11\%$; Table S5). Focusing on the contributions of phytoplankton chemotaxonomic groups biomass to integrated TChla for each size class (Fig. 4a), haptophytes stood out in the three size classes, constituting the dominant and ubiquitous group among all size classes

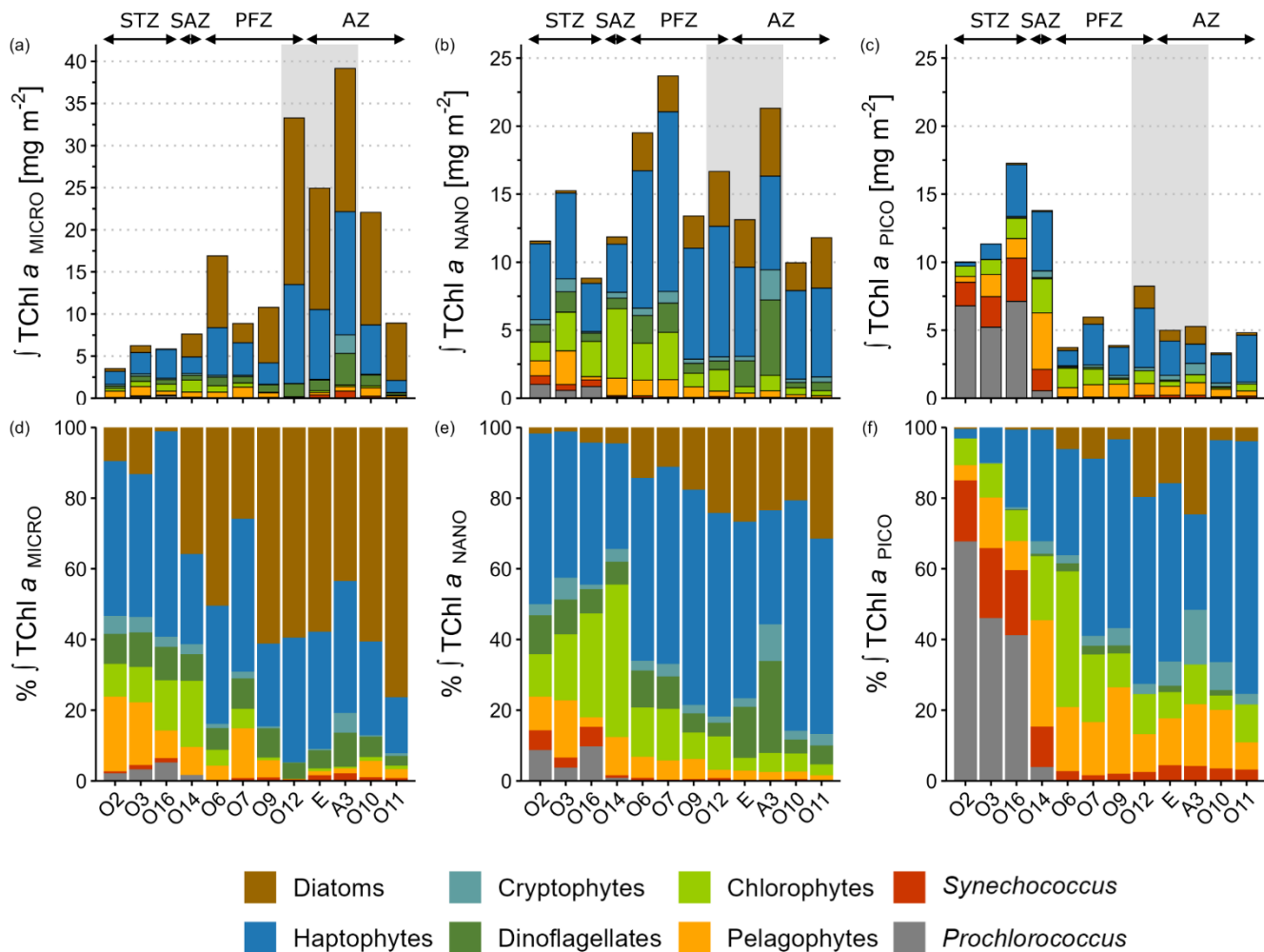
across the study area (Fig. 4a). Focusing on the contributions of each size class to the biomass of the chemotaxonomic groups averaged over the study area (Fig. 4b), each chemotaxonomic group was distributed among each size class with contrasting relative contributions. Diatoms biomass was mostly associated with the microphytoplankton, accounting for $67\% \pm 21\%$ of total diatom biomass. Haptophytes, cryptophytes and chlorophytes biomass were mostly found in the nanophytoplankton, while dinoflagellates biomass was distributed evenly and almost exclusively in the nano- and microphytoplankton (Fig. 4b). Pelagophytes biomass was mainly found in the picophytoplankton, yet nano- and microphytoplankton contributions to total pelagophytes biomass remained notable. As expected, cyanobacteria (*Prochlorococcus* and *Synechococcus*) biomass was mainly distributed in the picophytoplankton, however a small fraction ($< 3.5\%$) was also detected in the nano- and microphytoplankton biomass (Fig. 4a-b) but also surprisingly detected in the nano- and microphytoplankton.



355 **Figure 4: Insights into the size structure of phytoplankton chemotaxonomic groups using integrated biomass over the $Z_{EL0.01\%}$ across the global study area ($n = 12$). (a) Circular diagrams of average relative contributions (%) of phytoplankton chemotaxonomic groups to integrated TChl a for the micro-, the nano- and the picophytoplankton size classes. (b) Barplots of average relative contributions (%) of the size classes to the biomass of each phytoplankton chemotaxonomic group. Vertical bars indicate mean relative contribution + SD. Within a given group, mean relative contribution that are not significantly different ($p \geq 0.05$) are labelled with the same letter. Note that *Prochlorococcus* data in the barplots were computed from the STZ and SAZ ($n = 4$), *i.e.* only where**
360 ***Prochlorococcus* biomass was detected.**

3.3.2 Spatial distribution of integrated phytoplankton chemotaxonomic groups biomass

In the STZ, where integrated TChl a_{TOTAL} was dominated by pico- ($43\% \pm 10\%$) and nanophytoplankton ($40\% \pm 11\%$), TChl a_{PICO} was dominated by cyanobacteria ($70\% \pm 13\%$) whereas TChl a_{NANO} was mainly sustained by haptophytes ($43\% \pm 4\%$) and chlorophytes ($20\% \pm 9\%$) (Fig. 5e and 5f). In the SAZ, despite similar TChl a size structure compared to STZ,
365 TChl a_{PICO} was mainly driven by haptophytes (32%) and pelagophytes (30%) while TChl a_{NANO} was mainly sustained by chlorophytes (43%) and haptophytes (30%). In the offshore PFZ and AZ where integrated TChl a_{TOTAL} was dominated by nano- ($46\% \pm 12\%$) and microphytoplankton ($40\% \pm 14\%$), TChl a_{NANO} was firstly sustained by haptophytes ($58\% \pm 5\%$) followed by diatoms ($19\% \pm 8\%$), whereas TChl a_{MICRO} was firstly driven by diatoms ($55\% \pm 19\%$) followed by haptophytes ($29\% \pm 10\%$) (Fig. 5d-e). In the KER region where TChl a_{TOTAL} was dominated by microphytoplankton ($58\% \pm 1\%$), TChl a_{MICRO} was
370 dominated by diatoms and haptophytes whose relative contributions were respectively $54\% \pm 9\%$ and $35\% \pm 2\%$ (Fig. 5d).



375 **Figure 5: Spatial distribution of phytoplankton taxonomic groups of (a-c) integrated TChla and (d-f) relative contribution to integrated TChla over the $Z_{EL0.01\%}$ for the micro- (a, d), the nano- (b, e) and the picophytoplankton (c, f) size classes. Mind the scale differences of TChla for the microphytoplankton compared to nano- and pico-. Stations were grouped according to their hydrographic zone and biogeochemical region. The grey box covers the stations located in the Kerguelen region. STZ, Subtropical Zone; SAZ, Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone.**

380 The size structure of phytoplankton chemotaxonomic groups biomass shifted within each size class across the study area. The microphytoplankton community shifted from haptophyte dominance in the STZ ($48 \pm 9\%$ of TChla_{MICRO}) towards diatom dominance in the PFZ, AZ and KER ($54 \pm 15\%$) (Fig. 5d). Within the nanophytoplankton, chlorophytes were the secondary contributors in the STZ ($20\% \pm 9\%$ of TChla_{NANO}), but were replaced by diatoms in the PFZ, AZ and KER region ($21 \pm 7\%$) (Fig. 5e). The picophytoplankton community shifted from cyanobacteria dominance in the STZ ($70 \pm 13\%$ of TChla_{PICO}) to haptophyte dominance in the PFZ and AZ ($50 \pm 15\%$) (Fig. 5f). This shift across the study area was also observed for the total fraction (Fig. S4). Indeed, the SAZ acted as a “boundary zone” within the study area, delineating distinct

community structures. North of the SAZ, the community in the STZ appeared relatively diversified, with four groups (cyanobacteria, haptophytes, chlorophytes and pelagophytes) each contributing more than 10% to TChla_{TOTAL}. In contrast, south of the SAZ, the community in the PFZ, AZ and KER region appeared relatively less diversified, with only two groups (diatoms and haptophytes) contributing more than 10 % to TChla_{TOTAL} (Fig. S4b). In the SAZ, the community at O14 was relatively diversified, with four groups (haptophytes, chlorophytes, pelagophytes and diatoms) each contributing more than 10% to TChla_{TOTAL}, alongside a marked increase in diatom biomass and a concurrent decline in cyanobacteria.

3.4 Links between the size structure of phytoplankton chemotaxonomic groups biomass and primary production

Correlation coefficients were computed between volumetric NPP_{TOTAL} and phytoplankton chemotaxonomic groups biomass for each size class (Table 4). Across the study area, NPP_{TOTAL} was mainly driven by the biomass of nano- and microphytoplankton (Table 3). For these two size classes, NPP_{TOTAL} showed the highest correlation coefficients with the biomass of haptophytes, dinoflagellates and diatoms. In the STZ, NPP_{TOTAL} was significantly correlated with TChla in all size classes (Table 3), specifically with the TChla_{PICO} of cyanobacteria (*Prochlorococcus* and *Synechococcus*) and chlorophytes; with the TChla_{NANO} of haptophytes, dinoflagellates and chlorophytes; and with the TChla_{MICRO} of dinoflagellates, haptophytes and diatoms (Table 4). No significant correlations were found in the SAZ. In the PFZ, NPP_{TOTAL} was significantly correlated with TChla_{NANO} and TChla_{MICRO} (Table 3), specifically with the TChla_{NANO} of diatoms, haptophytes and *Synechococcus*, and with the TChla_{MICRO} of diatoms, and negatively correlated with the TChla_{MICRO} of *Synechococcus*. In the AZ and KER region, similar correlation patterns were observed: NPP_{TOTAL} was mainly correlated with the TChla_{NANO} of haptophytes and by the TChla_{MICRO} of haptophytes, diatoms and dinoflagellates (Table 4).

Table 4: Spearman's rank correlation coefficients between volumetric NPP_{TOTAL} and the phytoplankton chemotaxonomic groups biomass for each size class following the different zones and regions of the study area. Significant results are presented in bold font.

Area Stations	Global study area n = 72	STZ O2; O3; O16 n = 18	SAZ O14 n = 6	PFZ O6; O7; O9 n = 18	AZ O10; O11 n = 12	KER O12; A3; E n = 18
<i>Prochlorococcus</i>						
NPP _{TOTAL} vs. <i>Prochlorococcus</i> PICO	-0.18	0.54 *	0.14	NA	NA	NA
NPP _{TOTAL} vs. <i>Prochlorococcus</i> NANO	-0.05	0.45	0.15	NA	NA	NA
NPP _{TOTAL} vs. <i>Prochlorococcus</i> MICRO	-0.05	0.12	-0.03	NA	NA	NA
<i>Synechococcus</i>						
NPP _{TOTAL} vs. <i>Synechococcus</i> PICO	0.30 *	0.76 ***	0.49	0.88 ***	0.65 *	0.65 **
NPP _{TOTAL} vs. <i>Synechococcus</i> NANO	0.37 **	0.41	0.38	0.48 *	0.22	0.65 **
NPP _{TOTAL} vs. <i>Synechococcus</i> MICRO	0.01	0.08	NA	-0.87 ***	0.15	0.17
Pelagophytes						
NPP _{TOTAL} vs. Pelagophytes PICO	0.42 ***	0.45	-0.71	0.15	0.67 *	0.34
NPP _{TOTAL} vs. Pelagophytes NANO	0.14	0.13	-0.46	-0.05	0.02	0.36
NPP _{TOTAL} vs. Pelagophytes MICRO	-0.01	0.37	-0.14	-0.30	0.35	-0.30
Chlorophytes						

NPP _{TOTAL} vs. Chlorophytes _{PICO}	0.33 **	0.56 *	-0.83	0.22	-0.41	0.78 ***
NPP _{TOTAL} vs. Chlorophytes _{NANO}	0.44 ***	0.61 **	-0.09	0.17	0.28	0.87 ***
NPP _{TOTAL} vs. Chlorophytes _{MICRO}	0.18	0.56 *	0.54	0.05	0.74 **	-0.39
Dinoflagellates						
NPP _{TOTAL} vs. Dinoflagellates _{PICO}	0.18	0.00	0.26	-0.28	0.45	-0.48
NPP _{TOTAL} vs. Dinoflagellates _{NANO}	0.62 ***	0.71 **	0.54	0.38	0.67 *	0.40
NPP _{TOTAL} vs. Dinoflagellates _{MICRO}	0.74 ***	0.86 ***	0.31	0.37	0.83 ***	0.70 **
Cryptophytes						
NPP _{TOTAL} vs. Cryptophytes _{PICO}	0.49 ***	-0.31	-0.31	0.20	0.71 **	0.30
NPP _{TOTAL} vs. Cryptophytes _{NANO}	0.49 ***	0.39	0.06	0.24	0.22	0.57 *
NPP _{TOTAL} vs. Cryptophytes _{MICRO}	0.07	0.29	-0.03	-0.26	-0.23	-0.11
Haptophytes						
NPP _{TOTAL} vs. Haptophytes _{PICO}	0.33 **	0.24	0.20	0.29	0.27	0.11
NPP _{TOTAL} vs. Haptophytes _{NANO}	0.66 ***	0.82 ***	0.37	0.50 *	0.78 **	0.74 ***
NPP _{TOTAL} vs. Haptophytes _{MICRO}	0.76 ***	0.82 ***	0.49	0.40	0.88 ***	0.80 ***
Diatoms						
NPP _{TOTAL} vs. Diatoms _{PICO}	0.48 ***	0.00	0.07	0.33	0.15	0.78 ***
NPP _{TOTAL} vs. Diatoms _{NANO}	0.53 ***	0.17	-0.14	0.67 **	0.42	0.68 **
NPP _{TOTAL} vs. Diatoms _{MICRO}	0.57 ***	0.68 **	0.83	0.49 *	0.79 **	0.77 ***

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Significance level: * for < 0.05; ** for < 0.01; *** for < 0.001. STZ, Subtropical Zone; SAZ, Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone; KER, Kerguelen region.

4 Discussion

4.1 Understanding the key aspects of phytoplankton biomass and productivity in association with size structure—Analyzing the interplay between phytoplankton biomass and productivity in relation to size structure

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4.1.1 Vertical size classes decoupling of NPP^{TChla}

At several offshore stations in the STZ (O16), SAZ (O14), PFZ (O6, O7, O9) and AZ (O11) In all zones within the study area, except in the STZ, NPP^{TChla}_{MICRO} peaked at depth and coincided with minima in NPP^{TChla}_{NANO} and NPP^{TChla}_{PICO} below the SML while NPP^{TChla}_{NANO} and NPP^{TChla}_{PICO} were minimal (Fig. 2k-o). These maximums could reflect the adaptability of microphytoplankton in low-light environments to take advantage from the nutrients diapycnal diffusion (Tagliabue et al., 2014). At O6, O9 (PFZ) and all stations in the AZ and KER O11, diatoms were the main contributor to TChla_{MICRO} at these NPP^{TChla} maximums (data not shown). Large diatoms are known to thrive in such environmental niches thanks to their high growth efficiency under low-light conditions (Fisher and Halsey, 2016), their ability to regulate buoyancy (Villareal et al., 1996) and to exploit nutrient pulses through enhanced uptake and storage (Kemp and Villareal, 2013). However, haptophytes were the main contributor to TChla_{MICRO} at O16, O14 (SAZ) and O7 (PFZ), where NPP^{TChla}_{MICRO} peaked. For these stations, several hypotheses could explain our results. First, haptophytes have been shown to produce transparent exopolymer particles and form microphytoplankton size aggregates (Riebesell et al., 1995; Leblanc et al., 2009). Second, some *Phaeocystis* species such as *P. globosa* or *P. antarctica* are haptophytes known to form microphytoplankton

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size colonies from nano- and picophytoplankton size single cells, in response to environmental factors such as high irradiance and iron depletion (Feng et al., 2010; Bender et al., 2018), grazing (Long et al., 2007) or NO_x limitation (Riegman et al., 1992). We rule out the latter hypothesis for explaining colonies formation at O14 and O7, as they featured HN-LSi-LC conditions. Also, Schlüter et al. (2011) reported during late austral spring that one station (37.5°S, 72.5°E), relatively close to O16 (35.18°S, 73.37°E), was influenced by Southern Ocean waters and mainly sustained by haptophytes biomass. Although O16 exhibited distinct LNLC conditions, we cannot rule out the possibility of a potential Southern Ocean water mass in spring, favouring the formation of *Phaeocystis* colonies and shaping upstream the size structure. Further studies are needed to evaluate the recurrent or exceptional aspect of this outstanding feature and the preceding hypotheses.

4.1.2 ~~Global features~~ Overall patterns of phytoplankton biomass and productivity size structures across the study area

Across the study area, microphytoplankton was the main contributor of NPP_{TOTAL} ($56 \pm 12\%$) while the main contributors to TChl_a_{TOTAL} were nano- ($40 \pm 11\%$) and micro- ($37 \pm 18\%$). At the scale of the study area, our results in TChl_a size structure are in agreement similar with previous studies conducted during the austral summer, in the South Indian Ocean using phytoplankton functional pigments approaches to the bulk fraction (Mishra et al., 2020), and in the South Atlantic and the Atlantic sector of the Southern Ocean from size-fractionation approaches (Froneman et al., 2001). However, the NPP size structure in our study differed from that of TChl_a, while Froneman et al. (2001) reported that NPP displayed similar size structure with TChl_a. This concerns especially the microphytoplankton, as its contribution to NPP_{TOTAL} in our study was superior than of TChl_a_{TOTAL}. This result suggested that microphytoplankton could be more efficient in CO₂ fixation than the other size classes, which corroborate with previous studies from *in situ* experiments (Cermeño et al., 2005) and photophysiological models (Uitz et al., 2010). More specifically, the higher microphytoplankton photosynthetic efficiencies might be associated with a higher photochemical efficiency characteristic of certain taxonomic groups such as diatoms (Cermeño et al., 2005). We support this hypothesis as microphytoplankton diatoms formed the main contributor of phytoplankton bulk biomass bulk TChl_a biomass in our study, by representing 20% of TChl_a_{TOTAL} (Table S5).

Pigment chemotaxonomy has constituted a valuable tool for estimating the contribution of phytoplankton groups to TChl_a_{TOTAL} and analysing phytoplankton communities (Higgins et al., 2011; Kramer et al., 2024). Yet its application remained limited to the bulk fraction. Our study coupling pigment chemotaxonomy with size fractionation brings novel insights to dive deeper into the size structures of the phytoplankton community and of the phytoplankton chemotaxonomic groups. To our knowledge, Rodríguez et al. (2006) and Nunes et al. (2019) are the only two studies that have applied is the only study using these approaches – with CHEMTAX algorithm and two size classes ($< 3 \mu\text{m}$ and $> 3 \mu\text{m}$) – to investigate phytoplankton communities in the northwestern Iberian basin and in the surface Atlantic Ocean, respectively. Along with the latter study, we raise the importance Consistent with these studies, our results highlight that each phytoplankton chemotaxonomic group was not strictly associated to with one specific size class (Fig. 4). These results underline the limitations limits of phytoplankton functional type approaches used to estimate phytoplankton size structure from bulk measurements (e.g. Uitz et al., 2006; Hirata et al., 2011). For instance, diatoms and dinoflagellates, which are commonly associated with the

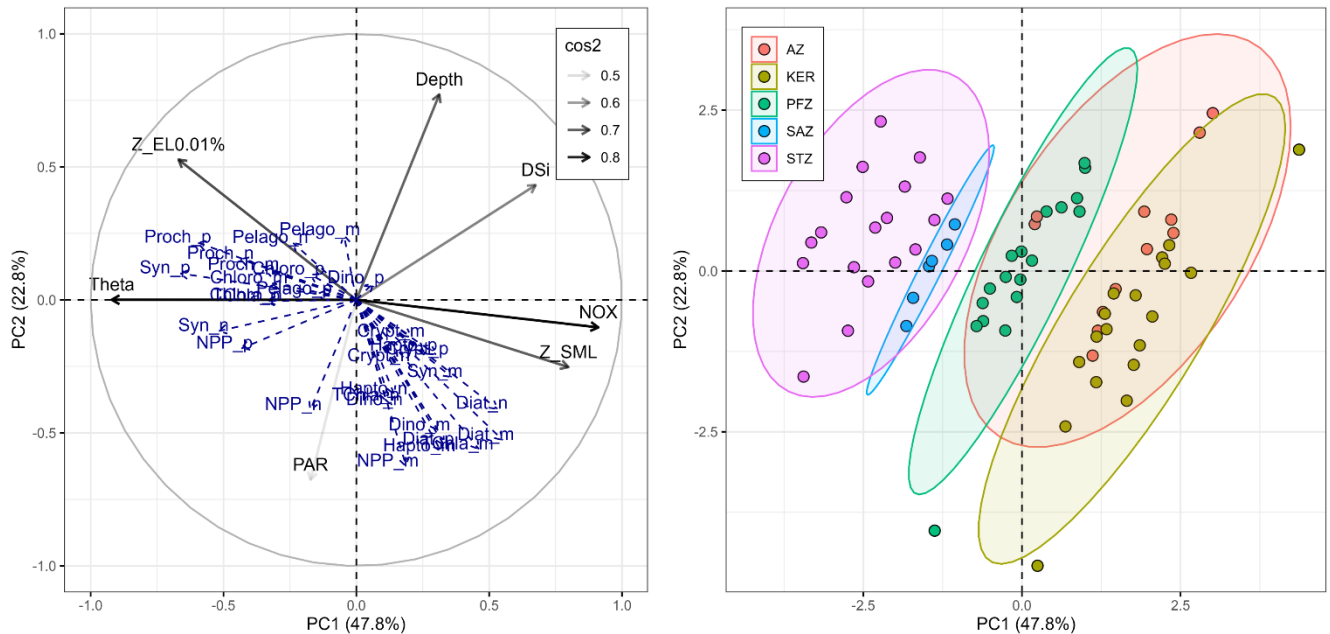
microphytoplankton in ~~such these~~ approaches, were also distributed in the pico- and nanophytoplankton **size classes** (Fig. 4). **This likely reflects the presence of nanoplanktonic dinoflagellate genera such as *Amphidinium*, *Gymnodinium*, *Protoperidinium* and *Prorocentrum* which have been reported in the Indian sector of the Southern Ocean (Georges et al., 2014; Hörstmann et al., 2021; Sreerag et al., 2023). Additionally, pico- and nanoplanktonic diatom genera such as *Minidiscus* and *Fragilariopsis*, as well as bolidophytes, a eukaryotic picophytoplankton group genetically very close to diatoms and sharing a similar pigments composition (Guillou et al., 1999), have previously been observed in the South Indian and South Atlantic Oceans (Hinz et al., 2012; Leblanc et al., 2018; Nunes et al., 2019; Deteix et al., 2024). Also, the presence of haptophytes in the picophytoplankton could be attributed to some coccolithophore genera such as small *Emiliana*, and to other genera such as *Chrysochromulina* and *Phaeocystis* (Poulton et al., 2007; Hinz et al., 2012; Patil et al., 2017; Hörstmann et al., 2021). Notably ~~Indeed~~, Nunes et al. (2019) ~~have shown demonstrated~~ that phytoplankton functional types approaches ~~based on using~~ bulk measurements predicted a high ~~contribution proportion~~ of nano- and microphytoplankton in the Atlantic sector of the Southern Ocean, while the size fractionation approach indicated the dominance of picophytoplankton.**

Furthermore, **our findings revealed that *Prochlorococcus*, ~~and~~ *Synechococcus* and chlorophytes** were mainly distributed in the picophytoplankton, but were also detected in the nano- and microphytoplankton (Fig. 4). This result, also reported **in previous studies (Rodríguez et al., 2006; Nunes et al., 2019) by Nunes et al. (2019)**, can be explained by the size fractionation methodology, as the 3 µm and 20 µm pore sizes may retain a part of these organisms **due to aggregation and/or adhesion**. In addition, **the attribution of pigments like zeaxanthin – associated with *Synechococcus* in this study – to larger size classes may be influenced by the presence of this pigment in nanophytoplankton (e.g. UCYN-B; UCYN-A in symbiosis within nanophytoplankton haptophytes) and microphytoplankton (e.g. *Trichodesmium* spp.; diatom diazotroph associations) previously detected in the STZ of the South Indian Ocean (Metzl et al., 2022; Chowdhury et al., 2024) or in some diatoms under high irradiance (Lohr and Wilhelm, 1999). ~~zeaxanthin, the pigment attributed to *Synechococcus* in the phytoclass algorithm, is also present in microphytoplankton cyanobacteria such as *Trichodesmium* spp. (Jeffrey et al. 2011) and in low concentrations in some Diatoms under high irradiance (Lohr and Wilhelm, 1999) which could explain the attribution of *Synechococcus* in microphytoplankton.~~ Thus, our result underline the importance of interpreting phytoplankton size structure data in the context of methodological constraints. The presence of picophytoplankton groups in larger size classes and the dominance of haptophytes in the picophytoplankton underscore the need for complementary validation using microscopy, flow cytometry or molecular techniques.**

4.1.3 ~~Inter-zonal spatial variability~~ **Geographical distribution of phytoplankton biomass and productivity size structures in relation with environmental factors**

~~As expected~~, The size structures of ~~the~~ integrated biomass and primary production clearly shifted between the oligotrophic subtropical waters and the Southern Ocean waters, **consistent with previous studies conducted in the Indian and Atlantic sectors of the Southern Ocean (Froneman et al., 2001; Mishra et al., 2017, 2020).** Result from the

490 multivariate analysis showed that **potential temperature (θ), DIC and NO_x concentration (and DIP due to its strong correlation with NO_x, see section 2.6)** were the major factors ~~in describing this~~ **driving the** spatial variability between the different zones (Fig. 6). Indeed, temperature, ~~salinity and macronutrients~~ **NO_x concentration** are ~~known~~ **recognized as key** factors to shape phytoplankton biomass and productivity size structures, ~~notably~~ **with picophytoplankton usually found prevalent** in warm and oligotrophic waters (Marañón, 2009; Hörstmann et al., 2021; Berthelot et al., 2025). ~~The spatial variability in the size structures of TChla and NPP was also observed in the Atlantic basin.~~ In our study, the TChla and NPP size structures in the PFZ, AZ and KER were mainly sustained by nano- (TChla: 40 ± 12%; NPP: 30 ± 12%) and microphytoplankton (TChla: 47 ± 14%; NPP: 66 ± 13%), which were consistent with previous studies **conducted** in the Atlantic and Indian sectors of the Southern Ocean, **encompassing both HNLC and HN-LSi-LC low-productivity waters as well as high-productivity waters near the Crozet and Kerguelen Islands** (Froneman et al., 2001, 2004; Seeyave et al., 2007; Uitz et al., 2009). By contrast, **the TChla size structure in the SAZ was mainly dominated by pico- (41%) and nanophytoplankton (36%), consistent with observations from other sectors of the SAZ in the Atlantic (Froneman et al., 2001) and western Pacific sectors (Boyd et al., 1999; McKay et al., 2005; Gutiérrez-Rodríguez et al., 2020). Similarly,** the TChla size structure in the STZ was mainly driven by the pico- (43 ± 10%) and nanophytoplankton (40 ± 10%). To our knowledge, there is no size-fractionated data for biomass and NPP in the literature in the STZ of the ~~SIO~~ **South Indian Ocean**. 505 Nevertheless, our results **were similar to those of Froneman et al. (2001) in the South Atlantic STZ, which reported a TChla size structure driven by pico- (49 ± 10%) and nanophytoplankton (39 ± 6%), but differed from other studies conducted in the northern and southern subtropical Atlantic** ~~differed from previous studies in the subtropical Atlantic,~~ where picophytoplankton accounted for ~~55~~ **60–75%** of TChla_{TOTAL} (Marañón et al., 2001; Morán et al., 2004). **As temperature and NO_x concentrations were similar between our study and the latter, several hypotheses could explain** 510 ~~the discrepancies~~ **differences** in TChla size structure **between the Atlantic and the Indian basins may be attributed to factors** such as regional-scale hydrodynamics **and/or** atmospheric inputs (Marañón, 2009). Nevertheless, Zhang et al. (2012) reported a latitudinal variability of TChla size structure in the western Pacific, with picophytoplankton being less dominant in subtropical than in tropical regions. For all that, extensive researches are needed in the ~~SIO~~ **South Indian Ocean** to better understand the potential factors in shaping the size structures of phytoplankton biomass and productivity, especially in the 515 STZ.



520 **Figure 6: Principal Component Analysis illustrating the relationships between explanatory variables and supplementary descriptors across the global study area. The first principal component (PC1) axis explains 50.5 47.8% of the variance and the second principal component (PC2) axis explains 20.7 22.8% of the variance. On the left panel, the black arrows indicate the explanatory variables (environmental factors) with their transparency defined by their \cos^2 : the better the variables are well represented by the principal components, the higher the \cos^2 . The blue arrows show the supplementary descriptors: NPP, TChla and phytoplankton chemotaxonomic groups biomass in each size class. On the right panel, the colour of each point represents the zone of each sample (n = 72).**

Phytoplankton chemotaxonomic groups biomass also varied in association with changes in TChla size structure.

525 Cyanobacteria, pelagophytes and chlorophytes mainly sustained picophytoplankton in the STZ – typical for **LNLC oligotrophic** areas with low mixing – while diatoms, haptophytes and dinoflagellates mostly sustained nano- and microphytoplankton in the PFZ, AZ and KER region – typical in areas where these opportunistic taxa are particularly well suited to take advantage of excess nutrient (Fig. 5 and 6) (Schlüter et al., 2011; Leblanc et al., 2018). Possible species that may account for much of the biomass of these phytoplankton chemotaxonomic groups include: *Synechococcus* and

530 *Prochlorococcus* for cyanobacteria; *Pelagomonas*, *Micromonas* for pelagophytes; *Chloroparvula*, *Chloropicon* for chlorophytes; *Chaetoceros*, *Corethron*, *Coscinodiscus*, *Eucampia*, *Fragilariopsis*, *Thalassiosira* for diatoms; *Gephyrocapsa*, *Chrysochromulina*, *Phaeocystis* for haptophytes; and, *Amphidinium*, *Gymnodinium*, *Protoperidinium*, *Prorocentrum* for dinoflagellates (Armand et al., 2008; Lasbleiz et al., 2016; Patil et al., 2017; Irion et al., 2020; Hörstmann et al., 2021; Sreerag et al., 2023, 2025; Thyssen et al. 2024). Recent studies have nevertheless underlined

535 that some eukaryotic picophytoplankton groups, such as prasinophytes – belonging to the green algae lineage within chlorophytes – can also benefit from enhanced nutrient conditions (e.g. ammonium; Irion et al., 2020) or deep-mixing and low-light regimes in HNLC open ocean waters (Gutiérrez-Rodríguez et al., 2023). Also, when focusing on the size

structure of phytoplankton chemotaxonomic groups biomass, several common features were observed between Nunes et al. (2019) in the South Atlantic Ocean and our study in the **SIØ South Indian Ocean**, for similar latitudes. First, we observed that **Haptophytes haptophytes** was the main and ubiquitous group within each size class across the **SIØ study area**; a feature also observed by Nunes et al. (2019) across the Atlantic Ocean. Second, Nunes et al. (2019) reported in the subtropical and tropical Atlantic Ocean the dominance of cyanobacteria in the picophytoplankton (70 % of TChla_{PICO}), and the dominance of haptophytes and dinoflagellates in the > 3 µm fraction (63% of TChla_{NANO+MICRO}). These results are in good agreement with ours in the STZ as cyanobacteria represented 70%± 13% of TChla_{PICO} (Fig. 5f) and the sum of haptophytes and dinoflagellates represented 53 ± 6% of TChla_{NANO} and 57 ± 10% of TChla_{MICRO} (Fig. 5d and 5e). Third, we observed noteworthy contributions of diatoms to TChla_{PICO} in KER (20 ± 4%; Fig. 5f). Nunes et al. (2019) reported similar findings in the Atlantic sector of the Southern Ocean in Patagonian waters (~ 40% of TChla_{PICO}) and explained this result by the presence of picophytoplankton diatoms **such as *Minidiscus sp.* and bolidophytes (see section 4.1.2) Parmales, a picophytoplankton group genetically very close to diatoms and sharing similar pigments composition (Guillou et al., 1999). This explanation is supported by Deteix et al. (2024) who found that < 5 µm particles accounted for 47 ± 23% of total biogenic silica within the 0–200 m layer in the Indian sector of the Southern Ocean, corroborated by SEM-based identification of picophytoplankton diatoms.** Together, these findings across two ocean basins highlight the utility of combining pigment chemotaxonomy with size fractionation to reveal size-specific shifts in phytoplankton communities from subtropical to polar regions. The methodological consistency and alignment of results between these two studies offers promising avenues to refine global assessments of phytoplankton size structure and composition.

4.2 Intra-zonal variability of phytoplankton biomass and productivity

4.2.1 The Subtropical Zone

Stations O2 and O3, located in the western STZ at similar longitudes, exhibited strong differences in TChla stocks and NPP fluxes, despite comparable size structures of TChla and NPP. The integrated TChla_{TOTAL} and NPP_{TOTAL} at O3 were respectively 31% and 110% higher than at O2, primarily due to increases in the nano- (TChla: +32%; NPP: + 98%) and microphytoplankton (TChla: +77%; NPP: +217%) (Fig. 3). However, results from phytoplankton chemotaxonomic groups biomass did not display any noticeable shifts between O2 and O3 (Fig. 5). These differences were likely driven by higher nutrient contents at O3 (NO_x: +115%; DIP: +67%; DSi: +49%; Table S6). Satellite-derived sea surface height data (GLORYS product) indicated the presence of a cyclonic eddy at O3 characterized by a shallower Z_{SML} (Table 2) and nitracline depth than at O2 (data not shown), leading to nutrient upwelling and enhanced productivity and biomass. These hydrographic and biogeochemical features are consistent with previous observations of cyclonic eddies in the Mozambique Channel and Basin, **which are characterized by a shallower Z_{SML} and nitracline, and a deeper euphotic zone** (Lamont and Barlow, 2017). Our NPP fluxes are **in agreement with similar to** previous studies, reporting a 20–100% increase in integrated NPP_{TOTAL} in cyclonic eddies compared to non-eddy areas in the Bay of Bengal (Prasanna Kumar et al., 2007; Sarma et al., 2020), in the

570 **SIIO South Indian Ocean** (Dalabehara and Sarma, 2021) **and in the subtropical North Pacific Ocean** (Landry et al., 2008).
Moreover, Sarma et al. (2020) reported no significant differences in the NPP size structure between cyclonic eddy and non-
eddy areas, which supports our findings. About TChla, there is a lack of previous studies focusing on eddies in the Indian
Ocean to compare with our dataset. Nevertheless, Vaillancourt et al. (2003) reported a similar 28% increase of integrated
TChla in cyclonic eddy compared to non-eddy areas in the subtropical North Pacific Ocean. **In addition, Beatty et al., (2025)**
575 **reported, in the latter region, based on amplicon sequencing data, that protistan community composition showed no**
response to eddy forcing in the water column, which is consistent with our results from phytoplankton chemotaxonomic
group biomass.

4.2.2 The Polar Frontal Zone

Stations O6, O7 and O9 follow a west-east transect, from the Crozet Plateau toward the northwest continental margin
580 of Kerguelen Plateau (Fig. 1). The lower integrated TChla_{TOTAL} observed at O9 compared to O6 and O7 may be attributed to
the island mass effect, where the persistent micronutrients supply downstream of Crozet shape phytoplankton biomass that
decline with distance, as micronutrients become depleted in the SML (Graham et al., 2015; Robinson et al., 2016).
Notwithstanding, the TChla size structure at O7 differed from O6 and O9, despite similar NPP_{TOTAL} and NPP size structure.
Indeed, at O7, the microphytoplankton contribution to TChla_{TOTAL} was reduced while that of nano- increased (Fig. 3; Table
585 S3). The decrease in the TChla_{MICRO} contribution at O7 was due to the decrease of microphytoplankton diatoms biomass by
4.3–6.2 mg m⁻² compared to O6 and O9 (Fig. 5a). Conversely, the TChla_{NANO} contribution increase was caused by the increase
of nanophytoplankton haptophytes and chlorophytes biomass by 3.9–7.5 mg m⁻² in comparison to O6 and O9 (Fig. 5b). This
community shift corroborated with lower integrated DSi content over the Z_{EL0.01%} at O7, on average 60% lower than at O6 and
O9 (Table S6). This decrease at O7 likely resulted from a low DSi surface water mass intrusion from the SAZ, leading to the
590 growth limitation of microphytoplankton diatoms in favour of a non-silicifying nanophytoplankton community dominated by
haptophytes. This transect is known to be influenced by the southern branch of the SAF current (Park et al., 1993), especially
around 55–58°E where a signal of higher SST and lower fCO₂ has been previously observed (Poisson et al., 1993; Leseurre et
al., 2022). Indeed, underway continuous measurements during SOCARB recorded an SST increase and fCO₂ decrease between
Crozet and O7 around 54–56°E (data not shown).

595 4.2.3 The Antarctic Zone and the Kerguelen bloom area

The HN-LSi-LC station O10, located southwest of the Kerguelen plateau, and the KER stations (A3, E and
O12), exhibited similar NPP size structure, with a dominance of the microphytoplankton (75% ± 10%), although
NPP_{TOTAL} was approximately 2.5 times higher at the KER stations (Fig. 3b, Table S3). Similarly, the TChla size
structure at O10 and the KER stations was similar, with a dominance of microphytoplankton (59% ± 2%) dominated
600 **by diatoms, although TChla_{TOTAL} was approximately 1.6 times higher at the KER stations (Fig. 3a and 5d, Table S3).**
No major differences were observed in the chemotaxonomic biomass structure – except a slightly higher contribution

of pelagophytes in the TChla_{MICRO} at O10 compared to the KER stations (Fig. 5d). In contrast, the offshore HNLC station O11 displayed distinct size structures relative to the other stations. Both NPP_{TOTAL} and TChla_{TOTAL} were dominated by nanophytoplankton (mainly haptophytes and diatoms) with respective contributions of 50% and 57%.
605 In addition, both NPP_{TOTAL} and TChla_{TOTAL} at O11 were lower than those measured at station O10. Our results are consistent with the study by Uitz et al. (2009), conducted during the austral summer, which reported a dominance of microphytoplankton (mainly diatoms) in the Fe-fertilized waters of the Kerguelen Plateau and an increasing contribution of nanophytoplankton at offshore HNLC stations.

We now compare the southeastern and northeastern blooms in KER, at stations A3 and O12, respectively. The
610 highest integrated TChla and NPP at A3 and O12 reflected the well-documented natural Fe fertilization. Despite sharing similar TChla and NPP size structures, integrated NPP displayed variability, as integrated NPP_{TOTAL} at A3 was 70% lower compared to O12 (Fig. 3). **This difference may not be attributed to the phenology, as satellite-derived surface TChla (MODIS product) did not highlight major differences neither in the timing, nor in the magnitude of phytoplankton biomass (Fig. S5).** Previous studies raised potential factors in explaining the spatial variability in integrated NPP in iron-fertilized areas, such as Si concentrations, phytoplankton community shifts, **grazing pressure** or light-mixing regime (*e.g.* Seeyave et al., 2007).
615 as Si concentrations, phytoplankton community shifts, **grazing pressure** or light-mixing regime (*e.g.* Seeyave et al., 2007). First, A3 and O12 exhibited ~~suboptimal~~ DSi/NO_x ratios in the SML **lower than the Brzezinski ratio** (Table 2), indicating a potential Si limitation; **this indicates that Si availability does not explain the observed difference in NPP_{TOTAL} and outlying the latter Si availability hypothesis.** Second, phytoplankton chemotaxonomic groups biomass displayed a noticeable ~~shift~~ **difference** in the phytoplankton community structure at A3 compared to O12. The relative contributions of dinoflagellates and cryptophytes to integrated bulk biomass increased by 17% – to the detriment of diatoms and haptophytes by 18% – primarily due to increases in the nanophytoplankton (31%) (Fig. 5; Fig. S4). ~~This shift may not be attributed to the phenology, as satellite-derived surface TChla (MODIS product) did not highlight major differences neither in the timing, nor in the magnitude of phytoplankton biomass (Fig. S5).~~ Third, to investigate the light-mixing regime, we computed the ratio of the diadinoxanthin (DD) and diatoxanthin (DT) concentrations to TChla ((DD+DT):TChla). ~~as an indicator of the mixing processes in the water column (Moline, 1998). Briefly, DD and DT have little chemotaxonomic values but occupy a photoprotective function, with concentrations changing rapidly with irradiance (Demers et al., 1991). Given that most phytoplankton contain DD and DT, the (DD+DT):TChla ratio provides additional information on the vertical mixing rates of the water column along with the light regime (Moline, 1998).~~ **Although DD and DT have limited chemotaxonomic values, they have a photoprotective role, with concentrations that respond rapidly to changes in irradiance (Demers et al., 1991). Because most phytoplankton contain these pigments, the (DD+DT):TChla ratio provides useful information on the vertical mixing rates in the water column along with the light regime (Moline, 1998).** The (DD+DT):TChla_{TOTAL} ratio at A3 was homogeneous within the SML (Fig. 7a), indicating that the vertical mixing rate was – or had recently been – faster than the photoprotective response (Moline, 1998). Our result corroborated with Uitz et al. (2009), which also studied A3 in late austral summer 2005 and underlined the lack of relationship between the bloom occurrence and the light-mixing regime previously described by Park et al. (2008). In contrary, the (DD+DT):TChla ratio at O12 decreased with depth within the SML (Fig. 7b), implying that the
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vertical mixing rate was – or had recently been – slower than the photoprotective response (Moline, 1998). Therefore, the variability in integrated NPP_{TOTAL} between A3 and O12 could result from contrasting phytoplankton communities and/or light-mixing regimes. Our results highlighted the heterogeneous distribution of phytoplankton communities within the nano- and microphytoplankton size classes in similar productive regimes around the Kerguelen Plateau in late austral summer, which was previously raised only during austral spring by Lasbleiz et al. (2014).

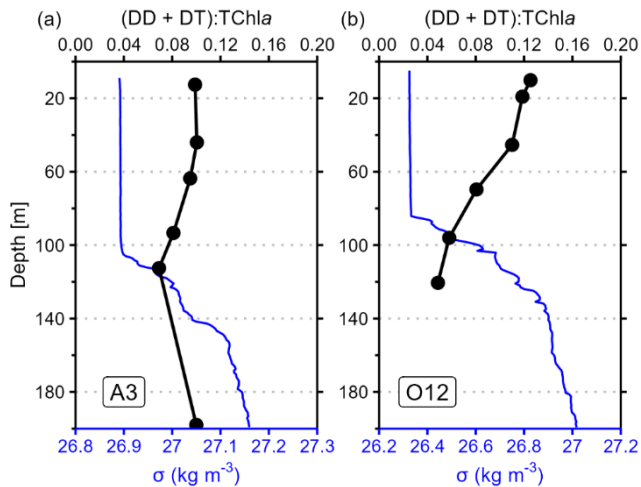


Figure 7: Vertical profiles of photoacclimation index $((DD + DT):TChla)$ in black and anomaly density (σ) in blue for stations A3 (a) and O12 (b).

4.3 Influence of the phytoplankton biomass size structure on NPP

Previously, we demonstrated firstly that NPP_{TOTAL} was mainly determined by the biomass of nano- and microphytoplankton across the study area, more specifically in the PFZ, AZ and KER region (Table 3), and highlighting their key role in driving NPP_{TOTAL} in the **SIIO South Indian Ocean**. Our results are in line with previous studies conducted during austral summer where microphytoplankton biomass drove primary production in iron-fertilised areas, and both nano- and micro- biomass were the drivers of primary production in iron-depleted areas (Froneman et al., 2001, 2004; Korb et al., 2005; Seeyave et al., 2007; Uitz et al., 2009; Shiomoto et al., 2023). However, these studies investigating the relationships between NPP and TChla size structure focused on the Southern Ocean, especially in geographically restricted region (Seeyave et al., 2007; Uitz et al., 2009) or in areas outside the Indian Sector (Froneman et al., 2001, 2004; Korb et al., 2005). While Shiomoto et al. (2023) brings a substantial contribution in the Indian sector of the Southern Ocean south of 60 °S, our study extends these researches northwards of the **SIIO South Indian Ocean**, up to the SAZ and STZ. Non-significative correlations in the SAZ between NPP_{TOTAL} and TChla size structure were likely due to the small sample number ($n = 6$), thus limiting any interpretation. Nevertheless, our study showed in the STZ that even though phytoplankton biomass size structure was mainly described by the pico- and nanophytoplankton, the biomass of each size class would play a significant role in driving NPP_{TOTAL}

(Table 3), including the microphytoplankton despite its small contribution to TChl a_{TOTAL} ($17 \pm 3\%$; Table S3). These results contrast with previous studies in subtropical domains suggesting that NPP $_{TOTAL}$ was mainly determined by the biomass of
660 pico- and nanophytoplankton (Froneman et al., 2001; Marañón et al., 2001).

Coupling between ~~NPP primary production~~ and phytoplankton community size structure provides an in-depth comprehension of the main phytoplanktonic contributors on the conditioning of NPP. Among the previous studies, Seeyave et al. (2007) and Uitz et al. (2009) investigated the relationships between NPP and phytoplankton community size structure from pigments concentrations. This involves assumptions of the phytoplankton chemotaxonomic affiliation, because certain
665 pigments are major components in many taxa (Higgins et al., 2011). To address this gap, Takao et al. (2012) used satellite data to estimate the spatiotemporal distribution of NPP and four phytoplankton chemotaxonomic groups biomass (*Prochlorococcus*, *Synechococcus*, ~~Haptophytes and Diatoms~~ **haptophytes and diatoms**), from the STZ to the AZ over 1997–2007. Our study **including fills a gap in this field, as our** *in situ* data coupled with the size fractionation approach provides a refined perspective on the phytoplankton community size structure. For instance, among the biomass of nano- and
670 microphytoplankton which drove NPP $_{TOTAL}$ in the global study area, the biomass of haptophytes, dinoflagellates and diatoms displayed the highest correlations with NPP $_{TOTAL}$ (Table 4), highlighting the key roles of these chemotaxonomic groups in driving NPP $_{TOTAL}$ in the ~~SIO~~ **South Indian Ocean**. Moreover, the significant correlations of NPP $_{TOTAL}$ with ~~Diatoms and Haptophytes~~ **diatoms and haptophytes** biomass **for the nano- and microphytoplankton** found in the PFZ, AZ and KER are consistent with the latter studies, but our size fractionation approach underlines the heterogeneity of the relationships in
675 between these zones for each size class (Table 4). Furthermore, while Takao et al. (2012) restricted their study to only four phytoplankton groups biomass due to the limits of the satellite approach, our results showed additional relationships of NPP $_{TOTAL}$ with the biomass of secondary phytoplankton groups in the AZ and KER such as ~~Chlorophytes, Dinoflagellates and Cryptophytes~~ **chlorophytes, dinoflagellates and cryptophytes**. Therefore, our findings contribute to a better understanding of the role of phytoplankton community size structure in modulating primary production in the ~~SIO~~ **South Indian Ocean**,
680 highlighting that NPP was influenced by the phytoplankton size structure and was not necessarily driven by a single dominant phytoplankton group within a given zone.

**Nevertheless, the relationship between NPP and phytoplankton TChl a biomass size structure should be interpreted with caution, as it is influenced by ecological and physiological factors such as the carbon to TChl a ratio (C:TChl a) and the growth rates. For instance, C:TChl a ratio in phytoplankton varies with temperature, irradiance and the degree of nutrient limitation, being the lowest under high temperature, low irradiance and nutrient-replete
685 conditions (Geider, 1987; Geider et al., 1997; Jakobsen and Markager, 2016; Landry et al., 2022). Moreover, the C:TChl a ratio depends on cell size and taxonomy, with larger cells having higher C:TChl a ratio than smaller cells (*e.g.* Geider, 1987; Yingling et al., 2025). Consequently, observed correlations between size-fractionated TChl a biomass and NPP may be partly influenced by differences in the C:TChl a ratio among size classes and taxa. Similarly, growth rate
690 displays taxonomic dependence, with diatoms, cryptophytes and chlorophytes exhibiting higher rates than dinoflagellates, haptophytes and pelagophytes in the Southern Ocean (*e.g.* Latasa et al., 2014; Gutiérrez-Rodríguez et**

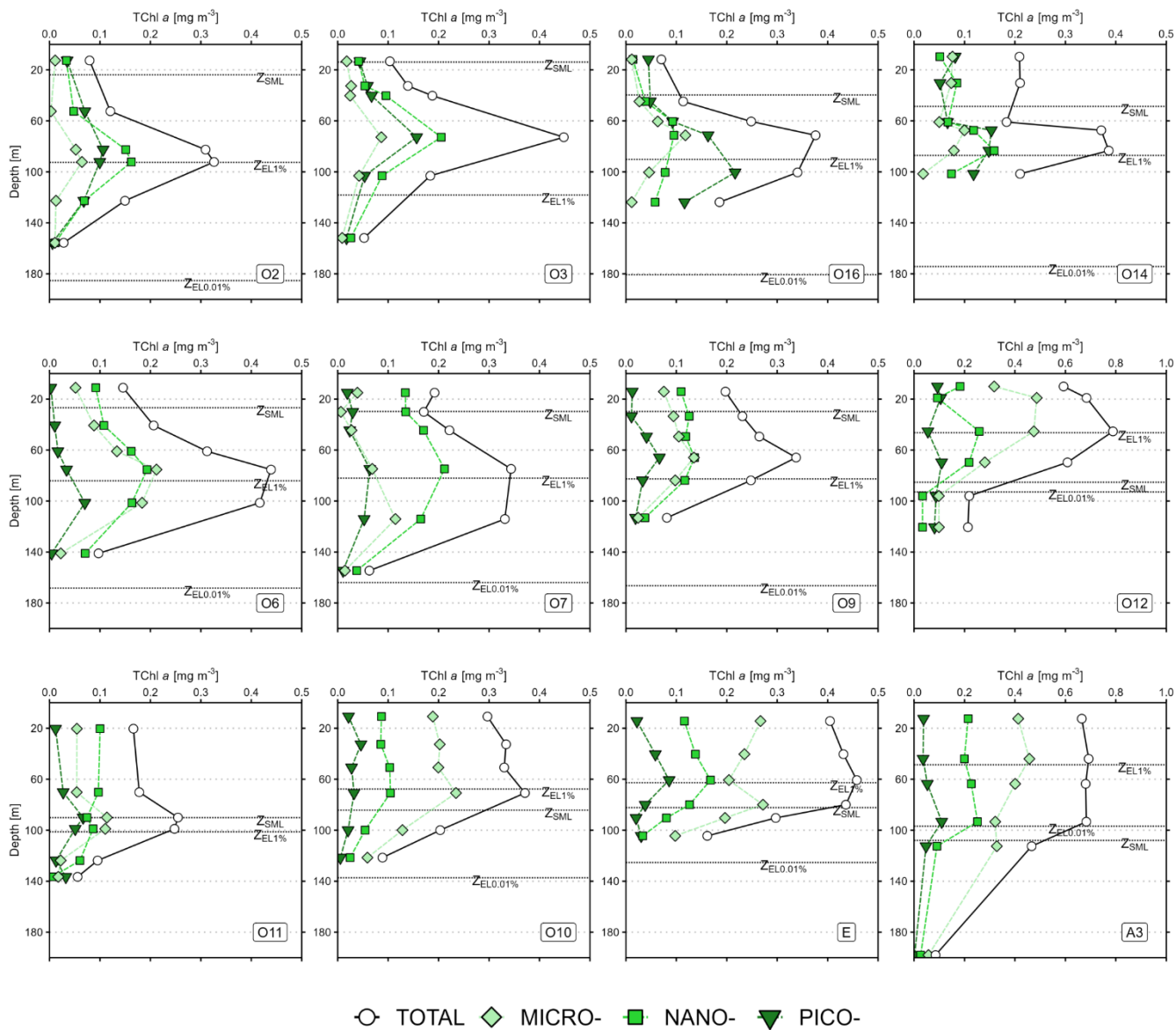
al., 2023). As a result, high growth rates can lead to elevated NPP even when TChl a is low, while slow-growing taxa may accumulate TChl a without contributing proportionally to NPP (Behrenfeld et al., 2005). Consequently, additional field studies using the size fractionation approach combined with measurements of C:TChl a ratios and growth rates across size classes and phytoplankton groups are needed to improve our understanding ~~complement our current knowledge~~ on the influence of phytoplankton biomass size structure on NPP, especially in the SAZ and STZ where NPP and phytoplankton data remain sparse.

5 Conclusion

Using a size fractionation approach, the size structures of phytoplankton algal biomass and primary production were assessed in the ~~SIO~~ South Indian Ocean – including the Indian Sector of the Southern Oceans – during the austral summer 2023, to describe their spatial variability and study the links between primary production and phytoplankton biomass size structure. Across the study area, integrated TChl a size structure was mainly described by the nano- and microphytoplankton size classes, while integrated NPP size structure was dominated by the micro- size class. Furthermore, TChl a size structure exhibited a greater spatial variability compared to NPP size structure. Using the novel pigment chemotaxonomy tool phytoclass (Hayward et al., 2023) coupled with the size fractionation approach, we determined that haptophytes were the main and ubiquitous group in each size class in the ~~SIO~~ South Indian Ocean, and that the remaining phytoplankton community shifted within each size class across the ~~SIO~~ study area. On the one hand, integrated TChl a in the STZ was described by pico- and nanophytoplankton, more specifically composed of cyanobacteria (*Prochlorococcus* and *Synechococcus*) in the pico- and of haptophytes and chlorophytes in the nanophytoplankton. On the other hand, integrated TChl a in the PFZ and AZ was described by nano- and microphytoplankton and featured a community dominated by diatoms and haptophytes. Our results also underline the intra-zonal variability of phytoplankton biomass and productivity through bottom-up processes, such as the occurrence of a cyclonic eddy in the STZ or the intrusion of a DSI-depleted water mass in the PFZ. When focusing on the links between NPP and TChl a size structure, we demonstrated that NPP_{TOTAL} was mainly determined by the biomass of nano- and microphytoplankton across the study area, more specifically by the biomass of haptophytes, dinoflagellates and diatoms within these size classes. When deciphering these relationships within each zone, our results not only were consistent from previous studies, but also exhibited additional relationships with secondary phytoplankton groups, which could not be identified before due to limitations of previous methodologies.

This study paves the way for a better comprehension of the primary production and phytoplankton community size structure in the ~~SIO~~ South Indian Ocean, as the size fractionation approach allows to better quantify the impact of the structure and dynamics of the phytoplankton community and their role in the BCP. Furthermore, the concordant results of phytoplankton community size structures between Nunes et al. (2019) in the South Atlantic Ocean and this study in the ~~SIO~~ South Indian Ocean using similar approaches provide promising perspectives in refining the size structure of phytoplankton community at a global scale. In this way, we strongly encourage the marine biogeochemical community, if possible, to use the size

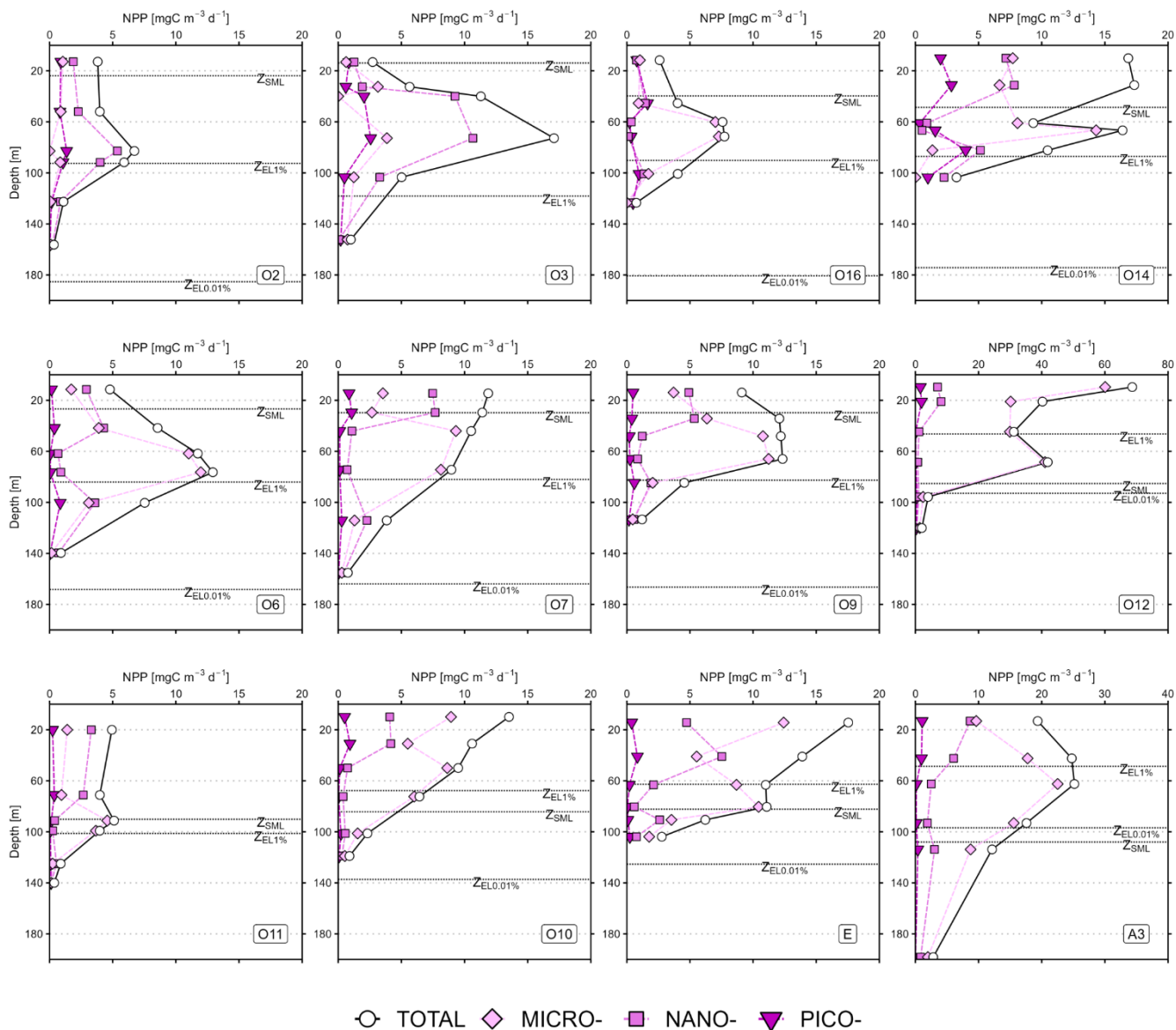
fractionation approach to evaluate the phytoplankton community and its associated fluxes. Complementary to SOCARB, these
725 data will be coupled in future works with cytometry and DNA metabarcoding data, to address a more detailed taxonomic
description of the phytoplankton community, such as evaluating the spatial variability of the community within the
haptophytes, which were found in this study to be the main and ubiquitous group in the **SIØ South Indian Ocean**.



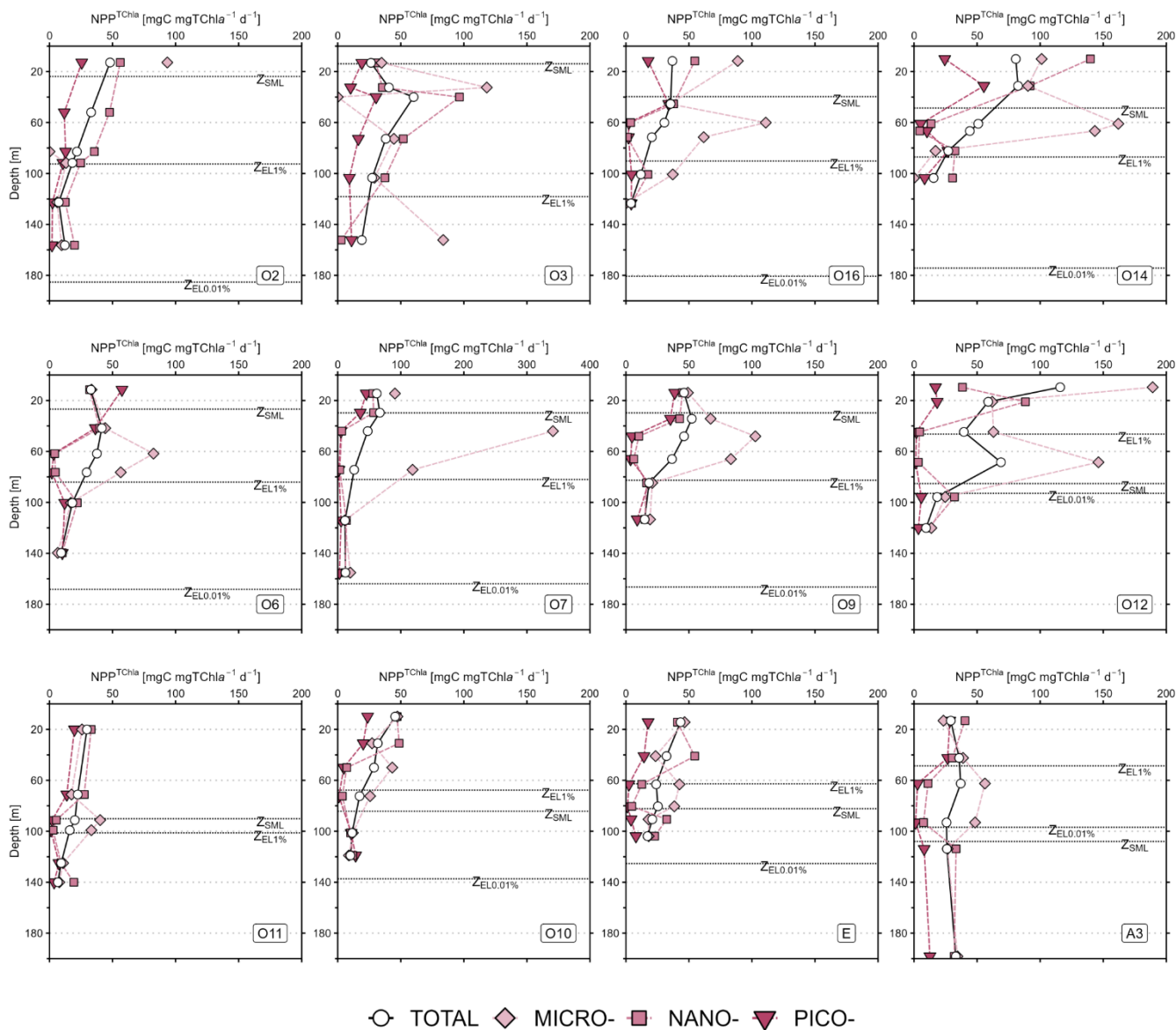
Appendix A: Vertical profiles of TChl_a, NPP and TChl_a-normalized NPP for all SOCARB stations.

730

Figure A1. Vertical profiles of total chlorophyll *a* (TChl_a) at the SOCARB stations. Mind the scale differences at O12 and A3. The dashed lines represent the depth of the mixed layer (Z_{SML}), the depth of the 1% euphotic layer ($Z_{EL1\%}$) and the depth of the 0.01 % euphotic layer ($Z_{EL0.01\%}$).



735 **Figure A2.** Vertical profiles of net primary production (NPP) for the SOCARB stations. Mind the scale differences at O12 and A3. The dashed lines represent the depth of the mixed layer (Z_{SML}), the depth of the 1% euphotic layer ($Z_{EL1\%}$) and the depth of the 0.01% euphotic layer ($Z_{EL0.01\%}$).



740

Figure A3. Vertical profiles of TChla-normalised net primary production (NPP^{TChla}) for the SOCARB stations. Mind the scale differences at O7. The dashed lines represent the depth of the mixed layer (Z_{SML}), the depth of the 1% euphotic layer ($Z_{EL1\%}$) and the depth of the 0.01% euphotic layer ($Z_{EL0.01\%}$).

Data Availability

Data available in this article will be subsequently submitted to the SEANOE database.

745 Author contribution

Valentin Deteix: Formal analysis, investigation, methodology, validation, visualization, writing – original draft. **Céline Ridame:** Conceptualization, formal analysis, funding acquisition, investigation, methodology, supervision, validation, visualization, writing – review and editing. **Celine Dimier:** Investigation, methodology, writing – review and editing. **Claire Lo Monaco:** Funding acquisition, investigation, project administration, writing – review and editing. **Aline Tribollet:** Supervision. **Frédéric Planchon:** Funding acquisition, investigation, project administration, writing – review and editing.

Competing interests

The authors declare that they have no conflict of interest.

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