

Interactive comment on « Southern Ocean biological pump over the last glacial cycle from new diatom transfer functions » by Rembauville and Pichat.

Authors response to Reviewer 1

We thank the anonymous reviewer #1 for reviewing our manuscript and the constructive comments that helped us improve the manuscript. All the modifications appear on the new version of the manuscript and the supplementary information attached as a supplement to this answer.

R1-Cx: Reviewer comment, **R1-Rx:** authors response, **Change made :** **change to the manuscript.**

General comments

R1-C1. The manuscript by Rembauville and Pichat aims to reconstruct past deep-ocean particulate organic carbon (POC) flux and the particulate inorganic carbon-to-particulate organic carbon (PIC/POC) export ratio using diatom assemblages preserved in sediment cores. First, the authors identify statistical relationships between the relative abundances of diatom species and organic carbon fluxes measured in several sediment traps deployed at depths of 1000–2000 m. Second, they apply these statistical relationships to the relative abundances of diatoms in several sediment cores to estimate variations in POC flux and PIC/POC from 150 ka to the present, depending on the core examined. Third, they compare the new diatom-based reconstructions with established palaeoproductivity records (%TOC, %CaCO₃, $\delta^{15}\text{N}_{\text{db}}$, Ba/Fe) previously published for the same cores. Overall, the new records broadly reproduce the patterns observed in the published palaeoproductivity records. One of the main findings of the manuscript is that this new approach reconstructs an increase in the biological carbon pump in the Antarctic Zone (AZ) during glacial periods, which contrasts with decades of research on this topic. The authors propose several hypotheses to explain these unexpected results, which is commendable. Such a potential paradigm shift would certainly stimulate further discussion.

However, the results and interpretations rely heavily on the robustness of the transfer function, which is based here on a purely statistical approach with limited ecological or biogeochemical justification and appears to be biased at several levels.

R1-R1. We thank the reviewer for the careful reading of the manuscript and the identification of the potentially important implications of our findings. We detail below a point-by-point response to address the questions and remarks associated to the transfer functions calibration and application.

R1-C2. First, the transfer function is developed using the relative abundances of diatoms and POC fluxes. However, the metric used by the authors is inappropriate, as diatom relative abundances have little direct biogeochemical meaning. The more appropriate metric would be the flux of diatom species or, preferably, the flux of diatom biovolumes. These fluxes determine the amount of biogenic silica (BSi) and POC exported to the deep ocean, as demonstrated by the authors themselves in previous work (Rembauville et al., 2015) and by several other studies (Rigual-Hernandez et al., 2015, 2016). Indeed, the link between relative abundances—i.e. the proportion of

each species within the total diatom assemblage—and POC flux (and even more so the PIC/POC ratio) remains unclear. Some studies have even reported the absence of a relationship between diatom relative abundances and POC flux (e.g. Grigorov et al., 2014; their Figure 5). For example, the same proportion of *Fragilariopsis kerguelensis*, the dominant diatom species in the open Southern Ocean, could occur in samples with very different absolute diatom abundances (millions of diatoms per litre of seawater) or export fluxes (millions of diatoms per litre per day). In such a scenario, a relative abundance of 50% *F. kerguelensis* in a flux of 10^6 diatoms $\text{m}^{-3} \text{d}^{-1}$ would export far less BSi and POC than the same 50% proportion in a flux of 150×10^6 diatoms $\text{m}^{-3} \text{d}^{-1}$. However, this fundamental difference is disregarded when relative abundances are used instead of fluxes. This issue is reflected in Figure 2 of the present study, where high POC values in the WSC correspond to a wide range of *C. pennatum* relative abundances, while low POC values from 47°S to P2 are associated with markedly different diatom assemblages.

R1-R2. The comment made by the reviewer is indeed true and valid for direct biomass measurements and/or fluxes reconstruction in sediment traps. As underlined by the reviewer, a direct quantitative conversion of diatom fluxes into chemical fluxes was notably used for POC fluxes based on diatom and faecal pellets fluxes and biovolume (Rembauville et al., 2015, 2016b) and PIC fluxes based on coccolithophores and foraminifer fluxes (Rembauville et al., 2016a). However the quantitative estimation of organic carbon flux from biovolumes needs a precise determination of the full vs. empty frustule fraction for each diatom species together with an absolute estimation of cell fluxes. These two key variables are not available in sediment cores. Hence, we propose a method that circumvent this problem and relies on the use of diatom relative abundance from counting. To clarify the difference between sediment trap “classic” approach and our new approach for sediment, we added this justification in the manuscript.

Change made l. 165-173: “Previous studies reported the direct quantitative link between plankton community structure and carbon export fluxes in sediment trap samples (e.g. Rembauville et al., 2015, 2016a, b). Such an approach needs a precise quantification of the full and empty diatom frustule flux together with the consideration of other flux vectors such as faecal pellets to estimate biovolumes and calculate carbon fluxes. The full/empty frustule distinction, the faecal pellets abundance, and the absolute fluxes are not available in sediment cores. Here, we use an alternative approach and suggest that the diatom community integrates the ecosystem structure that is the ultimate driver of the export fluxes. We do not formulate explicit mechanistic relationships between diatoms and POC or PIC fluxes. Rather, we consider that diatom community structure is correlated with biotic (e.g. other phytoplankton, zooplankton, calcifiers, bacteria) and abiotic conditions (hydrological zones, micronutrient availability) that altogether drive the biological pump and carbonate counter-pump.”

See also R1-R12 and modification made to answer the comment:

Change made l. 321-324: “Species associated with high scores on factors used in the MLR are consistent with the ones that have both high partial correlation coefficients in the PLSR and a high importance in the GBR. This suggests that the same ecological processes link the diatom community composition and the chemical fluxes in the three transfer functions, resulting in comparable dynamics in the reconstructed variables.”

R1-C3. The reconstruction of the PIC/POC ratio from diatom assemblages is even more tentative, given that diatoms do not precipitate CaCO_3 . As biogenic silica and CaCO_3 production and burial are currently concentrated south and north of the Polar Front Zone (PFZ), respectively (Ragueneau et al., 2000), and generally show an anti-correlation at glacial–interglacial timescales (Choi et al., 2025), estimating PIC/POC from diatom assemblages appears to rely on purely statistical relationships rather than on a clear mechanistic basis.

R1-R3. The rationale behind the use of diatom communities to reconstruct the PIC:POC export ratio is that diatom species distribution is strongly constrained by hydrological conditions as revealed by the factorial analysis. Thereby it catches part of the variance of calcifying plankton distribution. This relationship is indeed purely statistical as it is often the case in transfer functions. The study by Choi et al. (2025) mentioned by the Reviewer reports a decrease in PIC content and an increase in TOC content during glacial periods such as MIS 2 and MIS4. These results are in good agreement with our findings of lower PIC:POC export ratio during glacial periods, which comfort the idea that the approach we propose is robust. We modified the manuscript to take the reviewer remark into account.

Change made l. 486-488: “A decrease in PIC content and an increase in TOC content during MIS 2 and MIS 4 was reported in multiple sediment cores located in the Indian Sector (Choi et al., 2025). These results are in agreement with our reconstructions of a lower glacial PIC:POC export ratio.

Change made l. 345-347: “Although the calcifying plankton is not explicitly taken into account in this study, these results suggest that diatom communities, partially shaped by hydrological zones, appears to capture efficiently the global changes in ecosystem structure that set the magnitude of the carbonate counter-pump.”

R1-C4. Second, the modern relationships between diatom assemblages and geochemical fluxes are derived from sediment traps deployed at depths of 1000–2000 m. The authors state that there is little flux attenuation and minimal modification of diatom assemblages below these depths; however, this assertion contradicts several previous studies. Indeed, a significant loss of small, lightly silicified diatoms (e.g. *P. lineola*, *T. gracilis*) and a concomitant enrichment of heavily silicified taxa (e.g. *A. tabularis*, *T. lentiginosa*, *Chaetoceros* resting spores) has been documented between deep sediment traps (1500 m in the PFZ or 3800 m in the SAZ) and surface sediments (Rigual-Hernandez et al., 2016). This selective preservation highlights the importance of species such as *T. lentiginosa* in the export of biogenic silica (BSi) (Shukla, 2016), and potentially of organic carbon (C_{org}) if stoichiometric relationships are preserved through time.

R1-R4. We do not state that there is little attenuation of diatom flux below 2000 m but rather that dedicated studies reported little change of both POC and PIC fluxes between 1000-2000 m (see l. 101-106). On the contrary the comparison of the sediment trap and sediment core diatom dataset clearly suggests a selective dissolution/preservation of certain species, supporting the need for a selection of a common list of informative species in both sediment trap and sediment core datasets. This is indicated in the original version of the manuscript : “*The slope of the rarefaction curve is steeper in the sediment core dataset when compared to the sediment trap data, with the most abundant species in the cores characterized by a heavily silicified frustule (e.g. Fragilariopsis and large Thalassiosira species). These results confirm previous observations of selective dissolution of*

lightly silicified species in the deep ocean below the sediment traps depth (Rigual-Hernández et al., 2016; Warnock and Krueger, 2020; Ran et al., 2024). Hence, the selection of informative species in both datasets is a critical preliminary step before calibrating the transfer functions. The resulting rather small number of informative species (here 22) is due to the merging of the sediment trap and sediment core datasets in which the most abundant species are different.”

Additionally, one key finding of previous sediment trap studies in the SO is that the BSi:POC export ratio is highly variable at the species level. It results from both physiological constraints, e.g. the level of silicification being species-specific and related to environmental conditions such as iron limitation, and ecological constraints, e.g. some species are specifically targeted by grazers resulting in high empty:full cell ratio in the exported material). The case of *T. lentiginosa* is a very good example of a species exported with an empty:full cell ratio > 20 around both Kerguelen (Rembauville et al., 2015) and South Georgia islands (Rembauville et al., 2016b), hence preventing the use of the absolute frustule flux of this species (and the BSi flux) to reconstruct the POC flux.

Change made I. 299 : Typo corrected “curse” replaced by “curve”.

Change made I. 302 : The reference to Rigual-Hernández et al. (2016) was added.

R1-C5. Third, the POC flux and PIC/POC ratio reconstructed using the transfer function are compared with several palaeoproductivity records. However, none of the proxy records used represents the same metric, as the authors rely on %TOC, %CaCO₃, and $\delta^{15}\text{N}_{\text{db}}$. Both %TOC and %CaCO₃ are strongly affected by sedimentary dilution, whereas $\delta^{15}\text{N}_{\text{db}}$ is generally considered a more conservative proxy. To allow a more meaningful comparison, the authors should present TOC fluxes from the same cores or from nearby cores. In addition, several earlier studies reporting Corg fluxes have been omitted (Shimmield et al., 1994; Bareille et al., 1998; Anderson et al., 2002). These studies consistently indicate lower glacial export and burial in the Antarctic Zone (AZ), which contrasts with the interpretation proposed in the present manuscript.

R1-R5. It is true that the results from our transfer functions are compared to different paleoproductivity proxies for the cores used in the study. It reflects both the scarcity of available sediment cores in the studied area and the global inhomogeneity of the sediment cores datasets for paleoproductivity reconstructions. We used the available data published on public repositories. Unfortunately, the TOC content is only published for cores PS1768-8 and PS1786-1. Following the Reviewer’s recommendations we added the TOC content for core PS1768-8 to Fig. 9c (see below) and also discuss the potential dilution effect by detrital sediments for this core.

The study by Bareille et al. (1998) concerns the Indian Sector and concludes that: *“Integrated accumulation rates across the whole Indian sector of the Southern Ocean indicate that the burial of organic carbon which is held approximately constant, contrasts with lower biogenic silica and carbonate burial rates during glacial intervals”*. It does not support lower glacial POC exports but is consistent with lower PIC:POC export ratio during glacial intervals.

The study by Anderson et al. (2002) relies on ^{230}Th -normalized TOC accumulation rates, which in theory permits the reconstruction of a true vertical flux of TOC. However, in the studied area, the behavior of ^{230}Th is more complex as the ^{230}Th adsorption coefficient depends on the

chemical properties of the particles, with different affinities for CaCO and opal (Geibert and Usbeck, 2004). Furthermore the review by Costa et al. (2020) concludes that ^{230}Th is a powerful tool for reconstructing the bulk particles fluxes but needs refinements for specific organic carbon accumulation rates. It is clearly out of the scope of our study to discuss the use of ^{230}Th -normalized POC fluxes, and we added the important contribution by Anderson et al. (2002) as a reference in the introduction l. 48.

Change made l. 367-373: “The reconstructed POC flux is correlated with the TOC content during the Holocene and deglacial but not during the glacial maxima. Contrary to core PS1768-8 (Fig. 8), the reconstructed PIC:POC export ratio is not correlated with the CaCO_3 content (Fig. 9c). Decreases in the PIC:POC export ratio are associated with increases in the abundance of IRD during MIS 2. For this core, both the TOC and CaCO_3 content must be taken with caution due to 1) potential dilution effects by variable abundance of detrital sediments, especially during the last glacial and 2) the core depth (5862 m b.s.l.) which is deeper than the carbonate compensation depth, that can result in important CaCO_3 dissolution. Both processes could contribute to the low TOC and CaCO_3 contents observed in this core and partly explain their temporal variations.”

Change made to Figure 9 :

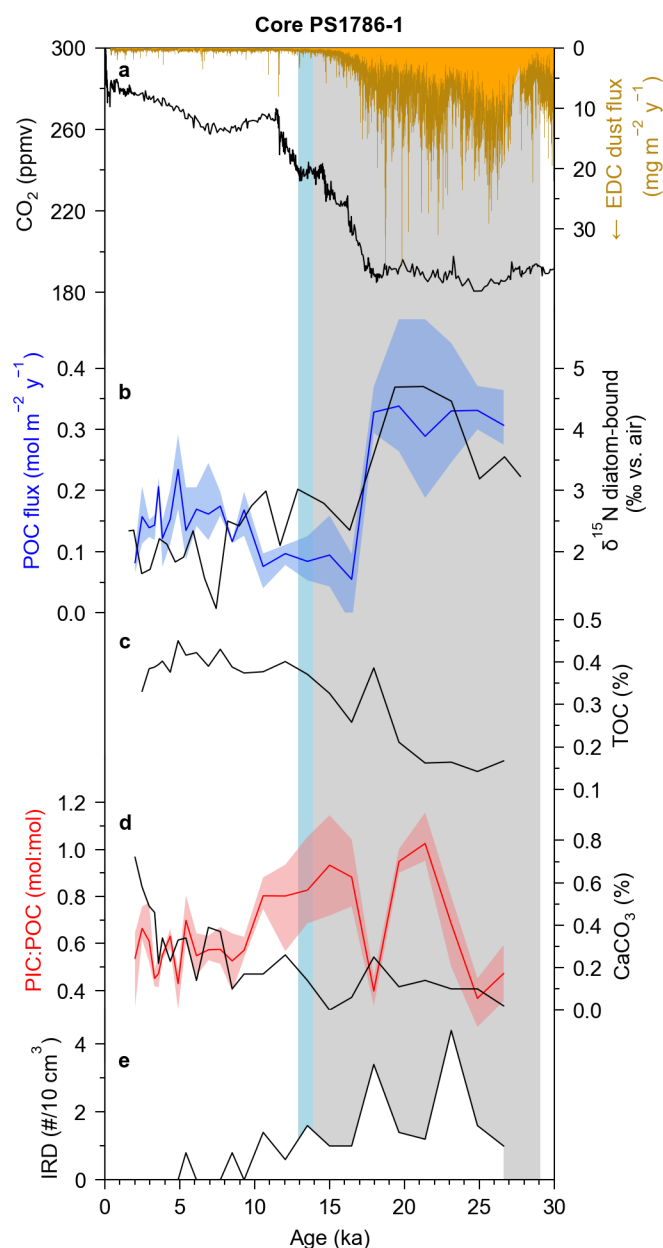


Figure 9. Comparison of the reconstructed POC flux and PIC:POC ratio with previously published data for core PS1786-1. a) Atmospheric CO₂ (black, Bereiter et al., 2015) and dust flux (brown, Lambert et al., 2012) from EPICA Dome C (EDC) ice core. b) Reconstructed deep-ocean POC flux (blue, this study) and diatom-bound $\delta^{15}\text{N}$ (black, Jacot Des Combes et al., 2008). c) **Total organic carbon (TOC) content (Grobe, 1996).** d) Reconstructed PIC:POC export ratio (red, this study) and sediment core CaCO₃ content (black, Grobe, 1996). e) Ice rafted debris (IRD) abundance (Grobe, 1996). In b) and c), the continuous line is the transfer functions average and the colored area is the transfer functions envelope. Grey and blue bars as in Fig. 6.

R1-C6. In conclusion, the manuscript presents a purely statistical approach that lacks a clear biogeochemical or ecological rationale. The methodology should employ more appropriate metrics—such as diatom fluxes or biovolume fluxes—which have a direct geochemical relevance for reconstructing POC export. In its current form, the approach relies on relative abundances, which do not adequately represent the magnitude of particle export. Furthermore, it is difficult to justify the reconstruction of the PIC/POC ratio from diatoms, particularly from diatom assemblages, given that diatoms do not produce CaCO_3 . The authors should also better constrain the potential loss and selective preservation of diatoms between the deepest sediment traps available and the surface sediments. Only once these issues are addressed could the resulting palaeoceanographic interpretations—currently at odds with previous studies on palaeoproductivity and nutrient supply—be evaluated using metrics that are comparable to those being reconstructed.

R1-R6. As stated in the Method section, the transfer functions do not rely on a direct mechanistic relationship between diatom fluxes and POC or PIC export, but rather on the statistical relationship between diatom community structure and ecosystem functioning that ultimately sets the biological pump and carbonate counter-pump intensities. This is a fundamental principle shared by all transfer functions based on microfossil records : the community structure is statistically correlated with a parameter, e.g. surface temperature, sea ice cover, pH, and the statistical relationship is used to reconstruct the parameter in the past. To our knowledge, all the existing transfer functions based on microfossils use species relative abundances (Imbrie and Kipp, 1971; Gasse et al., 1995; Crosta et al., 1998; Gersonde et al., 2005; Berner et al., 2008; Waelbroeck et al., 2009; Esper and Gersonde, 2014).

Concerning the potential loss and selective preservation of diatoms species between sediment traps and sediments, this limitation is taken into account by selecting the most abundant species in both the sediment trap and sediment cores datasets. This step drastically reduces the number of species used to calibrate transfer functions ($n = 22$), but ensures that the functions are calibrated and applied on comparable diatom communities only marginally affected by preservation issues. This is a conservative approach that certainly reduces the RMSE of the transfer functions but ensures more robust reconstructions. We now justify this choice more clearly in the methods.

Change made I. 148-160: “Our approach applies relationships between chemical fluxes and diatoms found in the mesopelagic/bathypelagic ocean (sediment traps) to sedimentary records. Indeed, the latter could potentially be affected by additional processes, e.g. diagenesis or sediment redistribution by deep-sea currents, that could modify the diatom community structure or the chemical fluxes. Diatoms are affected by selective grazing and dissolution during their sinking in the water column (Ran et al., 2024) and differential alteration of the frustule during early diagenesis (DeMaster et al., 1996; Pellegrino et al., 2024). For transfer functions calibration, the species present in both the sediment trap and sediment core datasets were first selected, i.e. 64 species/taxa groups (Fig. 3). Secondly, in order to avoid the bias associated with rare species and potential selective dissolution/preservation of species between the sediment trap and the surface sediments a filter was applied to isolate the abundant species shared by the two datasets. Species occurring with at least a relative abundance of 0.1 % in both datasets were selected (Esper and Gersonde, 2014). This final step resulted in a list of 22 informative species that we assume to be poorly affected by dissolution and diagenesis, ensuring a robust transfer from the sediment trap to the sediment core

datasets. The relative abundances of these informative species were rescaled to 100 % in the two datasets before using these data to calibrate the transfer functions.”

Minor comments (chronologically presented here below)

R1-C7. Line 77: Please further detail the role of diatoms in controlling the intensity and stoichiometry of the biological pump at the global scale.

R1-R7. Change made l. 83-86: “Diatom are major contributors to the global ocean primary production (Field et al., 1998; Uitz et al., 2010) and might contribute up to 40 % of the global POC export from the surface ocean (Jin et al., 2006). Furthermore, the diatom community structure has a strong influence on the biological pump intensity and stoichiometry through species-species strategies such as resting spore formation and highly variable Si:C ratio (Tréguer et al., 2018).”

R1-C8. Line 80: Please clarify what is meant by the deep ocean.

R1-R8. Change made l. 88: “In this study, we develop new transfer functions based on diatom community structure to reconstruct the deep-ocean (~1000 m) POC flux and PIC:POC export ratio.”

R1-C9. Line 106: The water depth between 1000 and 2000 m corresponds to the upper Circumpolar Deep Water (CDW), which is recirculated within the upper cell of the global meridional overturning circulation (MOC) (Marshall, 2012). Its residence time is on the order of a few hundred years. The apparent age of waters within this depth range is approximately 500 years today and around 1000 years during the Last Glacial Maximum (LGM) (Rafter, 2022). For carbon to be sequestered on climatically relevant timescales, export must reach deeper waters, namely the lower CDW and the lower cell of the MOC.

R1-R9. It is true that some sediment traps (MS2, MS3, MS4, 54S, Fig. R1) are located in the Upper Circumpolar Deep Water (UCDW) and that dissolved inorganic carbon (DIC) remineralized in these waters might be outgassed few hundred years later at the Antarctic divergence. However, other traps (MS5, P2, P3, WSC, 61S, PZB-1, see Figure below) are located in the Lower Circumpolar Deep Water (LCDW) fueling the antarctic bottom water (AABW) and therefore sequestering carbon for much longer timescale (up to millennia).

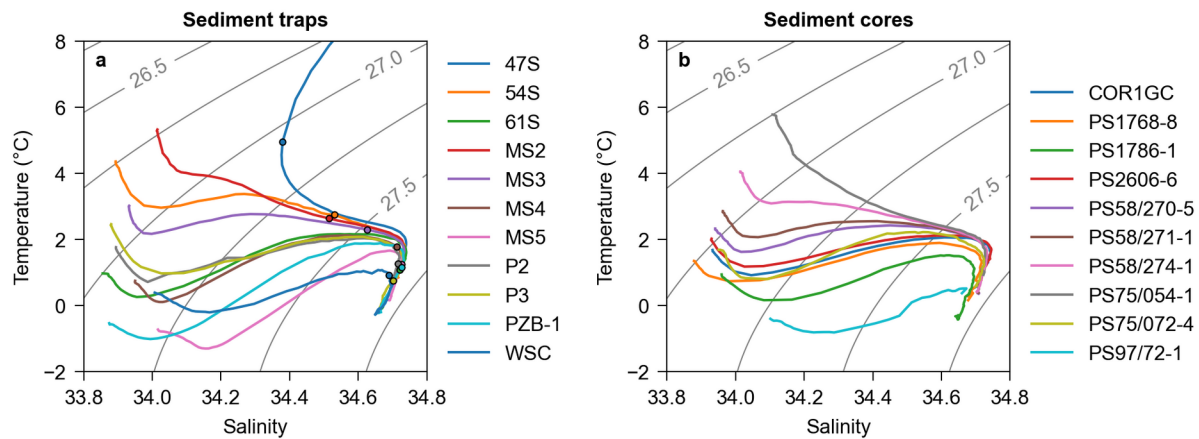


Figure R1: Temperature-Salinity diagram based on climatological data (World Ocean Atlas, 2023) extracted at the sediment trap (a) and the sediment core (b) locations. In (a), the dots represent the sediment trap location in the temperature/salinity space.

It is not possible to assess an homogeneous sequestration timescale for the entire sediment trap locations for two reasons : 1) as stated by Reviewer 1 the location is not homogeneous relative to the meridional overturning circulation (MOC) and 2) most of the particles remineralization occurs in the very upper part of the mesopelagic in the SO (Oetjens et al., 2025). . Hence, particles that reached ca. 1000-2000 m depth will only be marginally remineralized below that depth before reaching the antarctic bottom water (AABW) where the sequestration time reaches 1000 years (Siegel et al., 2021). Finally, the depth range of 1000-2000 m is considered as a standard depth for climate-relevant carbon sequestration at global scale in both observational (Henson et al., 2012) and modeling studies (Doney et al., 2024). We nuanced the original statement.

Change made l. 115-119: “Although some sediment traps considered in the study are located in the upper circumpolar deep water (UCDW) that latter reaches the atmosphere at the Antarctic divergence, we consider the compiled fluxes as representative of the deep ocean (~1000 to 2000 m) where carbon can be sequestrated over climate-relevant timescales from a few hundred years to millennia (Henson et al., 2012; Doney et al., 2024; Siegel et al., 2021).”

R1-C10. Line 139: Please provide more detail on the approach. Do you mean that the 22 informative species were rescaled to 100% and that the proportion of each species within this restricted assemblage was used as input data?

R1-R10. Change made l. 157-160: “This final step resulted in a list of 22 informative species that we assume to be poorly affected by dissolution and diagenesis, ensuring a robust transfer from the sediment trap to the sediment core datasets. The relative abundances of these informative species were rescaled to 100 % in the two datasets before using these data to calibrate the transfer functions.”

R1-C11. Section 2.3: Studies that develop new transfer functions generally include a more detailed methodological section to ensure both the robustness of the approach and its reproducibility. Here,

the methods—particularly the regression procedures—are not described in sufficient detail compared with similar studies (Esper et al., 2014; Ferry et al., 2015).

R1-R11. The procedure for factorial analysis followed by MLR and PLSR have been previously described in Imbrie and Kipp (1971) and Esper and Gersonde (2014). Moreover, we propose a quantitative justification for the choice of the number of factors in the factorial analysis (scree test, Fig. S1) and the PLSR (comparison with a null broken stick model, Fig. S2).

Concerning the robustness of the approach, this is a critical point given the restricted amount of data used for the calibration ($n = 44$). To our knowledge, this is the first transfer function study that uses train/test sets and bootstrapping technique to estimate transfer function error independently from the entire dataset (generally subjected to overfitting). For transparency and reproducibility, Python scripts are made publicly available

at : https://github.com/mathieu-rembauville/so_biological_pump.

Change made I. 526: “*The python scripts and the sediment trap and sediment core datasets are available at https://github.com/mathieu-rembauville/so_biological_pump.*”

R1-C12. It is also worth noting that MLR (or IKM) and PLSR (or WA, WA-PLS) typically perform best with linear models. However, diatom distributions in the Southern Ocean are known to be non-linear (Armand et al., 2005; Crosta et al., 2005; Esper et al., 2010) as well as in northern seas (Oksman et al., 2019), as are the associated species–temperature relationships (Esper et al., 2014; Oksman et al., 2019). This may explain the relatively poor performance of MLR and PLSR in the present study (Fig. 4). Are these methods, therefore, the most appropriate choices here?

R1-R12. The log-transformation of raw relative abundances partially reduces the non-linearity in the species-chemical fluxes relationship. It is true that MLR assumes linear relationships between predictors and responses variables. In the original paper by Imbrie and Kipp (1971), interaction terms and squared terms were added to the MLR model, thereby artificially introducing non-linearity. In the second paragraph of section 2.3, we explicitly explain why we do not integrate interaction and squared terms in the MLR to avoid the risk of overfitting given the restricted amount of data. For PLSR, it has been demonstrated that dimension reduction associated with projection on latent vectors prior to regression partially compensates for non linear relationships (Cook and Forzani, 2021). Finally, the MLR and PLSR are considered as standard and most used regression models to build diatom transfer functions (Gasse et al., 1995; Gersonde et al., 2005; Berner et al., 2008; Esper and Gersonde, 2014). The convergent response of the three transfer functions (Fig. 6) suggests that non linearity does not bias the reconstructed trends by MLR and PLSR. However, the higher RMSE and the negative values sometimes reported by these two methods might be due to non linearity in the learning set.

R1-C13. I am less familiar with decision-tree approaches, but the method does not appear to be sufficiently described or constrained (see Grenier et al., 2010, Water Quality Research Journal of Canada, 45(4), 413–425; Salonen et al., 2016, The Holocene, 26(7), 1040–1048). Overall, the transfer function is based on 11 sites and four seasons (i.e. 44 data points), which represents a rather limited dataset for calibration.

R1-R13. The critical choices associated with gradient boosting regression (tree depth, number of components) are detailed in the fourth paragraph of section 2.3 and illustrated by Fig. S3. To better constrain the importance of each species in the partial least square regression (PLSR) and the gradient boosting regression (GBR), we added the partial correlation coefficients and relative features importance in Table 3 and Fig. S4 and S5 (see figures below). The most important species in the GBR are consistent with species associated with high scores on factors 2 (SIZ and sea-ice related species) and factors 3 (bloom-forming and spore-forming species) from the factorial analysis, supporting that the same ecological processes link the diatom community composition and the chemical fluxes in the two transfer functions. This explains the comparable dynamics of the reconstructed variables.

Change made I. 229-239: “Species most positively correlated with POC export in the PLSR are *Actinocyclus actinochilus*, *Chaetoceros* subgenus *Hyalochaete*, *Fragilariopsis obliquecostata*, *Thalassiosira gracilis*, *Thalassiosira antarctica*, *Fragilariopsis rhombica*, and *Fragilariopsis curta* (Table 3, Fig. S4). All of them are positively associated with factors 2 (SIZ and ice-related species) and 3 (bloom-forming and spore-forming species). Species most positively associated with the PIC:POC export ratio in the PLSR are *Thalassiosira oestrupii*, *Shionodiscus trifultus*, and *Azpeitia tabularis*. All of them are positively associated with factor 1 (SAZ species).

The most important species ($\geq 10\%$ in importance) in the GBR for POC flux are *Actinocyclus actinochilus*, *Chaetoceros* subgenus *Hyalochaete*, *Fragilariopsis kerguelensis*, *Fragilariopsis obliquecostata* and *Thalassiosira gracilis* (Table 5, Fig. S4). Most of them are positively associated with factor 3 (bloom-forming and spore-forming species). The most structuring species in the GBR for the PIC:POC export ratio are *Fragilariopsis curta* and *Fragilariopsis separanda*. Both species are positively associated with factor 2 (SIZ and ice-related species).”

Change made I. 321-324: “Species associated with high scores on factors used in the MLR are consistent with the ones that have both a high partial correlation coefficients in the PLSR and a high importance in the GBR. This suggests that the same ecological processes link the diatom community composition and the chemical fluxes in the three transfer functions, resulting in comparable dynamics in the reconstructed variables.”

Change made to Table 3: Summary of transfer functions calibration : diatom scores on factors derived from the factor analysis (FA) with varimax rotation, partial correlation coefficients (β) from partial least square regression (PLSR), and features importance from gradient boosting regression (GBR). Major values are highlighted in bold.

Species	FA : scores on factors				PLSR : β coefficients		GBR : features importance (%)	
	F 1	F 2	F 3	F 4	POC	PIC:POC	POC	PIC:POC
<i>A. actinochilus</i>	-0.15	0.34	0.77	0.05	0.17	-0.06	29.8	0.0
<i>A. parvulus</i>	-0.19	0.03	-0.14	0.48	-0.09	-0.07	0.0	0.0
<i>A. tabularis</i>	0.94	-0.22	-0.15	-0.10	-0.02	0.08	0.3	1.8
<i>Chaetoceros</i> sub. <i>Hyalochaete</i>	0.13	-0.07	0.83	-0.05	0.15	0.03	12.3	1.1
<i>E. antarctica</i>	-0.39	-0.51	0.47	-0.18	0.04	0.07	0.1	0.2
<i>F. curta</i>	-0.22	0.81	0.14	0.17	0.07	-0.12	3.9	54.4
<i>F. kerguelensis</i>	0.09	-0.53	-0.37	0.02	-0.10	0.07	13.3	2.4
<i>F. obliquecostata</i>	-0.17	0.39	0.75	0.10	0.15	-0.07	16.9	6.3
<i>F. rhombica</i>	-0.13	0.58	0.38	0.53	0.10	-0.11	0.2	0.0
<i>Fragilariopsis ritscheri</i>	-0.07	0.71	-0.09	0.54	-0.01	-0.13	3.0	0.4
<i>F. separanda</i>	-0.20	0.63	0.06	0.27	0.06	-0.10	4.0	16.1
<i>N. directa</i>	-0.16	-0.52	0.00	0.17	0.01	0.07	0.00	0.22
<i>R. antennata</i>	0.12	0.04	0.01	0.63	-0.08	-0.04	3.1	0.4
<i>S. trifultus</i>	0.73	-0.05	0.06	-0.01	0.01	0.09	0.00	0.00
<i>T. nitzschioides</i> var <i>lanceolata</i>	0.31	-0.46	-0.04	0.15	-0.01	0.06	0.00	0.00
<i>T. antarctica</i>	-0.27	-0.05	0.79	-0.23	0.11	-0.01	1.5	0.2
<i>T. gracilis</i>	-0.44	0.51	0.20	-0.12	0.12	-0.03	9.0	1.8
<i>T. gracilis</i> var <i>expecta</i>	-0.05	0.08	0.02	0.99	-0.07	-0.08	0.00	4.76
<i>T. lentiginosa</i>	0.25	-0.12	-0.19	0.21	-0.01	0.04	0.8	0.1
<i>T. oestrupii</i>	0.88	-0.04	-0.12	-0.18	0.02	0.09	0.9	5.5
<i>T. oliverana</i>	0.10	-0.31	-0.28	0.34	-0.09	-0.05	0.00	4.28
<i>Tx. antarctica</i>	0.84	-0.09	-0.17	0.04	-0.04	0.06	0.7	0.0

We also added 2 figures (S4 and S5) in the supplementary Material.

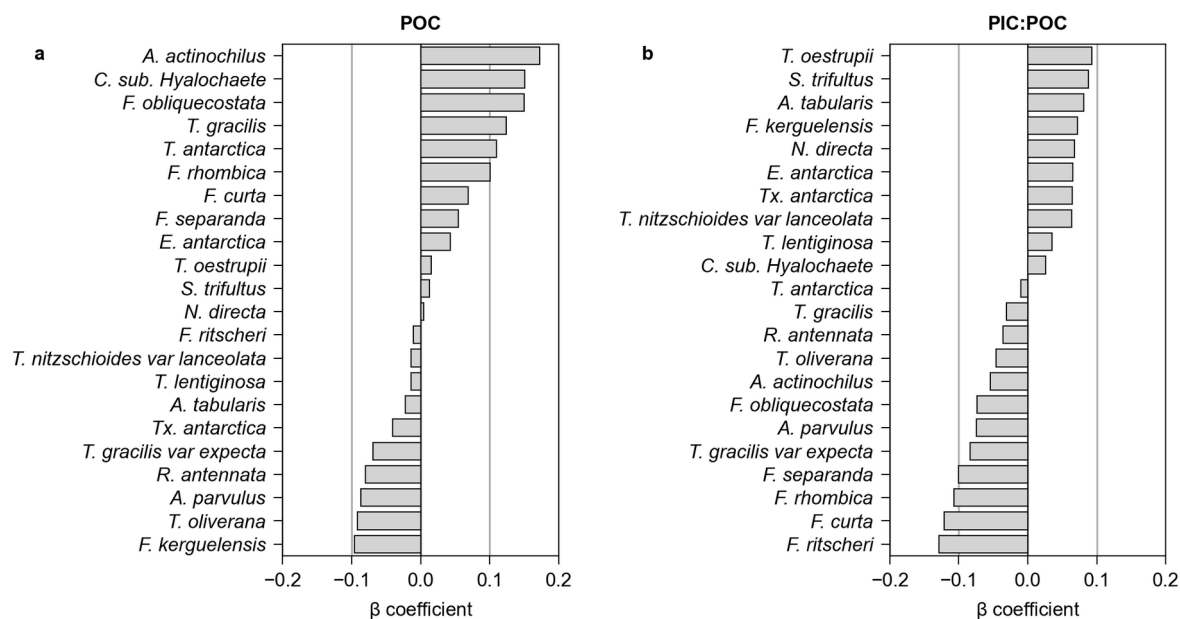


Figure S4. Sorted partial correlation coefficients (β) from the partial least square regression (PLSR) for a) the particulate organic carbon (POC) export flux and b) the particulate inorganic to organic (PIC:POC) export ratio.

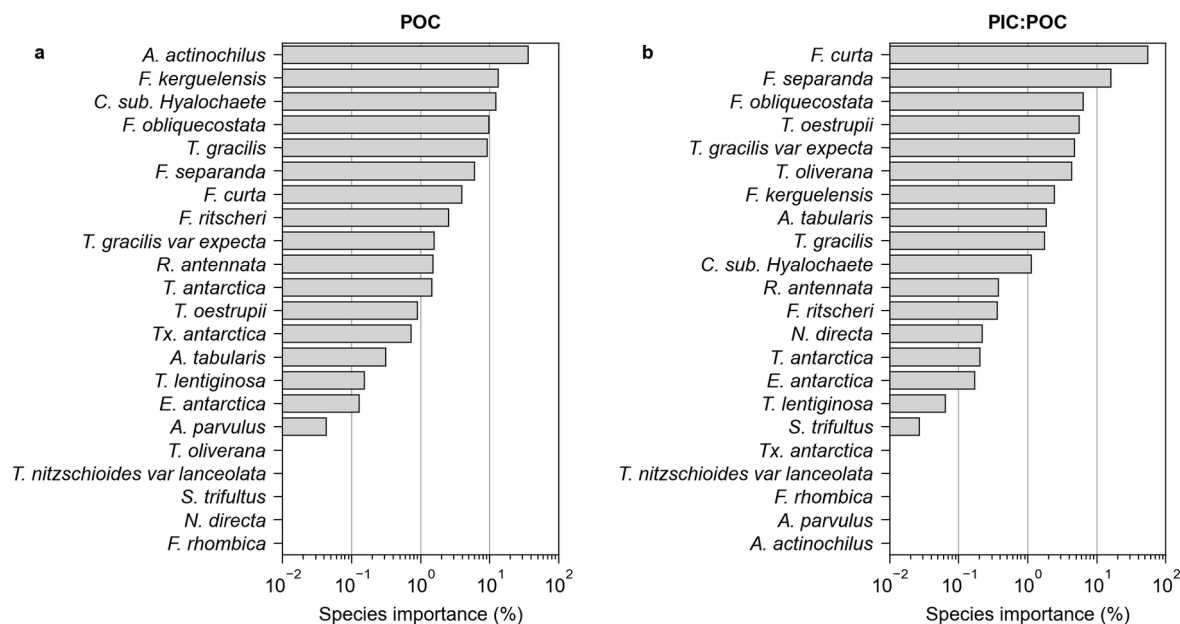
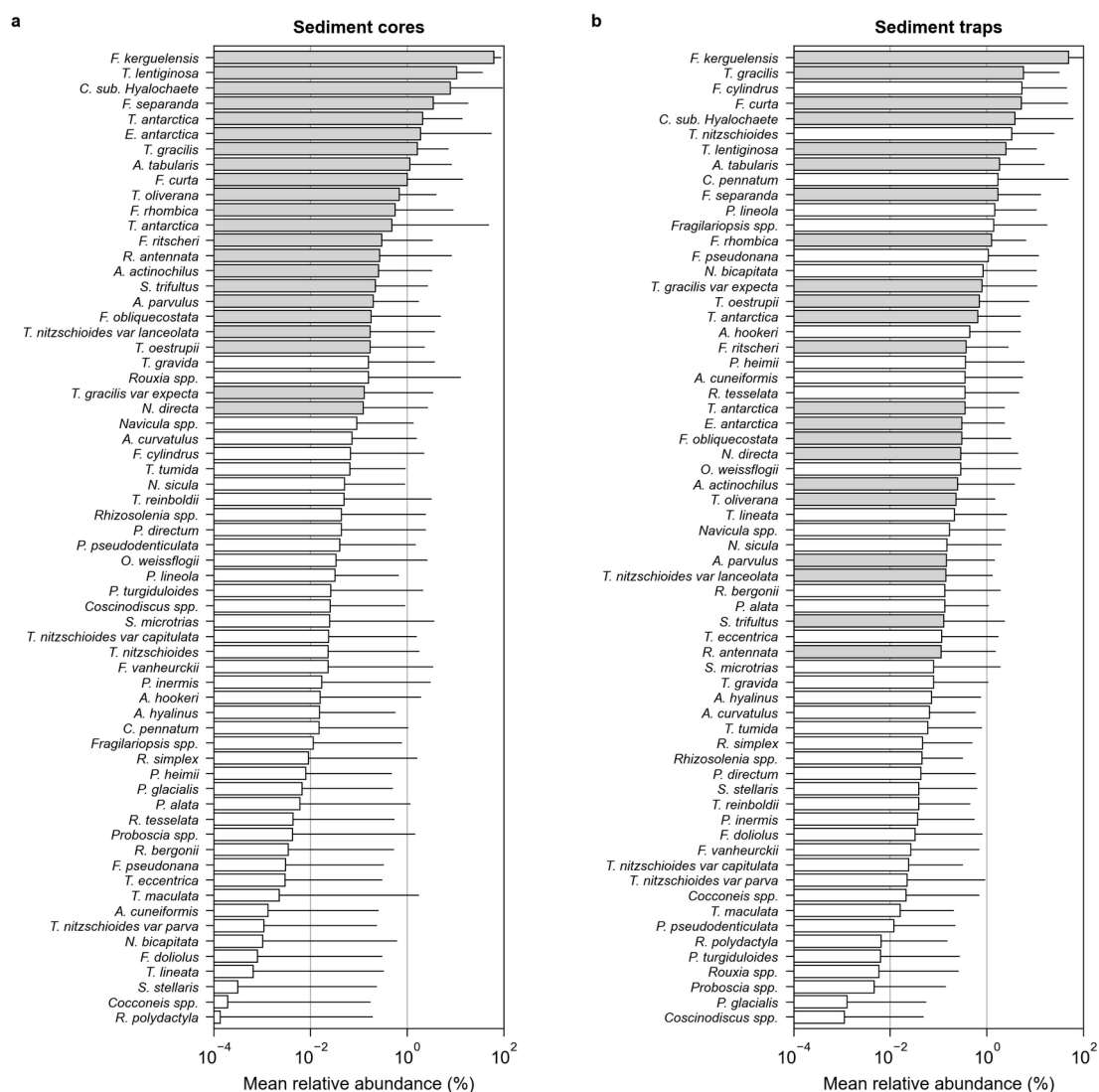


Figure S5. Sorted species relative importance in the gradient boosting regression (GBR) models for a) the particulate organic carbon (POC) export flux and b) the particulate inorganic to organic (PIC:POC) export ratio.

R1-C14. Table 3 and associated text: Most of the species with high loadings appear to be extremely rare in the sediment traps (<1%), based on the mean values presented in Figures 2 and 3. First, I would recommend presenting the ranges of relative abundances. Second, this suggests that the transfer function is largely driven by very rare taxa, which may have limited ecological and biogeochemical significance.

R1-R14. The comment of the reviewer made us realize that the mean relative abundance of a species is not a sufficient information because of the large range of relative abundance for each species. Hence, we added the highest relative abundance of each species to Fig. 3 (see modified figure below). We also added a supplementary figure with the relative abundance of diatoms species in the sediment cores (see R1-R25 below). It is worth noticing that the vast majority of the selected species for transfer functions calibration have highest relative abundances greater than 10 % in both the calibration (sediment traps) and the application (sediment cores) datasets. Consequently, contrary to the perception of the reviewer, the transfer functions are not driven by rare taxa.



Change made to Figure 3 caption: Mean relative abundance of diatom species (bars) and highest relative abundance (lines) reported in a) the sediment core and b) the sediment trap datasets. Grey bars represent species with a mean relative abundance higher than 0.1 % in both datasets.

R1-C15. In addition, the ecology of several species is not accurately described. In Factor 1 (SAZ), *S. trifultus* is not a typical SAZ species but rather a ubiquitous taxon, possibly because several varieties have been grouped. *Thalassiothrix antarctica* is a northern POOZ species (Grigorov et al., 2014) that has been used to infer past shifts in the Antarctic Polar Front (APF) position (Kemp et al., 2010; Duffy et al., 2025). In Factor 2 (sea ice), *F. separanda* is not strictly a sea-ice-associated species and can occur at temperatures up to 10 °C (Esper et al., 2010). In Factor 3 (POOZ), the bloom-forming species mentioned are typically abundant around the Antarctic coast and around the SAZ islands rather than in the open ocean (Armand et al., 2005; Buffen et al., 2007). *Fragilariopsis obliquecostata* is not a POOZ species but a sea-ice-associated taxon commonly used to infer the presence of summer sea ice (Gersonde and Zielinski, 2000).

R1-R15. Most of the references cited here (Armand et al., 2005; Buffen et al., 2007; Duffy et al., 2025; Esper et al., 2010) are based on surface sediment samples. As stated by Reviewer 1 in R1-C4, diatom communities deposited in surface sediments are prone 1) selective grazing in the water column, 2) selective dissolution both in the water column and the sediment, i.e. potentially leading to an over-representation of robust frustules, and 3) resuspension and lateral advection by deep currents. Although they are key archives for paleoceanographic applications, surface sediment samples are less representative of mixed layer communities than sediment trap samples that captures communities closer to the surface and at much shorter timescales. Figure R2 below compiles sediment trap data for the four species mentioned by Reviewer 1.

Shionodiscus trifultus: the species is clearly associated to the SAZ (2-4 % relative abundance) and winter samples from the northernmost site of the PFZ (MS2). Although *S. trifultus* is present up to the SIZ, the relative abundances are extremely low (<0.2 %). Hence, we argue that this taxon cannot be considered as “ubiquitous”.

Thalassiothrix antarctica: the taxon shows its highest relative abundances in the SAZ (2-5 %). Indeed, notable values < 1% are measured in the POOZ. Highest relative abundances for this species in warmer waters of the SAZ have been reported in the review by Kemp et al. (2006), both for modern communities [“Such diatoms may not be dominant in the waters approaching the fronts but are disrupted and concentrated at frontal zones, generally accumulating on the warm side of the front before sedimenting”] and during the early Matuyama diatom maximum (2.6-2 Ma) [“These deposits are interpreted to have formed beneath the frontal boundary between the cold upwelled water and the offshore warmer South Atlantic surface water during episodes of equatorward excursions of subantarctic waters, possibly also related to enhanced North Atlantic Deep Water production”].

We reformulated the first paragraph of section 3.1 accordingly.

Fragilariopsis separanda: although the species is present in the POOZ (< 3% relative abundance), the highest relative abundance is observed in the SIZ (8-13 %). We reformulated the first paragraph of section 3.1 accordingly.

Fragilariopsis obliquecostata: we agree that this species is strictly associated with the SIZ (0.5 – 3% relative abundance). It has been positively associated with factor 3 due to its co-occurrence with bloom-forming species in the WSC site. We reformulated the first paragraph of

section 3.1 accordingly. In particular for the bloom-forming species (factor 3), we now specify that they are abundant downstream island systems and close to the Antarctic coast.

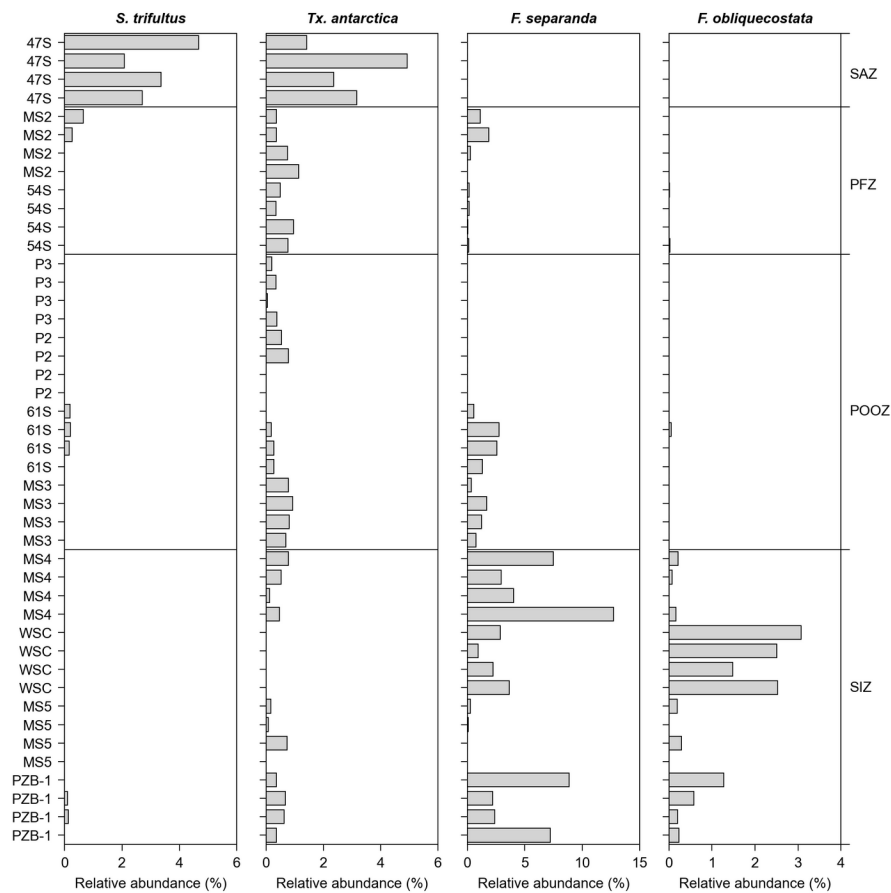


Figure R2. Seasonal averages of relative abundances of *Shionodiscus trifultus*, *Thalassiothrix antarctica*, *Fragilariopsis separanda* and *Fragilariopsis obliquecostata* from the sediment trap dataset. As in Fig. 2, sediment traps are sorted by location from north (top) to south (bottom) and for each sediment trap by season from spring (top) to winter (bottom).

Change made I. 214-228: “The species scores on factors from the factor analysis used in the MLR prediction are presented in Table 3. Factor 1 is characterized by warm-water species typical of the SAZ (*Azpeitia tabularis*, *Shionodiscus trifultus*) and small *Thalassiosira* species such as *Thalassiosira oestrupii*, together with the giant mat-forming species *Thalassiothrix antarctica* often observed at the warm side of the fronts. Factor 2 is associated with ice-related species *Fragilariopsis curta* together with other small *Fragilariopsis* species displaying generally highest relative abundances in the SIZ (*F. separanda*, *F. rhombica*). Factor 3 contains bloom-forming and resting spore forming species generally observed in naturally iron-fertilized locations close to island systems and around the Antarctic coast (*Chaetoceros* subgenus *Hyalochaete*, *Eucampia antarctica*, *Thalassiosira antarctica*) together with less abundant species generally found in the POOZ (e.g. *Actinocyclus actinochilus*). Factor 4 contains rare and large species sometimes associated with the PFZ such as *Asteromphalus parvulus* and *Rhizosolenia antennata*.”

R1-C16. There is also a significant issue related to the lumping together of varieties with distinct ecological signals (e.g. *E. antarctica* var. *recta* and var. *antarctica*, *T. antarctica* var. T1 and var. T2, *Hyalochaete* spp.).

R1-R16. We did not group varieties. This taxonomic level is simply not reported in the sediment traps and sediment cores publications (see the full list of 151 species/taxa in the supplementary material), therefore it cannot be used in the transfer functions calibration.

R1-C17. Line 278: It is not clear why deep-ocean POC export should be associated with small, sea-ice-related diatoms that are readily dissolved, thereby exposing their organic content to remineralisation. These small species rarely reach the sediments in high proportions, except on the Antarctic shelf (Burckle et al., 1987). Moreover, the slope between Corg flux and diatom flux in the AAZ MS4 trap—where *F. cylindrus* and *F. curta* are abundant (both in flux and relative abundance)—is much lower than in the SAZ MS2 trap, where *F. kerguelensis* and *Thalassiothrix* dominate. This suggests limited export associated with these sea-ice-related taxa.

R1-R17. When the entire raw sediment trap dataset is considered ($n = 256$), there is a highly significant statistical relationship ($p < 0.01$) between POC flux and log-transformed (*F. curta* + *F. cylindrus*) relative abundances (Fig. R3 below). To take the comment into account, we explain more clearly the potential ecological mechanism linking these small and lightly silicified diatoms with POC in the third paragraph of section 4.1.

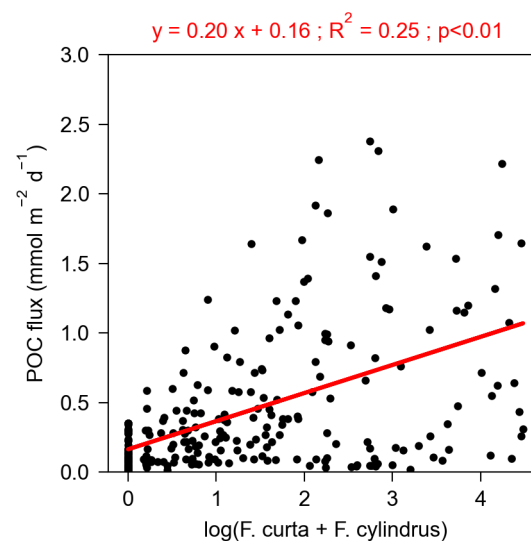


Figure R3. POC flux and relative abundance of *Fragilariopsis curta* and *Fragilariopsis cylindrus*. The red line represents a linear regression from ordinary least square model.

Change made l. 331-340: “Cold water varieties of *Chaetoceros* subgenus *Hyalochaete* and *Eucampia antarctica* were reported to be associated with ice-related species such as *Fragilariopsis curta* and *F. cylindrus* in both modern and glacial sediment cores samples (Leventer, 1991; Armand et al., 2005; Abelmann et al., 2006). Here, the taxonomic resolution does not allow to differentiate the cold water varieties, but a similar co-occurrence is observed in the sediment core dataset (Fig. S6). The POC flux is positively correlated with SIZ and ice-related species of factor 2 (*Fragilariopsis curta*, *F. obliquecostata*). Copepod and krill feed on these ice-associated diatoms in

summer (O'Brien et al., 2011; Schmidt et al., 2014; Pauli et al., 2021) and are efficient vectors of POC export through vertical migration and fecal pellet production (Smith et al., 2025). In this context, zooplankton-driven export can represent up to 90 % of the annual POC export in productive environments (Manno et al., 2015; Belcher et al., 2019). **The efficient POC export by zooplankton feeding on ice-related diatoms could explain the association of SIZ and ice-related diatom with POC export in the transfer functions.**

R1-C18. Line 283: The quantitative relationship was established between diatom fluxes—not relative abundances—and organic carbon fluxes.

R1-R18. Change made l. 328: “A direct quantitative link has already been established between diatom resting spore **vertical fluxes** and POC export pulses [...]”

R1-C19. Line 285: Only the cold-water varieties of *Hyalochaete* and *E. antarctica* are associated with sea ice. It is also worth noting that an inverse relationship is often observed between CRS and *F. curta* on the continental shelf (Leventer et al., 1993; Campagne et al., 2016; Torricella et al., 2024).

R1-R19. We now specify that the positive association between these species is only true for the cold-water varieties and that this level of taxonomic identification is not available in the sediment trap and sediment cores datasets (see R1-R17 and change associated).

R1-C20. Line 290: The correlation coefficients with Factor 1 (warm water; 0.033) and Factor 2 (sea ice; -0.149) are not significant (Table 4). How, then, can the PIC/POC ratio be reconstructed from diatom relative abundances?

R1-R20. These numbers are not significance levels, they are regression coefficients from the MLR (see Table 4 caption). Because the models are built on log-transformed and standardized diatom relative abundances, the regression coefficients are low. The full-model *p*-values (Fisher F-test) are given in the last column of Table 4. The two regression models for POC and PIC:POC are highly significant ($p < 0,01$), therefore the regression model has explanatory power and allows the reconstruction of the two variables.

Change made in caption of Table 4: “**The last column contains the regression model *p*-value for each variable (F-test).**”

R1-C21. Line 292: The terms northward and southward are not sufficiently informative; please specify the regions more precisely. To my knowledge, coccolithophores are nearly absent south of the Antarctic Polar Front (APF) (Eynaud et al., 1999; Saavedra-Pellitero et al., 2014), whereas planktic foraminifera (mainly *Neogloboquadrina pachyderma sinistral*) remain present (Niebler and Gersonde, 1998; Haddam et al., 2016).

R1-R21. We now specify “north of the polar front” and “south of the polar front”. The absolute coccoliths flux is not higher south of the polar front, but its relative contribution to the exported

calcifying community increases, mainly due to a decrease in the absolute flux of foraminifers (Rembauville et al., 2016a). We have reformulated this sentence for clarity.

Change made l. 342-345: “It has been previously reported that the PIC:POC export ratio increases north of the polar front concomitantly with an increase in the abundance of foraminifer and pteropod (Salter et al., 2014; Manno et al., 2022), whereas the PIC:POC export ratio is generally lower south of the polar front where the exported foraminifer flux decreases (Rembauville et al., 2016a).”

R1-C22. Line 295: This interpretation appears to rely purely on statistical relationships without an underlying ecological or biogeochemical rationale.

R1-R22. (See also R1-R3). Indeed, any microfossil-based transfer function is a statistical relationship between the response variables and the forcing variables. However, here we argue that the statistical relationships translate causalities. To clarify this point, we now specify that diatom community catches part of the hydrological variance and the ecological variance and that both processes could influence the PIC:POC export ratio.

Change made l. 345: “Although the calcifying plankton is not explicitly taken into account in this study, these results suggest that diatom communities, partially shaped by hydrological zones, appears to capture efficiently the global changes in ecosystem structure that set the magnitude of the carbonate counter-pump.”

R1-C23. Line 357: While this is correct, models tend to overestimate the geographical extent of the LGM high-export zone (Tagliabue et al., 2009) compared with observational data (Kohfeld et al., 2005).

R1-R23. It is out of the scope of our study to discuss the reliability of the models simulations in the SO. In our study, we take into account the substantial variations in model results by considering a large number of studies/references. The reconstructed POC flux based on our new transfer functions are within the model ranges, which gives us confidence in our results. The meta-analysis by Kohfeld et al. (2005) compiles different proxies at global scale and provides qualitative changes in the biological pump. It concludes to a lower biological pump in the Antarctic Zone during the last glacial maximum. We added the reference the introduction section.

Change made l. 51: “However, additional export proxies suggested a latitudinal response of the SO to glacial conditions : an increased biological pump in the SAZ due to dust-driven fertilization of phytoplankton growth, but a weaker biological pump in the AZ due to higher stratification and lower micronutrient enrichment (François et al., 1997; Anderson et al., 2002; Kohfeld et al., 2005; Jaccard et al., 2013; Sigman et al., 2021).”

R1-C24. Line 362: This statement is incorrect. These studies indicate an increase in the relative utilisation of nutrients (reflected by higher $\delta^{15}\text{N}_{\text{db}}$) in the Antarctic Zone due to reduced nutrient supply, as you also state in lines 376–378.

R1-R24. We corrected this mistake.

Change made l. 414: “Several studies previously proposed that during glacial or colder periods, export production increased in the SAZ due to iron fertilization while it decreased in the AZ due to **lower nitrate supply caused by** higher ocean vertical stratification (François et al., 1997; Jaccard et al., 2013; Gottschalk et al., 2016; Sigman et al., 2021).”

R1-C25. Lines 379–383: I recommend presenting the dominant diatom species in these cores to support this interpretation. For example, in core PS2606-6, CRS increases from 0% during the Holocene to ~10% during the glacial period; *E. antarctica* increases from 0 to ~10%; *F. curta* from 0 to ~6%; *F. kerguelensis* decreases from ~85% to ~50%; and *T. lentiginosa* increases from ~5% to ~15%. Based on these changes, it is not clear that there is a shift from “silica sinkers” to “carbon sinkers”, as silica-exporting taxa remain dominant during the glacial interval.

R1-R25. Following Reviewer 1 recommendation, we added a supplementary figure (Fig. S6, below) showing the relative abundance of diatoms species in the sediment cores. Fig. S6 shows that transfer functions are based on - and applied on – abundant taxa (e.g. species associated with factor 2 and 3 account for 20 to 60 % of the diatom community during glacial periods). For core PS2606-6, it is true that species considered as “carbon sinkers” are not dominant during MIS 2 but their relative abundance increases (from < 10 % to > 30 %). In other cores such as PS1786-1 and PS1768-8, they dominate the assemblage during glacial periods. We added this important point to section 4.3.

Change made l. 442-449: “**A change in diatom community structure during glacial periods has been previously described in all the open-ocean sediment cores considered here (Table 2). The contribution by lightly silicified, ice-related species (factor 2) and bloom forming species (factor 3) increases to reach 20-60 % of the diatom assemblage depending on the core (Fig. S6). Concomitantly, the relative abundance of the silica-sinker *Fragilariopsis kerguelensis* decreases. Hence, the reconstructed glacial increase of POC flux associated with a decrease in opal flux could be explained by a change in the diatom community characterized by an increased contribution from carbon sinkers and a decreasing contribution by silica sinkers, together with a higher zooplankton contribution to the total POC export flux.**”

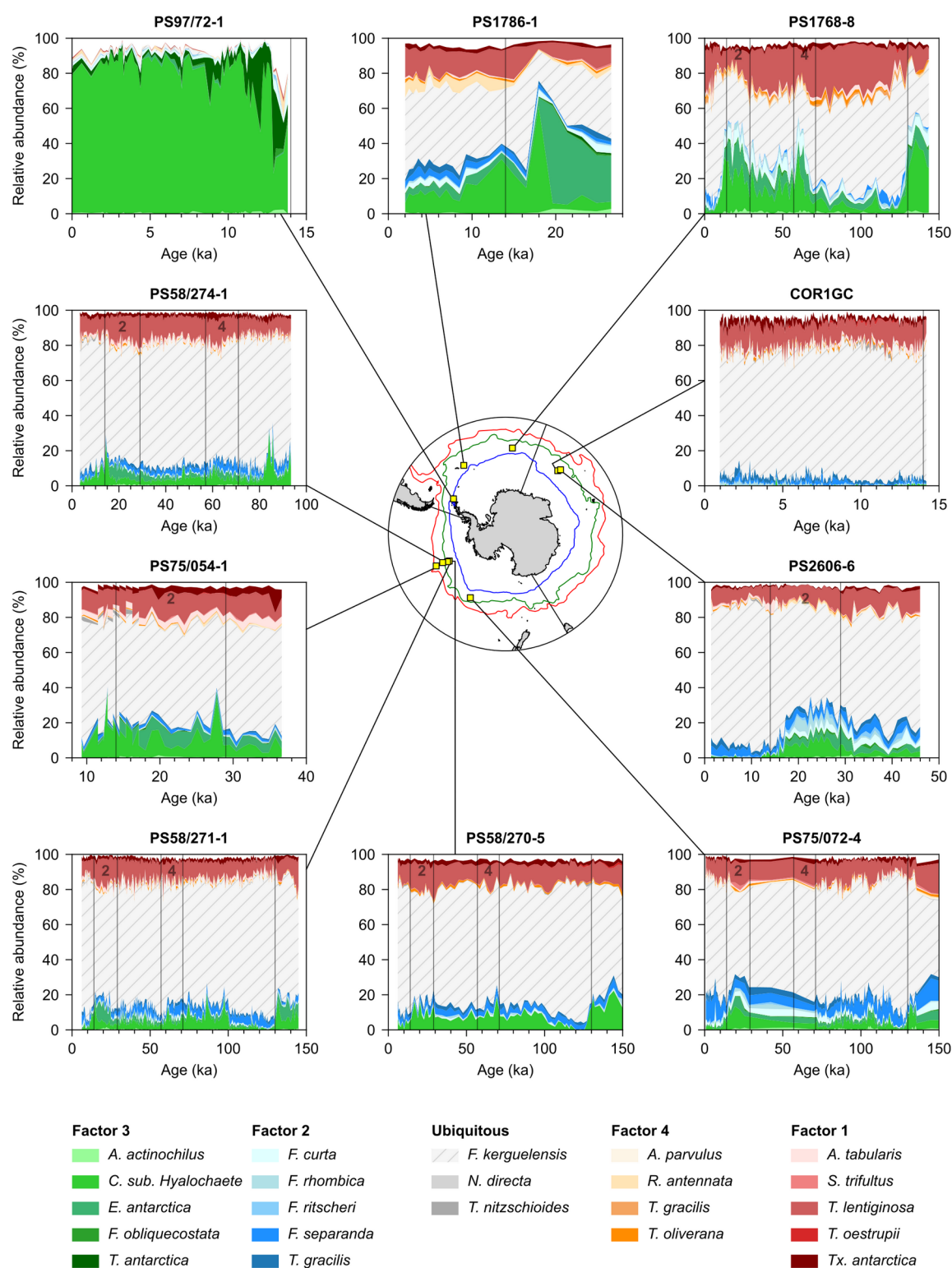


Figure S6 added. Relative abundance of the main diatom species in the sediment cores used to apply the transfer functions. The white area at the top of each panel represents rare species not considered in the transfer functions. Vertical lines and numbers denote marine isotopic stages (MIS). In the central map, colored lines represent hydrological fronts as in Fig. 1 : Subantarctic Front (red), Polar Front (green), September sea ice edge (blue).

R1-C26. Section 4.4: The interpretations rely heavily on the robustness of the transfer function, which currently appears to be based on an inappropriate metric. It would be important to determine whether the results—and therefore the palaeoceanographic interpretations—remain valid when diatom fluxes rather than relative abundances are used.

R1-R26. As stated in R1-R2 and R1-R6 the use of the relative abundance is a standard procedure in the development of transfer functions based on microfossil records. Moreover, diatom fluxes are not available for the sediment cores used in this study as well as in most cores of the Southern Ocean. The rationale is that the valve flux calculation in sediment core requires several parameters: 1) valves concentrations in the sediment (valve/g), 2) sediment density (g/cm^3) and 3) sediment accumulation rate (cm/ka) at very high resolution. Only diatom relative abundances are published or available on public repositories. Furthermore, it can be argued that sediment accumulation rate (3rd parameter mentioned above) can be largely biased by sediment redistribution by deep-water currents which is particularly true in the Southern Ocean (Francois et al., 2004; Dutkiewicz et al., 2016).

Following Reviewer 1 comments, we added ranges of relative abundances in Fig. 3 and relative abundances in sediment cores in Fig. S6. These additional data show that transfer functions are based on – and applied to – abundant species. We also added the partial correlation coefficients from PLSR and the importance of species in the GBR model in Table 5 and Fig. S4, which provide convergent results with the factorial analysis used in the MLR. We nuanced and precised the ecological rationale for higher POC export flux and lower PIC:POC export ratio in the AZ during glacial periods in the discussion. We hope that these modifications fulfill the Reviewer requirements.

Change made I. 534: “We thank the two anonymous Reviewers for the constructive comments that helped us improve the manuscript.”

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