



1 **Sedimentary organic matter signature hints at the phytoplankton-driven Biological**  
2 **Carbon Pump in the Central Arabian Sea**

3 **Medhavi Pandey<sup>1,2</sup>, Haimanti Biswas<sup>1,2\*</sup>, Daniel Birgel<sup>3</sup>, Nicole Burdanowitz<sup>3</sup>, Birgit**  
4 **Gaye<sup>3</sup>**

5 <sup>1</sup>CSIR National Institute of Oceanography, Biological Oceanography Division, Dona Paula, Goa  
6 403004. India.

7 <sup>2</sup>Academy of Scientific and Innovative Research (AcSIR), Ghaziabad-201002, India.

8 <sup>3</sup>Institute for Geology, Center for Earth System Research and Sustainability (CEN), Universität  
9 Hamburg, Bundesstraße55, 20146, Hamburg, Germany.

10 \*Corresponding Author's email: [haimanti.biswas.nio@gmail.com](mailto:haimanti.biswas.nio@gmail.com); [haimanti.biswas@nio.org](mailto:haimanti.biswas@nio.org)

11 **Abstract**

12 The Central Arabian Sea, a unique tropical basin is profoundly impacted by monsoon wind  
13 reversal affecting its surface circulation and biogeochemistry. Phytoplankton bloom associated  
14 with high biological productivity and particle flux occurs in the northern part of the central  
15 Arabian Sea due to summer monsoon-induced open ocean upwelling and winter convection.  
16 The core Oxygen Minimum Zone (OMZ) at the intermediate water depths is another important  
17 feature of the north-central Arabian Sea and fades southward. In this study, we **have attempted**  
18 to interlink how these factors collectively impact phytodetrital export to the sediment. Short  
19 sediment core top (1cm) samples representing the recent particle flux signatures were analyzed  
20 from 5 locations (21° to 11° N; 64° E) in the central Arabian Sea. The C<sub>37</sub> alkenone-based sea  
21 surface temperature (SST) proxy indicated cooler SST (27.6 ± 0.25 °C) in the north mostly due  
22 to upwelling (summer) and convective mixing (winter) and warmer (0.4 °C) in the south, which  
23 usually remains nutrient-poor. This trend was consistent with the satellite-derived average SST  
24 values (2017–2020). Lipid biomarker analysis **suggested** that dinoflagellates were the highest  
25 contributor as indicated in dinosterol and its degradative product dinostanol followed by  
26 brassicasterol, and C<sub>37</sub> alkenone representing diatoms, and coccolithophores, respectively. The  
27 **stations** in the north (21–15° N) that largely experience periodic phytoplankton blooms and **is**  
28 influenced by the thick OMZ revealed the highest contents of organic matter, diatom frustules  
29 (diversity and abundance) dominated by large thickly silicified cells (e.g. *Coscinodiscus* and  
30 *Rhizosolenia*), and phytoplankton organic biomarkers, **but** lower zooplankton biomarkers  
31 (cholesterol and cholestanol). Whereas relatively smaller chain-forming centric (e.g.  
32 *Thalassiosira*) and pennate (e.g. *Pseudo-nitzschia*, *Nitzschia*, *Thalassionema*) diatom frustules  
33 along with lower phytoplankton biomarker contents were found in the south where zooplankton  
34 biomarkers and silicious radiolarians were more abundant. The **probable** impacts of the  
35 presence of the OMZ along the sampling transect on particle flux related to the phytoplankton  
36 community, zooplankton grazing along with other factors have also been discussed.

37

38 **Keywords: Phytodetritus; North Indian Ocean; Monsoon; Biomarkers; Brassicasterol;**  
39 **Dinosterol**

40

41

42

43

44



## 45 Introduction

46 Marine phytoplankton modulate the global carbon cycle by fixing almost 48 Gt C annually  
47 (Singh and Ahluwalia, 2013) which corresponds to 50% of global primary production (Field et  
48 al., 1998; Behrenfeld et al., 2006). This amount of organic matter produced within the euphotic  
49 layers, where 1% of solar light arrives, supports the entire marine food chain including the  
50 benthic population. Nearly 10% of this organic matter (large and dense phytodetritus) sinks to  
51 the upper mesopelagic ocean and gets further fragmented by zooplankton and microbially  
52 remineralized on its descent into the deep ocean. Only 1–3% of this phytodetritus can reach the  
53 seafloor below 1000 m depth (Iversen, 2023) and can be stored for hundreds to millions of  
54 years (Buesseler, 1998) and is called sequestration flux. This way of trapping carbon from the  
55 atmosphere to the ocean interior mediated by phytoplankton is called the Biological Carbon  
56 Pump (BCP) (Volk and Hoffert, 1985; Le Moigne, 2019; Iversen, 2023 and references therein).  
57 However, the organic matter in the surface sediment can be further modified biogeochemically.  
58 The strength of BCP is governed by many factors, such as heterotrophic remineralization of  
59 organic matter, dissolved oxygen (DO) levels, temperature, phytoplankton community  
60 composition, cell size, and zooplankton activity (Marsay et al., 2015; Keil et al., 2016; Cavan  
61 et al., 2017; Engel et al., 2017; Iversen, 2023). Out of multiple factors controlling the efficacy  
62 of the BCP, phytoplankton community composition (that controls organic matter  
63 stoichiometry), zooplankton grazing (Cavan et al., 2017), and the presence of well-oxygenated  
64 water (Keil et al., 2016) are crucial. Thus, understanding the functioning of the marine BCP in  
65 productive marine ecosystems needs attention, particularly in the context of changing climate  
66 (Iversen, 2023).

67 Marine organic matter preserved in sediments in the forms of diatom frustules, dinoflagellate  
68 cysts, and organic biomarkers (sterols, alkenones) could be potential proxies for understanding  
69 organic matter transport from the surface to the deep sea floor (Liu et al., 2013; Hu et al., 2020;  
70 Xiong et al., 2020 and references therein). The responses of phytoplankton to changing climate  
71 as well as other environmental variables can be retrieved from the sediments and may help  
72 predict future primary production, community shifts in marine ecosystems, and the ocean's  
73 role as a carbon sink. The siliceous frustules of diatoms can be more resistant to grazing and  
74 degradation and can be better preserved in sediments. Sedimentary organic carbon, nitrogen,  
75 and their ratios, diatom frustules, and organic biomarkers (e.g. sterols and alkenones) are used  
76 to reconstruct past phytoplankton community shift and temperature (Schubert et al., 1998; Liu  
77 et al., 2013; Rodríguez-Miret et al., 2023). The lipid biomarkers of phytodetritus from the  
78 surface sediments can also provide valuable information about the surface processes  
79 controlling phytoplankton growth and their transport to the sediment (Xiong et al., 2020). For  
80 example in a study by Peng et al. (2023), phytoplankton community shift was evident in lipid  
81 biomarkers in the sediment core samples from the East China Sea. In a few studies, major  
82 phytoplankton lipid biomarkers like dinosterol, brassicasterol, and alkenone were also used to  
83 correlate their contents with palaeoproductivity and associated changes of the sea ice levels in  
84 the Arctic Ocean (Müller et al., 2011 and references therein).

85  
86 The Arabian Sea, the northwestern part of the Indian Ocean, is a unique marine province with  
87 several characteristic features, for instance, the direct influence of monsoon winds on  
88 oceanographic and biogeochemical processes, high productivity (McCreary et al., 2009), and  
89 one of the thickest (200–1200 m) oxygen minimum zones (OMZ) in modern oceans (Banse et  
90 al., 2014). The entire area experiences periodic reversals of monsoon winds and in its surface  
91 circulation. During the summer (SW) monsoon, a low-level atmospheric Jet (the Findlater Jet;  
92 Findlater, 1971) blows parallel to the Omani and Somalia coasts, generating coastal and open





93 ocean upwelling in its northern part. Subsequently, due to natural nutrient enrichment,  
94 phytoplankton blooms develop (Banse, 1987; Bhattathiri et al., 1996; Prasanna Kumar et al.,  
95 2000). In the winter (NE) monsoon, winds and surface circulation reverse and in the northern  
96 Arabian Sea the cooling and densification of surface water leads to convective mixing  
97 (Prasannakumar et al., 2001) that also fuels high phytoplankton growth (Madhupratap et al.,  
98 1996).

99

100 In the Arabian Sea, the magnitude of particle transfer to the deep sea floor is directly controlled  
101 by the surface processes (Schulte et al., 1999, Rixen et al., 2019a). The central Arabian Sea  
102 exhibits one of the highest particle flux rates ( $1.3\text{--}3.3\text{ g C m}^{-2}\text{ year}^{-1}$ ) (Haake et al., 1993)  
103 compared with other low-latitude seas (Rixen et al., 2019b). This is mostly associated with  
104 enhanced biological productivity governed by summer monsoon-induced upwelling and winter  
105 convection (Nair et al., 1989; Haake et al., 1993; Rixen et al., 2019a). Nevertheless, particle  
106 flux could vary significantly (Nair et al., 1989; Prah et al., 2000) during the intermonsoon and  
107 premonsoon due to prevailing oligotrophy (Prasanna Kumar and Narvekar, 2005).

108

109 The impacts of atmospheric forcings and consequent biological response in the central Arabian  
110 Sea have been studied thoroughly during the joint Global Ocean Flux Studies (JGOFS, from  
111 1987 to 2003). It was evident that the monsoon wind is the major controlling forcing of  
112 physical, chemical, and biological processes in the surface ocean (McCearry et al., 2009) with  
113 high spatial and seasonal variability (Prasanna Kumar and Narvekar, 2005). However, there  
114 was no further investigation in the last two decades, although ocean warming continued with  
115 high spatial variability (Roxy et al., 2016; Sharma et al., 2023 and references therein). Our  
116 previous study showed that diatom frustules retrieved from the surface sediments from the  
117 central (Pandey et al., 2023) and the eastern (Pandey and Biswas, 2023) Arabian Sea could be  
118 an efficient indicator of surface processes controlling euphotic phytoplankton communities.  
119 There are a few studies from the Arabian Sea characterizing sedimentary organic carbon using  
120 phytoplankton biomarkers (Schubert et al., 1998; Prah et al., 2000; Schulte et al., 1999; 2000)  
121 suggesting such proxies from the surface sediment may be quite useful to understand the spatial  
122 variability in organic matter transport. Prah et al. (2000) used phytoplankton biomarkers from  
123 sediment trap samples as well as from the surface sediments over a year from the central  
124 Arabian Sea ( $15^{\circ}59'N$ ,  $61^{\circ}30'E$ ) and showed the seasonal variability in surface water  
125 conditions that modified biological productivity. Nevertheless, the degradation of organic  
126 matter in the water column could be quite high during their descent through the water column  
127 pointed out by Wakeham et al. (2002) in their work on lipids from the water column of the  
128 western Arabian Sea.

129

130 Importantly, the Arabian Sea is warming at a faster pace compared to other oceanic regions  
131 (Roxy et al., 2016; Sharma et al., 2023), and how the phytoplankton-driven organic matter  
132 transport may respond to that change is still poorly understood. Furthermore, recent modeling  
133 studies hinted at the possibility of thinning of the OMZ in the Arabian Sea that may  
134 substantially impact organic matter degradation within the water column, specifically in the  
135 southern part (Roxy et al., 2016). To fill this gap, in the present study, we want to address three  
136 major questions 1) Which phytoplankton group dominates the sedimentary organic matter in  
137 the various stations of the transect from north to south? 2) Does high spatial variability in the  
138 phytoplankton community composition driven by physical forcing also impact organic matter  
139 transport? 3) What are the possible factors (hydrography, physicochemical conditions, and  
140 atmospheric forcings) being responsible for such spatial variability in organic matter transport  
141 in this region? To address these questions, we have measured key parameters from surface



142 sediments including lipid biomarkers, alkenone-based SST ~~reconstruction~~, and diatom  
143 frustules combined with our recent observations on hydrography, biogeochemistry, and  
144 phytoplankton community (Silori et al., 2021; 2022; Chowdhury et al., 2021; Pandey et al.,  
145 2023).  
146

## 147 2 Methodology

### 148 2.1. Sample collection

149  
150 During cruise SSD-068 (Dec 2019 to Jan 2020) with *RV. Sindhu Sadhana* five short sediment  
151 cores were obtained using a multicorer (Ocean Scientific International Limited Maxi Multi-  
152 corer; core tubes 60 cm, outer diameter 11 cm and 10 cm inner diameter) along a transect from  
153 11–21° N at 64° E (Fig. 1a). These short cores were collected at 21, 19, 15, 13, and 11° N with  
154 varying water depths between 3000–4500 m (Fig. 1a). The cores were subsampled onboard  
155 immediately at every 0.5 cm and were kept in pre-cleaned plastic containers at 0–4 °C. The  
156 advantages using multicorer is the better preservation of the topmost parts of the sediment core  
157 compared to other devices like box or gravity coring (Barnett et al., 1984). For this study we  
158 used the top 1 cm (0.5, 1) of the core for all related analyses.  
159

### 160 2.2. Analytical method

#### 161 2.2.1. Total inorganic carbon (TIC), total organic carbon (TOC), and total nitrogen (TN) 162 contents

163 Sediment samples were dried at 60 °C overnight and ground using agate mortar and pestle.  
164 Aliquots (10 mg) of sediment samples were taken in tin capsules. Total carbon (TC) and TN  
165 were measured using a CHN Elemental analyzer (Euro Vector EA3000 series analyzer) at the  
166 Central Analytical Facility of CSIR-National Institute of Oceanography, Goa, India) against  
167 soil reference material used for carbon and nitrogen (ThermoFisher Scientific, Cambridge, UK)  
168 with an analytical error of < 2%. The TIC contents were measured against the calcium  
169 carbonate (CaCO<sub>3</sub>) standard (Merck, Germany) in a coulometer attached to an acidification  
170 module (Model CM5015 (UIC, USA). The accuracy and precision obtained from the results  
171 were within ± 1.25%. TOC values were calculated by the difference between TC and TIC (TOC  
172 =TC-TIC).

#### 173 2.2.2. Analysis of silica-bearing organisms from sediments

174 The diatom frustules and other siliceous organisms from sediments were enumerated following  
175 the method by Armbrrecht et al.,-(2018). The dried sediment subsamples (50 mg) were taken in  
176 a 50 mL sterile polypropylene tube and were treated ~~chemically~~ with 10% HCl, 30% H<sub>2</sub>O<sub>2</sub>, and  
177 0.01 N anhydrous sodium diphosphate (Na<sub>4</sub>P<sub>2</sub>O<sub>7</sub>) for removing carbonate, organic matter, and  
178 fine clay, respectively. After each chemical treatment, samples were washed thrice with Milli-  
179 Q water. Finally, the residue remaining after the last rinse and decantation was diluted with  
180 Milli-Q to 10 mL and was homogenized. A small portion (1 mL) from this homogenized  
181 solution was analyzed under an inverted microscope (Nikon Ti2) in a Sedgewick rafter  
182 counting chamber (Pyser, UK) at 400–600× magnification. The classical identification keys by  
183 Tomas (1997), Desikachary (1989) and <http://www.algaebase.org> were used. No centrifugation  
184 was used in this process to restrict the breaking of frustules. Further, the diatoms more than  
185 half in size were considered complete valves (Abrantes and Sancetta, 1985). The diatom  
186 abundance was expressed as valves g<sup>-1</sup> dry sediment. Radiolarians were also enumerated along  
187 with diatom frustules and were represented as individuals g<sup>-1</sup>.





### 188 2.2.3 Biomarker analysis and temperature proxy

189 Lipid biomarker analyses were carried out at the Institute for Geology, University of Hamburg,  
190 Germany. About 11 to 19 g of freeze-dried and ground samples were used to obtain total lipid  
191 extracts (TLEs) by using an Accelerated Solvent Extractor (ASE200, DIONEX). Before  
192 extraction, ~~a known amount~~ (10 ng  $\mu\text{L}^{-1}$ ) of internal standards (14-heptacosanone,  
193 nonadecanol, and dialkylglycerol ether-18 (DAGE-18)) were added to the samples. The ASE  
194 extraction for each sample was carried out at 100°C and 1000 PSI for 5 minutes in 3 cycles by  
195 using the solvent mixture dichloromethane: methanol (DCM: MeOH, 9:1). The TLEs were  
196 then concentrated with rotary evaporation and ~~were~~ separated later into a hexane-soluble  
197 (adding *n*-hexane) and hexane-insoluble (adding DCM) fraction via  $\text{NaSO}_4$  column  
198 chromatography. To separate the hexane-soluble fraction into a neutral- and acid fraction via  
199 saponification (at 85°C for 2 hrs) a 5 % potassium hydroxide (KOH) in MeOH solution was  
200 added to this fraction. Then, the neutral fractions were obtained by adding *n*-hexane to the  
201 saponified fraction, vortexing, and pipetting the neutral fraction containing *n*-hexane layer into  
202 a new vial. The neutral fractions were then separated into apolar-, ketone-, (containing  
203 alkenones), and polar fractions (containing sterols, stanols) by column chromatography packed  
204 with deactivated silica gel (5 %  $\text{H}_2\text{O}$ , 60  $\mu\text{m}$  mesh) using the solvents *n*-hexane, DCM, and  
205 DCM:MeOH (1:1), respectively. We took 50% splits of the ketone- and polar fractions and put  
206 them together, as some of the sterols and added standards for the sterol fraction were found in  
207 the ketone fraction, too. For the derivatization of these fractions, a mixture of 200  $\mu\text{L}$  BSTFA:  
208 Pyridin (1:1) was added to the dried sample and heated at 80°C for 2 hrs followed by drying  
209 under an  $\text{N}_2$  environment.

210 To quantify the alkenones and sterols the samples were measured with a Thermo Scientific  
211 Trace 1310 gas chromatography coupled to a flame ionization detector (GC-FID) equipped  
212 with a Thermo Scientific TG-5MS column (30 m, 0.25 mm, 0.25  $\mu\text{m}$ ).  $\text{H}_2$  as carrier gas was  
213 used with a flow rate of 35  $\text{mL minute}^{-1}$  and the PTV injector started at 50°C ramped with  
214 10°C/s to 325°C in a splitless mode. For the alkenones, the initial GC temperature was  
215 programmed to 50°C (held 1 minute) and then ramped to a temperature of 230 °C with an  
216 increased rate of 20 °C  $\text{minute}^{-1}$ , then increased with 4.5°C  $\text{minute}^{-1}$  to 260 °C and finally  
217 increased the temperature with 6 °C  $\text{minute}^{-1}$  to 325°C which was held for 15 minutes. The  
218 peaks of alkenones were identified by comparing the retention time for peaks of the samples  
219 with a known working sediment standard. Quantification of the alkenones was done by using  
220 14-heptacosane and tetratriacontane with a known amount (10 ng  $\mu\text{L}^{-1}$ ) as external standards.  
221 Repeated measurements of the external standards yielded a quantification precision of 13 %  
222 (14-heptacosanone) and 8 % (tetratriacontane). The alkenone saturation index was calculated  
223 using the equation by Prahl et al. (1988):

$$224 \quad U_{37}^{k'} = \frac{C_{37:2}}{C_{37:2} + C_{37:3}}$$

225 to convert the  $U_{37}^{k'}$  index to SSTs we have used the core top calibration of Indian Ocean  
226 sediments (Sonzogni et al., 1997):

$$227 \quad SST = \frac{U_{37}^{k'} - 0.043}{0.033}$$

228 For each sample, at least a duplicate measurement was conducted, which yielded an average  
229 precision of 0.1°C (1SD). Replicate extractions of a working standard sediment (n=2) and its  
230 duplicate measurements of each replicate yielded to an average precision of 0.5°C (1 SD).





231 For the quantification of the sterols, the initial GC temperature was 50°C (held for 3 minutes)  
232 and then programmed to a final temperature of 325 °C (held for 20 minutes) with an increase  
233 of 6 °C **minutes**<sup>-1</sup>. To quantify the sterols we used nonadecanol and DAGE-18 with a known  
234 amount (10 ng µL) as external standards, with precision of 5.6 % and 4.9 %, respectively. To  
235 identify the sterols the mass spectra of each sample were investigated using a Thermo Scientific  
236 Trace GC Ultra coupled to a Thermo Scientific DSQ II mass spectrometer (GC-MS). He (2 mL  
237 minute<sup>-1</sup> flow rate) was used as carrier gas. The initial GC temperature was 50 °C (held for 3  
238 minutes) and ramped with 6 °C minute<sup>-1</sup> to 325 °C (held for 25 minutes). The mass spectra of  
239 the compounds were then compared with published mass spectral data.



240 For major four phytoplankton groups, brassicasterol, dinosterol, dinostanol and C<sub>37</sub> alkenone  
241 were used. For zooplankton cholesterol, and its degradative product cholestanol (Wittenborn  
242 et al., 2020) was used.



#### 243 2.2.4 Sea surface temperature (SST) from satellite imagery

244 The SST data was accessed from the climate reanalysis version 5 (ERA5) of the European  
245 Centre for Medium-Range Weather Forecasts (ECMWF) (C3S, 2017). ERA5 covers the time  
246 from 1979 to the present at a 0.25° × 0.25° grid. In this study, we used monthly mean of SST  
247 data covering a period from 2017–2020 (downloaded from:  
248 <https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=form>).

#### 249 2.2.5 Statistical analysis

250 The Shapiro-Wilk normality test and F test were used to check the normality and variance of  
251 individual datasets, respectively. The statistical significance between differences for various  
252 parameters was obtained using Single-factor Analysis of Variance (ANOVA) in Microsoft  
253 Excel at a 95% confidence level (probability  $p < 0.05$ ). The relationships between biotic  
254 (biomarkers, frustules, radiolarian, diatom community) and environmental (SST, TOC, TN,  
255 TIC, TOC:TN) variables were conducted using the CANOCO version 4.5 software (Ter Braak  
256 and Šmilauer, 2002). For explaining the correlation between the biotic and environmental  
257 variables a linear multivariate model RDA (Redundancy Analysis) was used.

### 258 3. Results

259 The sedimentary characteristics (TIC, TOC, TN), diatom frustule abundance, and diversity  
260 including radiolarian abundance from the **top 0–0.5 cm were already published earlier** (Pandey  
261 et al., 2023). In this study, we have analyzed the samples from 0.5–1 cm sediment depth and  
262 collectively shown an average representing the top 1 cm of the surface sediment (Table 1).  
263 Results of lipid biomarkers (0–0.5 and 0.5–1 cm) such as various phytosterols and the summed  
264 C<sub>37:2</sub> and C<sub>37:3</sub> alkenones as well as U<sub>37<sup>k</sup></sub>-derived sea surface temperature (SST) proxy are shown  
265 in Table 1. For further discussion of our results, the study area has been defined in two areas  
266 as the northern part (north of mean position of Findlater Jet) includes the sites 21, 19 and 15°  
267 N, whereas the southern part includes the sites 11, and 13 °N (Fig. 1a).

#### 268 3.1 Bulk sedimentary analysis and SST reconstruction

269 To compare with U<sub>37<sup>k</sup></sub> based-SST reconstruction, we also present **here** the SST values derived  
270 from the satellite (Fig. 1b) averaged for the **last three years (2017–2020). Assuming**  
271 the surface sediment usually represents the signature of recent time SST. High spatial variability  
272 in SST was observed from the north (mean 27.2°C) to the south (28°C). TIC contents (Fig. 2a)  
273 were slightly higher in the south (7.06 ± 0.63 %) compared to the north (5.15 ± 1.57 %) and  
274 this difference was statistically significant at a 94.7 % confidence level (single factor ANOVA  
275 analysis, Table 2). TOC contents (Fig. 2b) were substantially higher ( $p < 0.001$ ) above 15° N





276 (0.97 ± 0.06 %) reaching their highest value at 21° N and decreased southward (0.78 ± 0.005  
277 %). TN values (Fig. 2c) revealed a similar trend as TOC and decreased from 21° N (0.11 ±  
278 0.001 %) to 11° N (0.07 ± 0.009 %). The average TN value (0.06 ± 0.008 %) in the south was  
279 significantly lower ( $p < 0.001$ ) compared to the north (0.087 ± 0.018 %). The ratio of TOC and  
280 TN (Table 1) was the lowest (9.5 ± 0.18) in the north at 21° N and increased at the rest of the  
281 stations reaching >12. The  $U_{37}^{kw}$  based SST (Fig. 2d) shows an average value of 27.8 ± 0.3 °C.  
282 The coolest reconstructed SSTs (27.6 ± 0.25 °C) were found in the north and were nearly 0.4  
283 °C cooler compared to the south ( $p = 0.043$ ) (Table 2).

### 284 3.2 Lipid biomarkers

285 The lipid biomarkers brassicasterol (diatoms) (Fig. 2e), dinosterol (dinoflagellates) (Fig. 2f),  
286 dinostanol, the saturated, degradative product of dinosterol (Fig. 2g), and summed  $C_{37:2}$  and  $37:3$   
287 alkenones ( $C_{37}$  alkenone) (coccolithophores) (Fig. 2h) were present from north to south. The  
288 average dinosterol contents (98 ± 64 ng g<sup>-1</sup>) found in the surface sediment were the highest of  
289 the biomarkers followed by brassicasterol (64 ± 44 ng g<sup>-1</sup>) and  $C_{37}$  alkenones (39.4 ± 12 ng g<sup>-1</sup>)  
290 (Table 1). All studied lipid biomarkers showed significant linear positive correlations ( $R^2$   
291 = 0.62–0.96,  $p < 0.05$ ) with each other indicating their similar responses to environmental  
292 variables. Their concentrations were quite high at the northernmost station at 21° N (Fig. 2;  
293 Table 1) and decreased to their minimum values at 11° N. However, there were apparent trends  
294 of decrease from north to south of the sampling transect, but none of the biomarkers showed  
295 any statistically significant difference in their TOC normalized values between the stations.  
296 The sum of the major biomarkers grossly represents the major three phytoplankton groups,  
297 with the highest (33.9 ± 14.13 µg g<sup>-1</sup> TOC) at 21° N compared to other stations (19.96 ± 9.5  
298 µg g<sup>-1</sup> TOC). The TOC normalized values of dinosterol (16.53 ± 8.3 µg g<sup>-1</sup> TOC) and  
299 brassicasterol (12.37 ± 5.2 µg g<sup>-1</sup> TOC) were the highest at the northernmost station and  
300 decreased southward. However, the average values of dinosterol (north: 12.81 ± 6.3 µg g<sup>-1</sup>  
301 TOC; south 7.8 ± 4.47 µg g<sup>-1</sup> TOC) and brassicasterol (north: 8.64 ± 4.75 µg g<sup>-1</sup> TOC; south  
302 5.81 ± 3.48 µg g<sup>-1</sup> TOC) were not significantly different ( $p > 0.05$ ) (Table 2). The average ratios  
303 of dinosterol to brassicasterol and brassicasterol to alkenones were 1.5 and 1.6 (Table 1),  
304 respectively, without any significant north-south variability (Table 2).

### 305 3.3 Zooplankton proxies

306 We used two proxies representing zooplankton: 1) sterol biomarker (cholesterol (Fig. 2i), and  
307 its degradative product cholestanol (Fig. 2j)), although it may come from some other sources  
308 (Wittenborn et al., 2020) and 2) radiolarians. Cholesterol, mostly varied between 10 ± 2.5 µg  
309 g<sup>-1</sup> TOC (north) and 14.3 ± 5.8 µg g<sup>-1</sup> TOC (south) without any statistical significance. The  
310 TOC normalized values of cholestanol are lower in the northern (11.8 ± 6.3 µg g<sup>-1</sup> TOC) than  
311 in the southern part (15.9 ± 11.4 µg g<sup>-1</sup> TOC) and no significant correlation was noticed (Table  
312 2).

313 Radiolarian abundance (Fig. 2k) in the central Arabian Sea varied between 1.07 and 2.13 × 10<sup>4</sup>  
314 individuals g<sup>-1</sup> with the highest numbers at 13° N and the lowest at 21° N. Their occurrences  
315 were found to be higher at the southern stations (1.84 × 10<sup>4</sup> individuals g<sup>-1</sup>) compared to  
316 northern stations (1.10 × 10<sup>4</sup> individuals g<sup>-1</sup>) with statistical significance ( $p < 0.014$ ) (Table 2).  
317 The community was dominated by the genus *Tetrapyle* sp. and their abundance was higher in  
318 the south.

### 319 3.4 Diatom frustules: abundance and diversity

320 Diatoms frustules from the surface sediment showed high spatial variability in both abundance  
321 and diversity. The total frustule abundance in the central Arabian Sea (Supplementary Table 1;



322 Fig. 2l) ranged between  $2.78$  and  $6.36 \times 10^4$  valves  $g^{-1}$ . The highest frustule abundance was  
323 observed at  $19\text{--}21^\circ$  N and the least at  $11^\circ$  N. At station  $19^\circ$  N, the frustule abundance was the  
324 highest ( $6.36 \pm 0.2 \times 10^4$  valves  $g^{-1}$ ) among all stations (Table 1). The frustule numbers found  
325 in the north ( $5.46 \pm 0.95 \times 10^4$  valves  $g^{-1}$ ) were 1.67 times higher than in the south ( $p=0.009$ ).  
326 Diatom frustule diversity was calculated to understand the north-south distribution pattern and  
327 the average Shannon–Wiener diversity index ( $H'$ ) was  $1.6 \pm 0.1$  with the highest diversity at  
328  $21^\circ$  N (1.8) (Supplementary Fig. 1). Microscopic analysis revealed a total of 23 genera, with 9  
329 centric and 14 pennate diatoms. More than five-fold higher abundance of centric diatoms was  
330 observed than pennate at all the locations ( $p < 0.05$ ). The abundance of pennate diatoms was  
331 higher towards southern stations without any statistical significance.

332 The overall diatom community in the sediment samples from the central Arabian Sea  
333 (Supplementary Table 1; Fig. 3) was observed to be dominated by *Coscinodiscus* (40%),  
334 *Thalassiosira* (34%), *Pseudo-nitzschia* (6%), *Rhizosolenia* (4%), *Hemidiscus* (4%),  
335 *Thalassionema* (4%), and *Nitzschia* (3%). The northern stations were dominated by  
336 *Coscinodiscus* sp., whereas the two southernmost stations were dominated by *Thalassiosira*  
337 sp. In the north, the highest abundance ( $2.46 \times 10^4$  valves  $g^{-1}$ ) of *Coscinodiscus* sp. was  
338 observed ( $p < 0.05$ ) with the least abundance at  $11^\circ$  N ( $0.61 \times 10^4$  valves  $g^{-1}$ ). In the south,  
339 *Thalassiosira* seemed to dominate ( $1.59 \times 10^4$  valves  $g^{-1}$ ) without any statistical significance.  
340 The Bray-Curtis similarity index usually indicates the similarity in the distribution pattern of  
341 different diatom genera/species. The results revealed (Supplementary Fig. 2) that the two  
342 dominating diatom genera, i.e. *Coscinodiscus* sp. and *Thalassiosira* sp were grouped showing  
343 a similar distribution pattern. The commonly occurring pennate diatom *Pseudo-nitzschia* was  
344 present independently, whereas, *Rhizosolenia* and *Thalassionema* were clubbed. The other two  
345 major contributing diatom genera, *Hemidiscus* and *Nitzschia* revealed a similar pattern.

### 346 3.5 Statistical Analysis

347 In the RDA biplot (Fig. 4), Axis 1 and 2 explained most of the variability ( $\sim 97.2\%$ ). The biotic  
348 variables and abiotic variables show a distinct association. Interestingly, TOC, TN, the key  
349 phytoplankton biomarkers (dinosterol, brassicasterol, dinostanol, and alkenones), along with  
350 diatom frustules abundance, and the major genera were clubbed and were at the opposite axis  
351 where TIC, SST, cholesterol, and radiolarian were together. The association between the larger  
352 diatoms like *Coscinodiscus* and *Rhizosolenia* and organic matter including brassicasterol  
353 depicted that the organic matter flux was coupled with diatom fluxes. The positioning of  
354 *Thalassiosira* opposite these parameters also suggested that its abundance was higher in the  
355 south associated with warmer SSTs. TOC:TN ratio and TIC along with SST were together.

## 356 4. Discussion

### 357 4.1 Physical Forcing induced spatial variability in physicochemical properties

358 The alkenone-derived SST suggested a cooler northern part ( $19\text{--}21^\circ$  N) compared to the south  
359 along the sampling transect ( $64^\circ$  E, Fig. 2d). The annual average of satellite-derived SST also  
360 revealed a similar trend. Such variability in SST from north to south could be attributed to  
361 monsoon wind variability and related processes. During the summer monsoon, the  
362 physicochemical parameters (wind speed, SST, nutrients, mixed layer depths [MLDs]) along  
363  $64^\circ$  E show distinct north-south demarcation due to the presence of the Findlater Jet (Findlater,  
364 1971). In the northern flank of this jet axis, the maximum influence of upwelling is evidenced  
365 by the presence of cooler SSTs, high nutrient levels, and shallower MLDs (Silori et al., 2021;  
366 Chowdhury et al., 2021; Chowdhury et al., 2024). Along the axis ( $\sim 15\text{--}18^\circ$  N) of the Jet the  
367 highest wind speeds are recorded (Silori et al., 2021; Chowdhury et al., 2021; Chowdhury et







368 al., 2024). The coolest SST value at 15° N is most likely due to the advection of cool nutrient-  
369 rich upwelled waters from the western coastal Arabian Sea (Bauer et al., 1991). Furthermore,  
370 such high wind speeds for a prolonged period may also lead to evaporative heat loss leading to  
371 a decrease in SST. Contrarily, in the south downwelling induced deeper MLDs (>100 m),  
372 nutrient-poor waters along with higher SSTs are observed (Latasa and Bidigare, 1998;  
373 Chowdhury et al., 2021; Silori et al., 2021). During the winter monsoon, surface circulation  
374 reverses in this region, and in the northern Arabian Sea cold dry wind leads to evaporative  
375 cooling and subsequent convection leading to cooler SSTs, and high nutrient levels. At the  
376 same time, southern regions remain oligotrophic and warm. During the intermonsoon and  
377 premonsoon, SST increases and nutrient level reduces substantially along the entire transect  
378 (Prasannakumar and Narvekar, 2005).

## 379 4.2 Spatial variability in particle flux, and phytoplankton dynamics

### 380 4.2.1 Organic matter

381

382 The northernmost stations were the hotspots for particulate organic matter (POM) flux and sink  
383 to the sediment floor (Fig. 2). The positioning of SST in the RDA plot (Fig. 4) opposite TOC,  
384 TN, diatom frustules, and phytoplankton biomarkers also supported this fact. The north-south  
385 variability in phytodetritus flux could be also influenced by dissolved oxygen levels within the  
386 mesopelagic (Fig. 5) as it directly controls microbial degradation and zooplankton activity  
387 (Moriceau et al., 2018; Iversen, 2023). In our sampling transect, the northern stations are under  
388 the influence of intense OMZ and the intensity as well as the thickness reduces while moving  
389 southward (Banse et al., 2014). In their synthesis, Banse et al. (2014) showed that the median  
390 DO values within 150–500 m depth in the northern stations within the core OMZ vary between  
391 0.04 and 0.30 mL L<sup>-1</sup>. Conversely, in the south, these values increased to 0.24–0.72 mL L<sup>-1</sup>.  
392 Such spatial variability in OMZ distribution/intensity across the stations could substantially  
393 alter the rate of organic matter mineralization, zooplankton abundance (Cavan et al., 2017),  
394 and particle flux attenuation (François et al., 2002; Keil et al., 2016). Fast and efficient  
395 mineralization within the mesopelagic may allow less organic matter to be transported, whereas  
396 partial remineralization may lead to higher organic matter export flux (Ragueneau et al., 2006).  
397 Therefore, the northern station with an intense OMZ may have a higher preservation potential  
398 of organic matter compared to the south (Fig. 5) as mentioned by Schulte et al. (2000).

399

### 400 4.2.2 Phytoplankton biomarkers

401 TOC-normalized lipid biomarker contents collected from the surface sediment represent the  
402 relative contribution of individual phytoplankton groups to total organic matter transfer from  
403 the upper oceanic layers to the deep sea floor. In this study, total and TOC-normalized  
404 phytoplankton biomarkers revealed that dinoflagellates, diatoms, and coccolithophores were  
405 the dominant phytoplankton groups transferring carbon to the surface sediment (Fig. 2). All  
406 studies available from the Arabian Sea using biomarkers (Schubert et al., 1998; Schulte et al.,  
407 1999; 2000; Prah et al., 2000) showed that dinosterol contents were higher than brassicasterol,  
408 both in sediment core and trap samples, suggesting greater contributions of dinoflagellates  
409 compared to diatoms. In this study, nearly 1.5 times higher dinosterol contents compared to  
410 brassicasterol all along the transect also confirmed this. Likewise, the dominance of dinosterol,  
411 C<sub>37</sub>-alkenones, and some species-specific biomarkers for diatoms was found in sediment trap  
412 samples (2220 m depth) from the Central Arabian Sea (Prah et al., 2000), in two sediment core  
413 samples from the northeastern and southern Arabian Sea (Schulte et al., 1999). Further, a long  
414 sediment core from the northern Arabian Sea close to our sampling locations (22° 29.31' N,





415 65° 38.9' E) (Schubert et al., 1998) reported about the same dominating phytoplankton groups  
416 in the Arabian Sea over the past 0.2 million years.

417  
418 Since diatoms predominate over dinoflagellates during phytoplankton blooms (Chowdhury et  
419 al., 2021; 2024) a higher contribution of brassicasterol over dinosterol can be expected,  
420 however, it was the opposite in our study. This reverse trend can be explained by the seasonal  
421 succession of phytoplankton communities in surface layers mostly driven by nutrient  
422 stoichiometry related to monsoon wind forcings and grazing (Prahl et al., 2000; Rixen et al.,  
423 2019a). It should be noted that organic matter on the surface sediment accumulates throughout  
424 the year with variable depositional rates. Monsoon reversal also leads to changes in the  
425 phytoplankton community (Sawant and Madhupratap, 1996; Latasa and Bidigare, 1998) that  
426 may also affect the transfer of phytodetritus to the sea floor. Consequently, diatom frustules  
427 largely represent the signature of the most productive periods. However, the nutrient-poor  
428 phases are usually dominated by dinoflagellates and other calcifying nanophytoplankton.  
429 Dinoflagellates grow slowly in nutrient-poor warm waters and can remain there for longer  
430 periods (k-strategists) (Smayda and Reynolds, 2001; Glibert et al., 2016). Likewise, this  
431 situation can be compared to the southern stations, where high SSTs and oligotrophic  
432 conditions were more favorable for the growth of dinoflagellates (Chowdhury et al., 2021;  
433 2024). This is reflected south of the 15° N station by the occurrences of dinoflagellates like  
434 *Gymnodinium* sp. *Gyrodinium* sp, and *Katodinium* sp. with small cells (Garrison et al., 1998;  
435 Chowdhury et al., 2021).

436 Moreover, unlike diatoms, which are autotrophs, most dinoflagellates could be either  
437 heterotrophs or mixotrophs (Stoecker, 1999; Stoecker et al., 2017) which actively graze on  
438 smaller phytoplankton including diatoms and even could be detritivorous feeding on particles  
439 (García-Oliva et al., 2022). Mixotrophs could consume prey to meet their cellular nitrogen  
440 demand and can simultaneously perform photosynthesis to gain carbon (Stoecker et al., 2017).  
441 In the Arabian Sea dissolved inorganic nitrogen is the limiting nutrient and a significant part  
442 of the available nitrogen is lost due to strong denitrification within the OMZ (Ward et al., 2006).  
443 Therefore, particularly during the stratified oligotrophic phases like intermonsoon and  
444 premonsoon, when SST increases followed by stratification, nanophytoplankton, and  
445 dinoflagellates dominate over diatoms. Hence, the overall contribution of dinoflagellates on an  
446 annual basis could exceed diatoms as dinoflagellates are constantly present during both high-  
447 nutrient regimes and low-nutrient stratified warm water periods.

448 Another possible factor for the observed variability in brassicasterol to dinosterol could be due  
449 to differences in their labile nature. It was claimed that diatom-rich organic matter could be of  
450 higher lability (François et al., 2002) and may possess low transfer potential to the sea floor  
451 (Alonso-González et al., 2010). Contrary to this, it was also observed that compared to other  
452 phytoplankton (Cabrera-Brufau et al., 2021) diatom-rich organic matter is more of a refractory  
453 nature against mesopelagic microbial degradation. Moreover, the phytodetritus of diatom  
454 origin could be preferably eaten by the benthic communities than other phytoplankton groups  
455 (Nomaki et al., 2021) and could be one of the reasons for lower brassicasterol over dinosterol  
456 in the surface sediment. This is indeed difficult to conclude as we do not have enough  
457 experimental evidence supporting/contradicting these hypotheses.

458 In the central Arabian Sea, coccolithophores constitute an important part of the  
459 nanophytoplankton community (Andruleit et al., 2004; Mergulhao et al., 2006). The relatively  
460 high occurrences of substantial amounts of C<sub>37</sub>-alkenones all along the transect in our study  
461 indicate that coccolithophores may also contribute as a major part of sinking phytodetritus,  
462 with slightly higher values towards the north (Fig. 2h). Sediment trap studies from the south of



463 the Findlater Jet (Mergulhao et al., 2006) reported the flux of coccolithophores throughout the  
464 year justifying our observations.

#### 465 4.2.3 Diatom frustules

466 The highest abundance of diatom frustules coupled with TOC and TN contents were found in  
467 the northern stations (19-21° N), which most likely indicated higher organic matter transfer to  
468 the sediment compared to the southern stations. The RDA plot (Fig. 4) also revealed that the  
469 abundance of large centric diatoms like *Coscinodiscus*, *Rhizosolenia*, TOC, and TN contents  
470 as well as brassicasterol were grouped and correlated significantly. During both summer  
471 (Chowdhury et al., 2021) and winter monsoons (Sawant and Madhupratap, 1996) in the  
472 northern Arabian Sea, *Coscinodiscus* and *Rhizosolenia* are the major diatoms forming blooms  
473 and consequently, dominate the particle flux (opal/biogenic silica) (Rixen et al., 2019a). A  
474 higher abundance of large *Rhizosolenia* frustules was also seen in the sediment trap samples  
475 from the central Arabian Sea after the summer monsoon bloom (Rixen et al., 2019a). The  
476 contribution of heavily silicified diatom frustules may in addition provide ballasting effects  
477 (Smetacek, 1985; Tréguer et al., 2018) facilitating efficient organic matter export compared to  
478 other phytoplankton groups (Buesseler, 1998; Boyd and Newton, 1999; Zúñiga et al., 2021).  
479 Diatom bloom development in the Arabian Sea was found to be associated with dissolved silica  
480 (DSi) availability (Chowdhury et al., 2021) and the depth of the silicicline (Anju et al., 2020).  
481 The northern stations become DSi depleted (<2 μM) at the end of the bloom (Chowdhury et  
482 al., 2021) and may lead to a mass sinking of frustules (Smetacek, 1985; Krause et al., 2019) or  
483 they can be grazed and cell death may also occur due to viral attacks (Agusti and Duarte, 2000).  
484 On the other hand, the abundance of small chain-forming diatoms such as *Thalassiosira*,  
485 *Pseudo-nitzschia*, *Nitzschia*, and *Thalassionema*, enhanced in the surface sediment in the  
486 southern stations (Fig. 3) low nutrient conditions prevail even during summer and winter  
487 monsoons. During the intermonsoon and premonsoon oligotrophy intensifies in these regions  
488 supporting the growth of smaller diatoms or non-diatoms (Garrison et al., 1998; Tarran et al.,  
489 1999; Chowdhury et al., 2021) that could sink slower compared to the larger cells in the north  
490 (Buesseler and Boyd, 2009).

491 Moreover, diatom frustules may dissolve while sinking and usually the thickly silicified  
492 frustules reach the abyssal plain and can be preserved. Nevertheless, the organic coating  
493 that protects siliceous frustules from dissolution (Lewin, 1961), can be degraded by  
494 heterotrophic bacterial activity (Bidle and Azam, 1999; Roubeix et al., 2008). The presence of  
495 OMZ in the northern stations (200–1200m) could therefore slow down such dissolution  
496 facilitating frustules to reach the sea floor. On the other hand, in the south, small and thinly  
497 silicified diatom frustules (mostly due to DSi limitation) may be more fragile as they travel  
498 through the well-oxygenated water column and higher heterotrophic activity may enhance the  
499 risk of dissolution leading to reduced frustules abundance on the seabed. In addition to this, the  
500 almost 700 m deeper water column in the south compared to the north could enhance the scope  
501 of degradation of sinking particles. This is consistent with our observation.

#### 502 4.2.4 Zooplankton grazing

503  
504 The highest concentration of TOC-normalized cholesterol was found in the south indicating  
505 more zooplankton activity. In the RDA biplot, SST was clubbed with cholestanol and was on  
506 the same side of cholesterol indicating higher zooplankton activity in the south. The association  
507 of TIC with cholesterol indicates that calcareous zooplankton could also be a source of  
508 cholesterol. Consequently, a higher fecal matter production could enhance particle flux  
509 compared to the north. Nonetheless, a major part of the fecal matter could also be degraded  
510 within the upper mesopelagic layer as reported by Iversen et al. (2017). The authors observed



511 that more than 87% of fecal matter produced in the surface ocean can be lost via  
512 remineralization before reaching upper mesopelagic (300 m) in the Southern Ocean. Likewise,  
513 the warmer temperature in the mesopelagic of our study location could facilitate faster  
514 mineralization. Zooplankton grazing could largely alter the magnitude of carbon export flux  
515 (Moriceau et al., 2018). Thus, the low abundance of mesozooplankton within the OMZ may  
516 decrease defragmentation which in turn slows down the bacterial remineralization of  
517 phytodetritus allowing a higher amount of carbon to be exported to the abyssal plain (Cavan et  
518 al., 2017) (Fig. 5). Likewise, the lower zooplankton activity in the mesopelagic within the OMZ  
519 of the Arabian Sea (Wishner et al., 1998) may hinder particle fragmentation that usually  
520 accelerates degradation (Briggs et al., 2020). Likewise, at the northern stations, lower  
521 zooplankton abundance within the OMZ (Cavan et al., 2017) may restrict particle flux  
522 attenuation (Fig. 5).

523 In the western and central Arabian Sea, nearly 50–100% of the diatom population can be grazed  
524 by copepods (Landry et al., 1998; Smith et al., 1998; Gauns et al., 2005). Importantly, diatom  
525 cell size can be a crucial factor that determines their grazing rates. Copepods exhibit the highest  
526 grazing rate when the ratio between prey and predator body size remains 18:1 on average  
527 (Hansen et al., 1994). In the north and at the axis of the Findlater Jet, the higher availability of  
528 nutrients, particularly DSI could promote large and thickly silicified diatoms which are difficult  
529 to graze for copepods (Hansen et al., 1994; Ryderheim et al., 2022). Subsequently, large centric  
530 diatoms like *Coscinodiscus radiatus* and *Rhizosolenia* spp. could escape grazing by copepods  
531 (Jansen, 2008; Löder et al., 2011) and can sink to the sediment floor (Buesseler and Boyd,  
532 2009; Kemp et al., 2006). On the contrary, the bloom-forming diatoms with thinly silicified  
533 frustules like *Chaetoceros* and *Leptocylindrus* (Sawant and Madhupratap, 1996; Chowdhury  
534 et al., 2021) can be grazed easily and are usually not found in the sediment. However, the  
535 organic signature can be reflected in sedimentary biomarkers like brassicasterol. In the case of  
536 southern stations, smaller diatoms or non-diatoms could be consumed by microzooplankton  
537 (Swanberg and Anderson, 1985). Corroborating with this fact, the significantly higher number  
538 of radiolarians (Fig. 2k) which mostly consume smaller phytoplankton, bacterioplankton, and  
539 copepods (Caron et al., 1995) were higher in the south. A high abundance of radiolarians  
540 dominated by *Tetrapyle* sp. that are found under high salinity was also reported by a previous  
541 study from the Arabian Sea (Gupta, 2003).

542

#### 543 4.2.5 Influence of lateral advection

544

545 Since there is evidence of advected waters reaching from the western Arabian Sea to its central  
546 part, the chances of particle transport also need to be considered. Nitrogen-stable isotopic  
547 values of particulate organic matter ( $\delta^{15}\text{N}_{\text{POM}}$ , Silori et al. 2021) revealed that nutrient  
548 enrichment mostly takes place via advection from the upwelling system as well as entrainment  
549 close to the axis (16–18° N). Earlier studies also noticed the presence of slightly low saline  
550 waters in this region probably due to advection from the western Arabian Sea (Prasanna Kumar  
551 et al., 2000). Additionally, Silori et al. (2021) reported lower  $\delta^{15}\text{N}$  values of particulate nitrogen  
552 during summer monsoon at the stations influenced by the axis suggesting laterally advected  
553 dissolved inorganic nitrogen from the Somali upwelling region. However, so far there is no  
554 report claiming that particulate organic matter can be advected such a long distance (~600 km)  
555 without being grazed/remineralized/sinking. Contrarily, there is plenty of evidence showing a  
556 direct relation between phytoplankton bloom and particle flux in these regions (Haake et al.,  
557 1993; Rixen et al., 2019a). Thus, the possibility of lateral transport of phytoplankton or detritus  
558 from the western Arabian Sea to the seabed of the central Arabian Sea may be partly overruled.



559

560

## Conclusions

561 This study aims for the first time to elucidate phytoplankton-driven particle flux to the sea floor  
562 using sedimentary organic biomarkers from the central Arabian Sea. Such studies linking  
563 sedimentary organic matter to physical forcings and phytoplankton community have rarely  
564 been studied in the central Arabian Sea. Importantly, most of the studies using sediment traps  
565 focused on diatoms and coccolithophores, but neglected dinoflagellates (Nair et al., 1989). A  
566 few studies proposed that the diatom blooms could be replaced by dinoflagellates. On the other  
567 hand, another study (Schubert et al. 1998), revealed that the relative contribution of dinosterol  
568 was higher than brassicasterol over the last 0.2 million years in this basin. Following this  
569 concept, we crosschecked the organic matter from the top 1 cm of surface sediments from more  
570 locations across a spatially variable transect (from high to low productive). Our results also  
571 indicated that dinoflagellates have contributed more to the sedimentary phytodetritus compared  
572 to diatoms even in the recent past. We propose that diatoms and coccolithophores do contribute  
573 to sedimentary particle flux. However, the dinoflagellates dominate due to their smart survival  
574 strategies during poor nutrient supply. We show that the distinct spatial variability in physical  
575 forcing drives the phytoplankton bloom and the particle flux is also closely coupled with this  
576 fact. The northernmost station in the central Arabian Sea was found to be a hotspot for sinking  
577 particles followed by subsequent preservation mostly due to the prevailing OMZ (Fig. 5). Both  
578 summer and winter monsoon-induced phytoplankton bloom dominated by diatoms led to the  
579 sinking of large thickly silicified frustule on the sediment floor. We hypothesized that the low  
580 oxygen within the thick OMZ could slow down the dissolution of frustules as well as  
581 heterotrophic degradation and fragmentation by zooplankton leading to low flux attenuation.  
582 Contrarily, in the south, higher dissolved oxygen levels could facilitate faster remineralization  
583 and higher zooplankton activity resulting in more flux attenuation and reduced particle  
584 transport to the sea floor. Contrary to the global scenario of expanding OMZ, a recent modeling  
585 study (Vallivattathillam et al., 2023) showed that the southern part of the OMZ can get thinner  
586 in the future due to the higher supply of oxygen. Such changes could facilitate higher  
587 heterotrophic activities within the mesopelagic and thus could impact particle flux attenuation  
588 in this region and need to be investigated.

589

## Acknowledgments

590 MP was supported by the Department of Science and Technology (DST) - Inspire Fellowship.  
591 This study is an outcome of CSIR-NIO in-house program “Impact of Climate Change on the  
592 Physics, Biogeochemistry, and the Ecology of the North Indian Ocean (CliCONIO)” (MLP  
593 1802) funded by the Council of Scientific and Industrial Research (CSIR). We express our  
594 gratitude to the captain, scientists, technical staff, ship cell staff, deckhands, and the students  
595 onboard RV Sindhu Sadhana (SSD 068) for their constant help and support during the cruise.  
596 We are thankful to the Director, CSIR NIO for his kind support. Ms. Teja Naik is acknowledged  
597 for the technical help in using the Coulometer under the central analytical facility in CSIR,  
598 NIO, Goa. The contribution number is XXXX. NB was funded by the Deutsche  
599 Forschungsgemeinschaft (DFG, German Research Foundation) under Germany’s Excellence  
600 Strategy – EXC 2037 ‘CLICCS - Climate, Climatic Change, and Society’ – Project Number:  
601 390683824, contribution to the Center for Earth System Research and Sustainability (CEN) of  
602 Universität Hamburg. The author(s) wish to acknowledge use of the Ferret program for analysis  
603 and graphics in this paper. Ferret is a product of NOAA’s Pacific Marine Environmental  
604 Laboratory. (Information is available at <http://ferret.pmel.noaa.gov/Ferret/>).

605

606 **Availability of data and materials:** Data will be available on request





607 **Statements and Declarations**

608 **Competing Interests:** *The authors have no relevant financial or non-financial interests to*  
609 *disclose.*

610 **Ethical Approval: Not applicable**

611 **Consent to Participate: Not applicable**

612 **Consent to Publish: Not applicable**

613 **Authors' Contributions:** *MP: Conceptualization, sampling, sample analysis; formal*  
614 *analysis, data curation, writing original manuscript and editing; HB: Conceptualization; Fund*  
615 *acquisition; sampling; manuscript reviewing and editing; DB: sampling; manuscript*  
616 *reviewing and editing NB: Sample analysis, Conceptualization; manuscript reviewing and*  
617 *editing BG: Conceptualization; reviewing and editing*

618 **References**

- 619 1. Abrantes, F.F.G. and Sancetta, C.: Diatom assemblages in surface sediments reflect  
620 coastal upwelling off southern Portugal, *Oceanologica acta*, 8, 7–12, 1985.
- 621 2. Agustí, S. and Duarte, C.M.: Strong seasonality in phytoplankton cell lysis in the NW  
622 Mediterranean littoral, *Limnology and Oceanography*, 45, 940–947,  
623 <https://doi.org/10.4319/lo.2000.45.4.0940>, 2000.
- 624 3. Alonso-González, I.J., Aristegui, J., Lee, C., Sanchez-Vidal, A., Calafat, A., Fabrés, J.,  
625 Sangrá, P., Masqué, P., Hernández-Guerra, A. and Benítez-Barrios, V.: Role of slowly  
626 settling particles in the ocean carbon cycle, *Geophysical research letters*, 37,  
627 <https://doi.org/10.1029/2010GL043827>, 2010.
- 628 4. Andruleit, H., Rogalla, U. and Stäger, S.: From living communities to fossil  
629 assemblages: origin and fate of coccolithophores in the northern Arabian Sea,  
630 *Micropaleontology*, 50, 5–21, [https://doi.org/10.2113/50.Suppl\\_1.5](https://doi.org/10.2113/50.Suppl_1.5), 2004.
- 631 5. Anju, M., Sreeush, M.G., Valsala, V., Smitha, B.R., Hamza, F., Bharathi, G. and Naidu,  
632 C.V.: Understanding the role of nutrient limitation on plankton biomass over Arabian  
633 Sea via 1-D coupled biogeochemical model and bio-Argo observations, *Journal of*  
634 *Geophysical Research: Oceans*, 125, e2019JC015502,  
635 <https://doi.org/10.1029/2019JC015502>, 2020.
- 636 6. Armbrecht, L.H., Lowe, V., Escutia, C., Iwai, M., McKay, R. and Armand, L.K.:  
637 Variability in diatom and silicoflagellate assemblages during mid-Pliocene glacial-  
638 interglacial cycles determined in Hole U1361A of IODP Expedition 318, *Antarctic*  
639 *Wilkes Land Margin, Marine Micropaleontology*, 139, 28–41,  
640 <https://doi.org/10.1016/j.marmicro.2017.10.008>, 2018.
- 641 7. Banse, K.: Seasonality of phytoplankton chlorophyll in the central and northern  
642 Arabian Sea, *Deep Sea Research Part A, Oceanographic Research Papers*, 34, 713–723,  
643 [https://doi.org/10.1016/0198-0149\(87\)90032-X](https://doi.org/10.1016/0198-0149(87)90032-X), 1987.
- 644 8. Banse, K., Naqvi, S.W.A., Narvekar, P.V., Postel, J.R. and Jayakumar, D.A.: Oxygen  
645 minimum zone of the open Arabian Sea: variability of oxygen and nitrite from daily to  
646 decadal timescales, *Biogeosciences*, 11, 2237–2261, [https://doi.org/10.5194/bg-11-](https://doi.org/10.5194/bg-11-2237-2014)  
647 [2237-2014](https://doi.org/10.5194/bg-11-2237-2014), 2014.
- 648 9. Barnett, P.R.O., Watson, J. and Connelly, D.: A multiple corer for taking virtually  
649 undisturbed samples from shelf, bathyal and abyssal sediments, *Oceanologica acta*, 7,  
650 399–408, 1984.
- 651 10. Bauer, S., Hitchcock, G.L., Olson, D.B.: Influence of monsoonally-forced Ekman  
652 dynamics upon surface layer depth and plankton biomass distribution in the Arabian



- 653 Sea, Deep Sea Research, Part A Oceanographic Research Papers 38, 531–553,  
654 [https://doi.org/10.1016/0198-0149\(91\)90062-K](https://doi.org/10.1016/0198-0149(91)90062-K), 1991.
- 655 11. Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L.,  
656 Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M. and Boss, E.S.: Climate-  
657 driven trends in contemporary ocean productivity, *Nature*, 444, 752–755,  
658 <https://doi.org/10.1038/nature05317>, 2006.
- 659 12. Bhattathiri, P.M.A., Pant, A., Sawant, S., Gauns, M., Matondkar, S.G.P. and  
660 Mohanraju, R.: Phytoplankton production and chlorophyll, *Current Science*, 71, 1996.
- 661 13. Bidle, K.D. and Azam, F.: Accelerated dissolution of diatom silica by marine bacterial  
662 assemblages, *Nature*, 397, 508–512, <https://doi.org/10.1038/17351>, 1999.
- 663 14. Boyd, P.W. and Newton, P.P.: Does planktonic community structure determine  
664 downward particulate organic carbon flux in different oceanic provinces?, *Deep Sea*  
665 *Research Part I: Oceanographic Research Papers*, 46, 63–91,  
666 [https://doi.org/10.1016/S09670637\(98\)00066-1](https://doi.org/10.1016/S09670637(98)00066-1), 1999.
- 667 15. Briggs, N., Dall'Olmo, G. and Claustre, H.: Major role of particle fragmentation in  
668 regulating biological sequestration of CO<sub>2</sub> by the oceans, *Science*, 367, 791–793,  
669 <https://doi.org/10.1126/science.aay1790>, 2020.
- 670 16. Buesseler, K.O. and Boyd, P.W.: Shedding light on processes that control particle  
671 export and flux attenuation in the twilight zone of the open ocean, *Limnology and*  
672 *Oceanography*, 54, 1210–1232, <https://doi.org/10.4319/lo.2009.54.4.1210>, 2009.
- 673 17. Buesseler, K.O.: The decoupling of production and particulate export in the surface  
674 ocean, *Global Biogeochemical Cycles*, 12, 297–310,  
675 <https://doi.org/10.1029/97GB03366>, 1998.
- 676 18. Cabrera-Brufau, M., Arin, L., Sala, M.M., Cermeño, P. and Marrasé, C.: Diatom  
677 dominance enhances resistance of phytoplanktonic POM to mesopelagic microbial  
678 decomposition, *Frontiers in Marine Science*, 8, p.683354,  
679 <https://doi.org/10.3389/fmars.2021.683354>, 2021.
- 680 19. Caron, D.A., Michaels, A.F., Swanberg, N.R. and Howse, F.A.: Primary productivity  
681 by symbiont-bearing planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in  
682 surface waters near Bermuda, *Journal of Plankton Research*, 17, 103–129,  
683 <https://doi.org/10.1093/plankt/17.1.103>, 1995.
- 684 20. Cavan, E.L., Trimmer, M., Shelley, F. and Sanders, R.: Remineralization of particulate  
685 organic carbon in an ocean oxygen minimum zone. *Nature Communications*, 8(1),  
686 p.14847, <https://doi.org/10.1038/ncomms14847>, 2017.
- 687 21. Chowdhury, M., Biswas, H., Mitra, A., Silori, S., Sharma, D., Bandyopadhyay, D.,  
688 Shaik, A.U.R., Fernandes, V. and Narvekar, J.: Southwest monsoon-driven changes in  
689 the phytoplankton community structure in the central Arabian Sea (2017–2018): After  
690 two decades of JGOFS, *Progress in Oceanography*, 197, p.102654,  
691 <https://doi.org/10.1016/j.pocean.2021.102654>, 2021.
- 692 22. Chowdhury, M., Biswas, H., Silori, S. and Sharma, D.: Spatiotemporal variability in  
693 phytoplankton size class modulated by summer monsoon wind forcing in the central  
694 Arabian Sea, *Journal of Geophysical Research: Oceans*, 129, e2023JC019880,  
695 <https://doi.org/10.1029/2023JC019880>, 2024.
- 696 23. Copernicus Climate Change Service (C3S), ERA5: Fifth generation of ECMWF  
697 atmospheric reanalyses of the global climate, Copernicus Climate Change Service  
698 Climate Data Store (CDS), 2017.
- 699 24. Desikachary, T.V.: Atlas of Diatoms (Marine Diatoms of the Indian Ocean Region), 6,  
700 Madras Science Foundation, Madras Fasc, 1–13, 1989.



- 701 25. Engel, A., Wagner, H., Le Moigne, F.A. and Wilson, S.T.: Particle export fluxes to the  
702 oxygen minimum zone of the eastern tropical North Atlantic, *Biogeosciences*, 14,1825-  
703 1838, <https://doi.org/10.5194/bg-14-1825-2017>, 2017.
- 704 26. Field, C.B., Behrenfeld, M.J., Randerson, J.T. and Falkowski, P.: Primary production  
705 of the biosphere: integrating terrestrial and oceanic components, *Science*, 281, 237-  
706 240, <https://doi.org/10.1126/science.281.5374.237>, 1998.
- 707 27. Findlater, J.: Mean monthly airflow at low levels over the western Indian Ocean (No.  
708 116). HM Stationery Office, *Pure Appl. Geophys. PAGEOPH* 115, 1251-1262,  
709 <https://doi.org/10.1007/BF00874408>, 1971.
- 710 28. Francois, R., Honjo, S., Krishfield, R. and Manganini, S.: Factors controlling the flux  
711 of organic carbon to the bathypelagic zone of the ocean, *Global Biogeochemical*  
712 *Cycles*, 16, 34-1, <https://doi.org/10.1029/2001GB001722>, 2002.
- 713 29. García-Oliva, O., Hantzsche, F.M., Boersma, M. and Wirtz, K.W.: Phytoplankton and  
714 particle size spectra indicate intense mixotrophic dinoflagellates grazing from summer  
715 to winter. *Journal of Plankton Research*, 44, 224-240,  
716 <https://doi.org/10.1093/plankt/fbac013>, 2022.
- 717 30. Garrison, D.L., Gowing, M.M. and Hughes, M.P.: Nano-and microplankton in the  
718 northern Arabian Sea during the Southwest Monsoon, August-September 1995 A US-  
719 JGOFS study, *Deep Sea Research Part II: Topical Studies in Oceanography*, 45, 2269-  
720 2299, [https://doi.org/10.1016/S0967-0645\(98\)00071-X](https://doi.org/10.1016/S0967-0645(98)00071-X), 1998.
- 721 31. Gauns, M., Madhupratap, M., Ramaiah, N., Jyothibabu, R., Fernandes, V., Paul, J.T.  
722 and Kumar, S.P.: Comparative accounts of biological productivity characteristics and  
723 estimates of carbon fluxes in the Arabian Sea and the Bay of Bengal. *Deep Sea Research*  
724 *Part II: Topical Studies in Oceanography*, 52, 2003-2017,  
725 <https://doi.org/10.1016/j.dsr2.2005.05.009>, 2005.
- 726 32. Glibert, P.M., Wilkerson, F.P., Dugdale, R.C., Raven, J.A., Dupont, C.L., Leavitt, P.R.,  
727 Parker, A.E., Burkholder, J.M. and Kana, T.M.: Pluses and minuses of ammonium and  
728 nitrate uptake and assimilation by phytoplankton and implications for productivity and  
729 community composition, with emphasis on nitrogen-enriched conditions, *Limnology*  
730 *and Oceanography*, 61, 165-197, <https://doi.org/10.1002/lno.10203>, 2016.
- 731 33. Gupta, S.M.: Orbital frequencies in radiolarian assemblages of the central Indian  
732 Ocean: implications on the Indian summer monsoon, *Palaeogeography,*  
733 *Palaeoclimatology, Palaeoecology*, 197(1-2), 97-112, [https://doi.org/10.1016/S0031-](https://doi.org/10.1016/S0031-0182(03)00388-2)  
734 [0182\(03\)00388-2](https://doi.org/10.1016/S0031-0182(03)00388-2), 2003.
- 735 34. Haake, B., Ittekkot, V., Rixen, T., Ramaswamy, V., Nair, R.R. and Curry, W.B.:  
736 Seasonality and interannual variability of particle fluxes to the deep Arabian Sea, *Deep*  
737 *Sea Research Part I: Oceanographic Research Papers*, 40(7), 1323-1344,  
738 [https://doi.org/10.1016/0967-0637\(93\)90114-I](https://doi.org/10.1016/0967-0637(93)90114-I), 1993.
- 739 35. Hansen, B., Bjornsen, P.K. and Hansen, P.J.: The size ratio between planktonic  
740 predators and their prey, *Limnology and oceanography*, 39(2), 395-403,  
741 <https://doi.org/10.4319/lo.1994.39.2.0395>, 1994.
- 742 36. Hu, L., Liu, Y., Xiao, X., Gong, X., Zou, J., Bai, Y., Gorbarenko, S., Fahl, K., Stein, R.  
743 and Shi, X.: Sedimentary records of bulk organic matter and lipid biomarkers in the  
744 Bering Sea: A centennial perspective of sea-ice variability and phytoplankton  
745 community, *Marine Geology*, 429, 106308,  
746 <https://doi.org/10.1016/j.margeo.2020.106308>, 2020.
- 747 37. Iversen, M.H., Pakhomov, E.A., Hunt, B.P., Van der Jagt, H., Wolf-Gladrow, D. and  
748 Klaas, C.: Sinkers or floaters? Contribution from salp pellets to the export flux during  
749 a large bloom event in the Southern Ocean, *Deep Sea Research Part II: Topical Studies*  
750 *in Oceanography*, 138, 116-125, <https://doi.org/10.1016/j.dsr2.2016.12.004>, 2017.





- 751 38. Iversen, M.H.: Carbon Export in the Ocean: A Biologist's Perspective, *Annual Review*  
752 *of Marine Science*, 15, 357–381, [10.1146/annurev-marine-032122-035153](https://doi.org/10.1146/annurev-marine-032122-035153), 2023.
- 753 39. Jansen, S.: Copepods grazing on *Coscinodiscus wailesii*: a question of size?, *Helgoland*  
754 *Marine Research*, 62(3), 251–255, <https://doi.org/10.1007/s10152-008-0113-z>, 2008.
- 755 40. Keil, R.G., Neibauer, J.A., Biladeau, C., van der Elst, K. and Devol, A.H.: A multiproxy  
756 approach to understanding the "enhanced" flux of organic matter through the oxygen-  
757 deficient waters of the Arabian Sea, *Biogeosciences*, 13(7), 2077–2092,  
758 <https://doi.org/10.5194/bg-13-2077-2016>, 2016.
- 759 41. Kemp, A.E., Pearce, R.B., Grigorov, I., Rance, J., Lange, C.B., Quilty, P. and Salter, I.,  
760 Production of giant marine diatoms and their export at oceanic frontal zones:  
761 Implications for Si and C flux from stratified oceans, *Global Biogeochemical*  
762 *Cycles*, 20(4), <https://doi.org/10.1029/2006GB002698>, 2006.
- 763 42. Krause, J.W., Schulz, I.K., Rowe, K.A., Dobbins, W., Winding, M.H., Sejr, M.K.,  
764 Duarte, C.M. and Agustí, S.: Silicic acid limitation drives bloom termination and  
765 potential carbon sequestration in an Arctic bloom, *Scientific Reports*, 9(1), 8149,  
766 <https://doi.org/10.1038/s41598-019-44587-4>, 2019.
- 767 43. Landry, M.R., Brown, S.L., Campbell, L., Constantinou, J. and Liu, H.: Spatial patterns  
768 in phytoplankton growth and microzooplankton grazing in the Arabian Sea during  
769 monsoon forcing, *Deep Sea Research Part II: Topical Studies in Oceanography*, 45(10–  
770 11), 2353–2368, [https://doi.org/10.1016/S0967-0645\(98\)00074-5](https://doi.org/10.1016/S0967-0645(98)00074-5), 1998.
- 771 44. Latasa, M. and Bidigare, R.R.: A comparison of phytoplankton populations of the  
772 Arabian Sea during the Spring Intermonsoon and Southwest Monsoon of 1995 as  
773 described by HPLC-analyzed pigments, *Deep Sea Research Part II: Topical Studies in*  
774 *Oceanography*, 45(10-11), 2133–2170, [https://doi.org/10.1016/S0967-0645\(98\)00066-](https://doi.org/10.1016/S0967-0645(98)00066-6)  
775 [6](https://doi.org/10.1016/S0967-0645(98)00066-6), 1998.
- 776 45. Le Moigne, F.A.: Pathways of organic carbon downward transport by the oceanic  
777 biological carbon pump, *Frontiers in Marine Science*, 6, 634,  
778 <https://doi.org/10.3389/fmars.2019.00634>, 2019.
- 779 46. Lewin, J.C.: The dissolution of silica from diatom walls, *Geochimica et Cosmochimica*  
780 *Acta*, 21(3-4), 182–198, [https://doi.org/10.1016/S0016-7037\(61\)80054-9](https://doi.org/10.1016/S0016-7037(61)80054-9), 1961.
- 781 47. Liu, D., Shen, X., Di, B., Shi, Y., Keesing, J.K., Wang, Y. and Wang, Y.:  
782 Palaeoecological analysis of phytoplankton regime shifts in response to coastal  
783 eutrophication, *Marine Ecology Progress Series*, 475, 1–14,  
784 <https://doi.org/10.3354/meps10234>, 2013.
- 785 48. Löder, M.G., Meunier, C., Wiltshire, K.H., Boersma, M. and Aberle, N.: The role of  
786 ciliates, heterotrophic dinoflagellates and copepods in structuring spring plankton  
787 communities at Helgoland Roads, North Sea, *Marine biology*, 158, 1551–1580,  
788 <https://doi.org/10.1007/s00227-011-1670-2>, 2011.
- 789 49. Madhupratap, M., Kumar, S.P., Bhattathiri, P.M.A., Kumar, M.D., Raghukumar, S.,  
790 Nair, K.K.C. and Ramaiah, N.: Mechanism of the biological response to winter cooling  
791 in the northeastern Arabian Sea, *Nature*, 384(6609), 549–552,  
792 <https://doi.org/10.1038/384549a0>, 1996.
- 793 50. Marsay, C.M., Sanders, R.J., Henson, S.A., Pabortsava, K., Achterberg, E.P. and  
794 Lampitt, R.S.: Attenuation of sinking particulate organic carbon flux through the  
795 mesopelagic ocean, *Proceedings of the National Academy of Sciences*, 112(4), 1089–  
796 1094, <https://doi.org/10.1073/pnas.141531111>, 2015.
- 797 51. McCreary, J.P., Murtugudde, R., Vialard, J., Vinayachandran, P.N., Wiggert, J.D.,  
798 Hood, R.R., Shankar, D. and Shetye, S.: Biophysical processes in the Indian  
799 Ocean, *Indian Ocean biogeochemical processes and ecological variability*, 185, 9–32,  
800 <https://doi.org/10.1029/2008GM000768>, 2009.



- 801 52. Mergulhao, L.P., Mohan, R., Murty, V.S.N., Guptha, M.V.S. and Sinha, D.K.:  
802 Coccolithophores from the central Arabian Sea: Sediment trap results, *Journal of earth*  
803 *system science*, 115, 415–428, <https://doi.org/10.1007/BF02702870>, 2006.
- 804 53. Moriceau, B., Iversen, M.H., Gallinari, M., Evertsen, A.J.O., Le Goff, M., Beker, B.,  
805 Boutorh, J., Corvaisier, R., Coffineau, N., Donval, A. and Giering, S.L., Copepods  
806 boost the production but reduce the carbon export efficiency by diatoms, *Frontiers in*  
807 *Marine Science*, 5, 82, <https://doi.org/10.3389/fmars.2018.00082>, 2018.
- 808 54. Müller, J., Wagner, A., Fahl, K., Stein, R., Prange, M. and Lohmann, G.: Towards  
809 quantitative sea ice reconstructions in the northern North Atlantic: A combined  
810 biomarker and numerical modelling approach, *Earth and Planetary Science Letters*,  
811 306(3-4), 137–148, <https://doi.org/10.1016/j.epsl.2011.04.011>, 2011.
- 812 55. Nair, R.R., Ittekkot, V., Manganini, S.J., Ramaswamy, V., Haake, B., Degens, E.T.,  
813 Desai, B.T. and Honjo, S.: Increased particle flux to the deep ocean related to  
814 monsoons, *Nature*, 338(6218), 749–751, <https://doi.org/10.1038/338749a0>, 1989.
- 815 56. Nomaki, H., Rastelli, E., Ogawa, N.O., Matsui, Y., Tsuchiya, M., Manea, E.,  
816 Corinaldesi, C., Hirai, M., Ohkouchi, N., Danovaro, R. and Nunoura, T.: In situ  
817 experimental evidences for responses of abyssal benthic biota to shifts in phytodetritus  
818 compositions linked to global climate change, *Global Change Biology*, 27(23), 6139–  
819 6155, <https://doi.org/10.1111/gcb.15882>, 2021.
- 820 57. Pandey, M., Biswas, H. and Chowdhury, M.: Interlinking diatom frustule diversity from  
821 the abyss of the central Arabian Sea to surface processes: physical forcing and oxygen  
822 minimum zone, *Environmental Monitoring and Assessment*, 195(1), 161,  
823 <https://doi.org/10.1007/s10661-022-10749-7>, 2023.
- 824 58. Pandey, M. and Biswas, H.: May. An account of the key diatom frustules from the  
825 surface sediments of the Central and Eastern Arabian Sea and their biogeochemical  
826 significance, In *EGU General Assembly Conference Abstracts (EGU-131)*,  
827 <https://doi.org/10.5194/egusphere-egu23-131>, 2023.
- 828 59. Peng, P., Bi, R., Sachs, J.P., Shi, J., Luo, Y., Chen, W., Huh, C.A., Yu, M., Cao, Y.,  
829 Wang, Y. and Cao, Z.: Phytoplankton community changes in a coastal upwelling  
830 system during the last century, *Global and Planetary Change*, 224, 104101,  
831 <https://doi.org/10.1016/j.gloplacha.2023.104101>, 2023.
- 832 60. Prahl, F. G., Muehlhausen, L. A. and Zahnle, D. L.: Further evaluation of long-chain  
833 alkenones as indicators of paleoceanographic conditions, *Geochim. Cosmochim. Acta*,  
834 52(9), 2303–2310, doi:10.1016/0016-7037(88)90132-9, 1988.
- 835 61. Prahl, F.G., Dymond, J. and Sparrow, M.A.: Annual biomarker record for export  
836 production in the central Arabian Sea, *Deep Sea Research Part II: Topical Studies in*  
837 *Oceanography*, 47(7-8), 1581–1604, [https://doi.org/10.1016/S0967-0645\(99\)00155-1](https://doi.org/10.1016/S0967-0645(99)00155-1),  
838 2000.
- 839 62. Prasanna Kumar S., Madhupratap, M., Kumar, M.D., Gauns, M., Muraleedharan, P.M.,  
840 Sarma, V.V.S.S. and De Souza, S.N.: Physical control of primary productivity on a  
841 seasonal scale in central and eastern Arabian Sea, *Journal of Earth System*  
842 *Science*, 109, 433–441, <https://doi.org/10.1007/BF02708331>, 2000.
- 843 63. Prasanna Kumar. S., and Narvekar, J.: Seasonal variability of the mixed layer in the  
844 central Arabian Sea and its implication on nutrients and primary productivity, *Deep Sea*  
845 *Research Part II: Topical Studies in Oceanography*, 52(14-15), 1848–1861,  
846 <https://doi.org/10.1016/j.dsr2.2005.06.002>, 2005.
- 847 64. Prasanna Kumar. S., Ramaiah, N., Gauns, M., Sarma, V.V.S.S., Muraleedharan, P.M.,  
848 Raghukumar, S., Kumar, M.D. and Madhupratap, M.: Physical forcing of biological  
849 productivity in the Northern Arabian Sea during the Northeast Monsoon, *Deep Sea*



- 850 Research Part II: Topical Studies in Oceanography, 48(6-7), 1115–1126,  
851 [https://doi.org/10.1016/S0967-0645\(00\)00133-8](https://doi.org/10.1016/S0967-0645(00)00133-8), 2001.
- 852 65. Ragueneau, O., Schultes, S., Bidle, K., Claquin, P. and Moriceau, B.: Si and C  
853 interactions in the world ocean: Importance of ecological processes and implications  
854 for the role of diatoms in the biological pump, *Global Biogeochemical Cycles*, 20(4),  
855 <https://doi.org/10.1029/2006GB002688>, 2006.
- 856 66. Rixen, T., Gaye, B. and Emeis, K.C.: The monsoon, carbon fluxes, and the organic  
857 carbon pump in the northern Indian Ocean, *Progress in oceanography*, 175, 24–39,  
858 <https://doi.org/10.1016/j.pocean.2019.03.001>, 2019a.
- 859 67. Rixen, T., Gaye, B., Emeis, K.C. and Ramaswamy, V.: The ballast effect of lithogenic  
860 matter and its influences on the carbon fluxes in the Indian Ocean, *Biogeosciences*,  
861 16(2), 485–503, <https://doi.org/10.5194/bg-16-485-2019>, 2019b.
- 862 68. Rodríguez-Miret, X., del Carmen Trapote, M., Sigró, J. and Vegas-Vilarrúbia, T.:  
863 Diatom responses to warming, heavy rains and human impact in a Mediterranean lake  
864 since the preindustrial period, *Science of The Total Environment*, 884, 163685,  
865 <https://doi.org/10.1016/j.scitotenv.2023.163685>, 2023.
- 866 69. Roubex, V., Becquevort, S. and Lancelot, C.: Influence of bacteria and salinity on  
867 diatom biogenic silica dissolution in estuarine systems, *Biogeochemistry*, 88, 47–62,  
868 <https://doi.org/10.1007/s10533-008-9193-8>, 2008.
- 869 70. Roxy, M. K., Modi, A., Murtugudde, R., Valsala, V., Panickal, S., Kumar, S. P.,  
870 Ravichandran, M., Vichi, M., and Levy, M.: A reduction in marine primary productivity  
871 driven by rapid warming over the tropical Indian Ocean, *Geophysical Research Letters*,  
872 43, 826–833, <https://doi.org/10.1002/2015GL066979>, 2016.
- 873 71. Ryderheim, F., Grønning, J. and Kiørboe, T.: Thicker shells reduce copepod grazing on  
874 diatoms, *Limnology and Oceanography Letters*, 7(5), 435–442,  
875 <https://doi.org/10.1002/lol2.10243>, 2022.
- 876 72. Sawant, S. and Madhupratap, M.: Seasonality and composition of phytoplankton.  
877 *Current Science*, 71(11), 1996.
- 878 73. Schubert, C.J., Villanueva, J., Calvert, S.E., Cowie, G.L., Von Rad, U., Schulz, H.,  
879 Berner, U. and Erlenkeuser, H.: Stable phytoplankton community structure in the  
880 Arabian Sea over the past 200,000 years, *Nature*, 394(6693), 563–566,  
881 <https://doi.org/10.1038/29047>, 1998.
- 882 74. Schulte, S., Mangelsdorf, K. and Rullkötter, J.: Organic matter preservation on the  
883 Pakistan continental margin as revealed by biomarker geochemistry, *Organic*  
884 *Geochemistry*, 31(10), 1005–1022, [https://doi.org/10.1016/S0146-6380\(00\)00108-X](https://doi.org/10.1016/S0146-6380(00)00108-X),  
885 2000.
- 886 75. Schulte, S., Rostek, F., Bard, E., Rullkötter, J. and Marchal, O.: Variations of oxygen-  
887 minimum and primary productivity recorded in sediments of the Arabian Sea, *Earth*  
888 *and Planetary Science Letters*, 173(3), 205–221, [https://doi.org/10.1016/S0012-](https://doi.org/10.1016/S0012-821X(99)00232-0)  
889 [821X\(99\)00232-0](https://doi.org/10.1016/S0012-821X(99)00232-0), 1999.
- 890 76. Sharma, S., Ha, K.-J., Yamaguchi, R., Rodgers, K. B., Timmermann, A., and Chung,  
891 E.: Future Indian Ocean warming patterns, *Nature Communications*, 14, 1789,  
892 <https://doi.org/10.1038/s41467-023-37435-7>, 2023
- 893 77. Silori, S., Sharma, D., Chowdhury, M., Biswas, H., Cardinal, D. and Mandeng-Yogo,  
894 M.: Particulate organic matter dynamics and its isotopic signatures ( $\delta^{13}\text{C}_{\text{POC}}$  and  
895  $\delta^{15}\text{N}_{\text{PN}}$ ) in relation to physical forcing in the central Arabian Sea during SW monsoon  
896 (2017–2018), *Science of the Total Environment*, 785, 147326,  
897 <https://doi.org/10.1016/j.scitotenv.2021.147326>, 2021.



- 898 78. Singh, U.B. and Ahluwalia, A.S.: Microalgae: a promising tool for carbon  
899 sequestration, *Mitigation and Adaptation Strategies for Global Change*, 18(1), 73–95,  
900 <https://doi.org/10.1007/s11027-012-9393-3>, 2013.
- 901 79. Smayda, T.J. and Reynolds, C.S.: Community assembly in marine phytoplankton:  
902 application of recent models to harmful dinoflagellate blooms, *Journal of plankton*  
903 *research*, 23(5), 447–461, <https://doi.org/10.1093/plankt/23.5.447>, 2001.
- 904 80. Smetacek, V.S.: Role of sinking in diatom life-history cycles: ecological, evolutionary  
905 and geological significance, *Marine biology*, 84, 239–251,  
906 <https://doi.org/10.1007/BF00392493>, 1985.
- 907 81. Smith, S., Roman, M., Prusova, I., Wishner, K., Gowing, M., Codispoti, L.A., Barber,  
908 R., Marra, J. and Flagg, C.: Seasonal response of zooplankton to monsoonal reversals  
909 in the Arabian Sea, *Deep Sea Research Part II: Topical Studies in Oceanography*,  
910 45(10-11), 2369–2403, [https://doi.org/10.1016/S0967-0645\(98\)00075-7](https://doi.org/10.1016/S0967-0645(98)00075-7), 1998.
- 911 82. Sonzogni, C., Bard, E., Rostek, F., Lafont, R., Rosell-Mele, A. and Eglinton, G.: Core-  
912 top calibration of the alkenone index vs sea surface temperature in the Indian Ocean,  
913 *Deep Sea Res. Part II Top. Stud. Oceanogr.*, 44(6), 1445–1460, doi:10.1016/S0967-  
914 0645(97)00010-6, 1997.
- 915 83. Stoecker, D.K.: Mixotrophy among Dinoflagellates 1. *Journal of eukaryotic*  
916 *microbiology*, 46, 397–401, <https://doi.org/10.1111/j.1550-7408.1999.tb04619.x>, 1999.
- 917 84. Stoecker, D.K., Hansen, P.J., Caron, D.A. and Mitra, A.: Mixotrophy in the marine  
918 plankton, *Annual Review of Marine Science*, 9, 311–335,  
919 <https://doi.org/10.1146/annurev-marine-010816-060617>, 2017.
- 920 85. Swanberg, N.R. and Anderson, O.R.: The nutrition of radiolarians: Trophic activity of  
921 some solitary Spumellaria 1, *Limnology and Oceanography*, 30, 646–652,  
922 <https://doi.org/10.4319/lo.1985.30.3.0646>, 1985.
- 923 86. Tarran, G.A., Burkill, P.H., Edwards, E.S. and Woodward, E.M.S.: Phytoplankton  
924 community structure in the Arabian Sea during and after the SW monsoon, 1994, *Deep*  
925 *Sea Research Part II: Topical Studies in Oceanography*, 46, 655–676,  
926 [https://doi.org/10.1016/S0967-0645\(98\)00122-2](https://doi.org/10.1016/S0967-0645(98)00122-2), 1999.
- 927 87. Ter Braak, C.J. and Smilauer, P.: CANOCO reference manual and CanoDraw for  
928 Windows user's guide: software for canonical community ordination (version 4.5),  
929 www.canoco.com, 2002.
- 930 88. Tomas, C. R., (Ed.), *Identifying marine phytoplankton*. Elsevier, 1997.
- 931 89. Tréguer, P., Bowler, C., Moriceau, B., Dutkiewicz, S., Gehlen, M., Aumont, O., Bittner,  
932 L., Dugdale, R., Finkel, Z., Iudicone, D. and Jahn, O.: Influence of diatom diversity on  
933 the ocean biological carbon pump, *Nature Geoscience*, 11, 27–37,  
934 <https://doi.org/10.1038/s41561-017-0028-x>, 2018.
- 935 90. Vallivattathillam, P., Lachkar, Z. and Lévy, M.: Shrinking of the Arabian Sea oxygen  
936 minimum zone with climate change projected with a downscaled model, *Frontiers in*  
937 *Marine Science*, 10, 1123739, <https://doi.org/10.3389/fmars.2023.1123739>, 2023.
- 938 91. Volk, T. and Hoffert, M.I.: Ocean carbon pumps: Analysis of relative strengths and  
939 efficiencies in ocean-driven atmospheric CO<sub>2</sub> changes, *The carbon cycle and*  
940 *atmospheric CO<sub>2</sub>: Natural variations Archean to present*, 32, 99–110,  
941 <https://doi.org/10.1029/GM032p0099>, 1985.
- 942 92. Wakeham, S.G., Peterson, M.L., Hedges, J.I. and Lee, C.: Lipid biomarker fluxes in the  
943 Arabian Sea, with a comparison to the equatorial Pacific Ocean. *Deep Sea Research*  
944 *Part II: Topical Studies in Oceanography*, 49, 2265–2301,  
945 [https://doi.org/10.1016/S0967-0645\(02\)00037-1](https://doi.org/10.1016/S0967-0645(02)00037-1), 2002.



- 946 93. Ward, B.B., Devol, A.H., Rich, J.J., Chang, B.X., Bulow, S.E., Naik, H., Pratihary, A.  
947 and Jayakumar, A.: Denitrification as the dominant nitrogen loss process in the Arabian  
948 Sea, *Nature*, 461, 78–81, <https://doi.org/10.1038/nature08276>, 2009.
- 949 94. Wishner, K.F., Gowing, M.M. and Gelfman, C.: Mesozooplankton biomass in the upper  
950 1000 m in the Arabian Sea: overall seasonal and geographic patterns, and relationship  
951 to oxygen gradients, *Deep Sea Research Part II: Topical Studies in Oceanography*, 45,  
952 2405–2432, [https://doi.org/10.1016/S0967-0645\(98\)00078-2](https://doi.org/10.1016/S0967-0645(98)00078-2), 1998.
- 953 95. Wittenborn, A.K., Schmale, O. and Thiel, V.: Zooplankton impact on lipid biomarkers  
954 in water column vs. surface sediments of the stratified Eastern Gotland Basin (Central  
955 Baltic Sea), *Plos one*, 15, e0234110, <https://doi.org/10.1371/journal.pone.0234110>,  
956 2020.
- 957 96. Xiong, W., Mei, X., Meng, X., Chen, H. and Yang, H.: Phytoplankton biomarkers in  
958 surface sediments from Liaodong Bay and their potential as indicators of primary  
959 productivity, *Marine Pollution Bulletin*, 159, 111536,  
960 <https://doi.org/10.1016/j.marpolbul.2020.111536>, 2020.
- 961 97. Zúñiga, D., Sanchez-Vidal, A., Flexas, M.D.M., Carroll, D., Rufino, M.M., Spreen, G.,  
962 Calafat, A. and Abrantes, F.: Sinking diatom assemblages as a key driver for deep  
963 carbon and silicon export in the Scotia Sea (Southern Ocean), *Frontiers in Earth  
964 Science*, 9, 579198, <https://doi.org/10.3389/feart.2021.579198>, 2021.

965

966

967

968

969

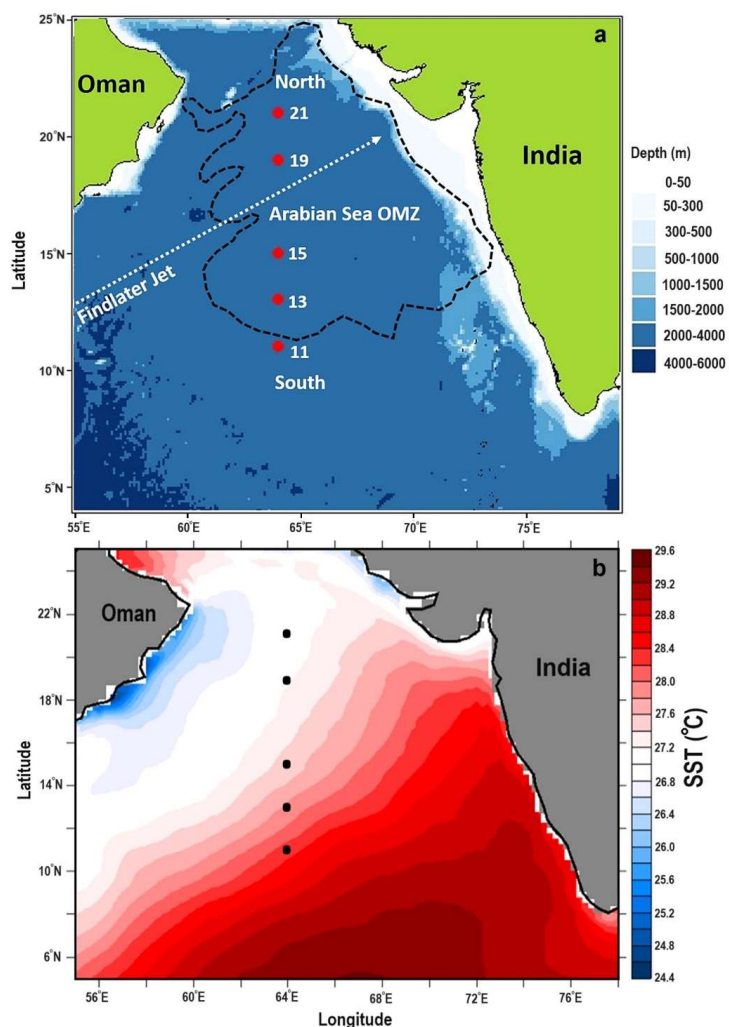
970

971

972

973

974



975

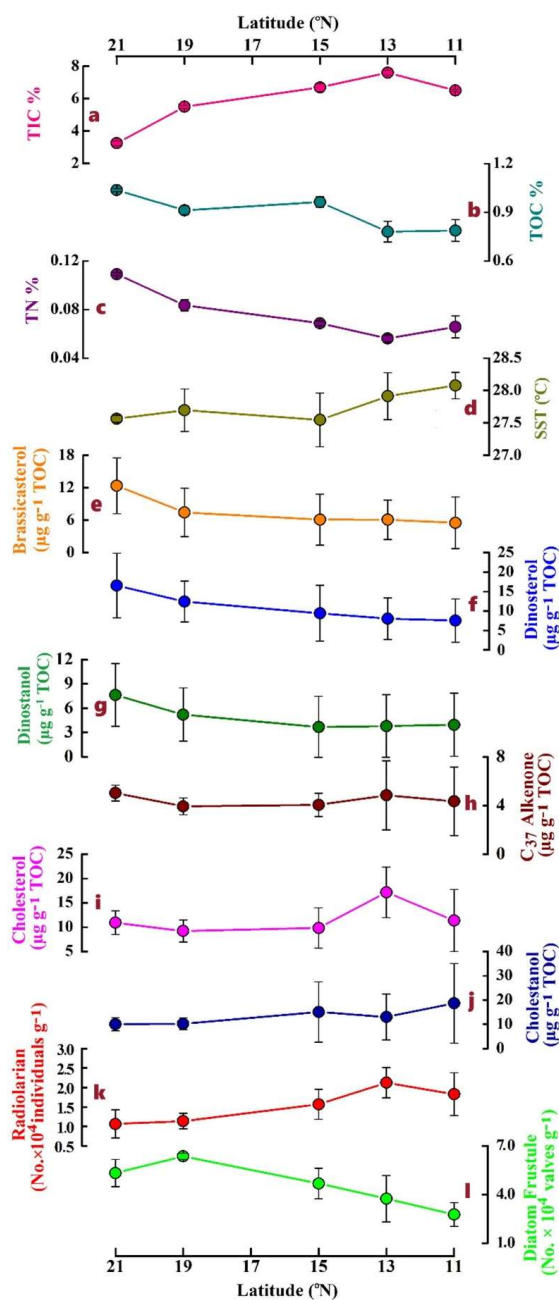
976

977 **Figure 1.** Map showing the study location in the Central Arabian Sea along 64° E transect  
978 during SSD-068 (Dec 2019) (a). The low-level atmospheric jet (Findlater Jet) is shown by a  
979 white dashed arrow and the boundary of the Oxygen Minimum Zone (OMZ) (0.5 mmol L<sup>-1</sup> O<sub>2</sub>  
980 concentration) is shown by a black dashed line. The average SST (2017-2020) values depicting  
981 spatial variability among the sampling stations from the north to south (b).

982



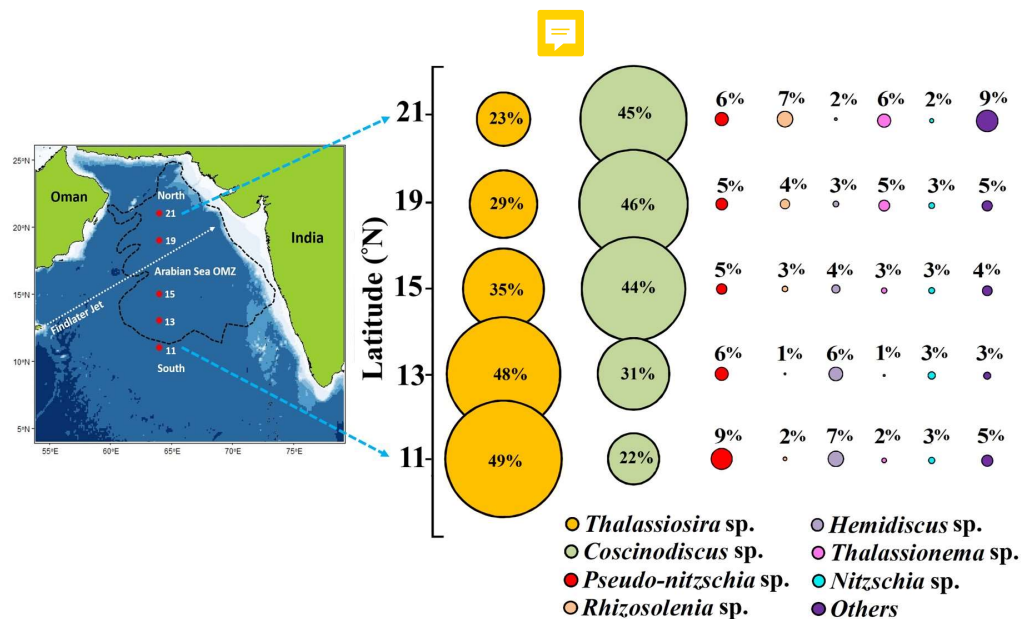
983  
984  
985  
986  
987  
988  
989  
990  
991  
992  
993  
994  
995  
996  
997  
998  
999  
1000  
1001  
1002  
1003  
1004  
1005  
1006  
1007  
1008  
1009



1010 **Figure 2.** The distribution of total inorganic carbon (TIC %) (a), total organic carbon (TOC %) (b), total nitrogen (TN%) (c), sea surface temperature (SST °C) (d), brassicasterol (e), dinosterol (f), dinostanol (g), C<sub>37</sub> alkenones (h), cholesterol (i), cholestanol (j), radiolarians (k), and diatom frustules (l) along the 64° E transect in the central Arabian Sea.



1014



1015

1016

1017

1018 **Figure 3.** The relative percentage of diatom frustules of major species (>3% of total  
 1019 abundance) from surface sediment samples (top 0.5, 1 cm) along the 64° E transect in the  
 1020 central Arabian Sea. Individual contributions from centric and pennate diatoms <3% were  
 1021 summed as “others”.

1022

1023

1024

1025

1026

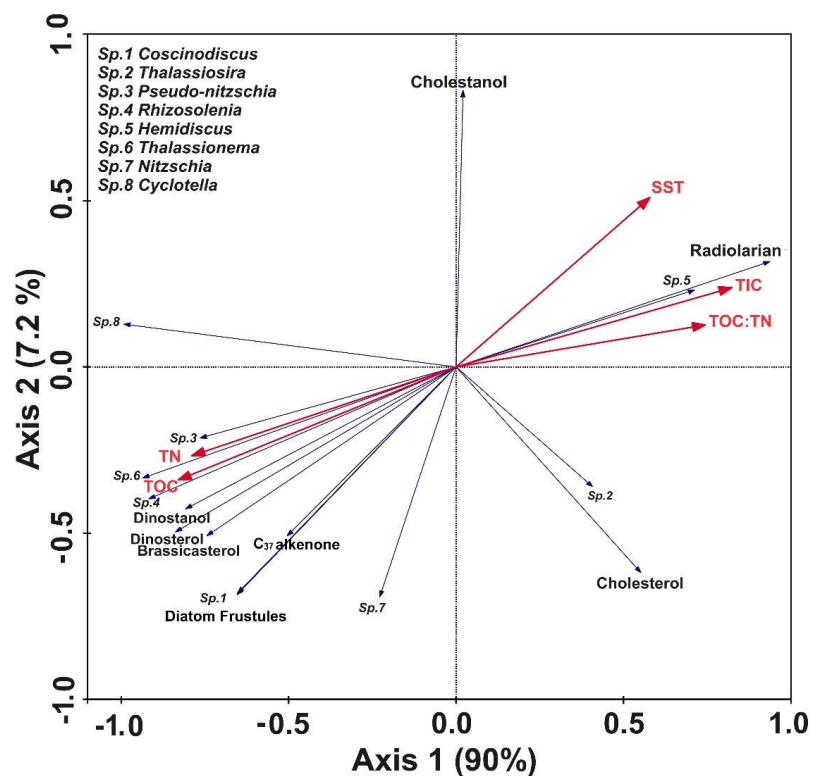
1027

1028

1029

1030





1031

1032

1033 **Figure 4.** RDA biplot shows the interrelationship between the biotic and abiotic factors. The  
1034 names of diatoms genera are marked as “Sp.” and are mentioned in the top left side of the  
1035 panel. Axis 1 and axis 2 explained nearly 97.2% of variability.



1036

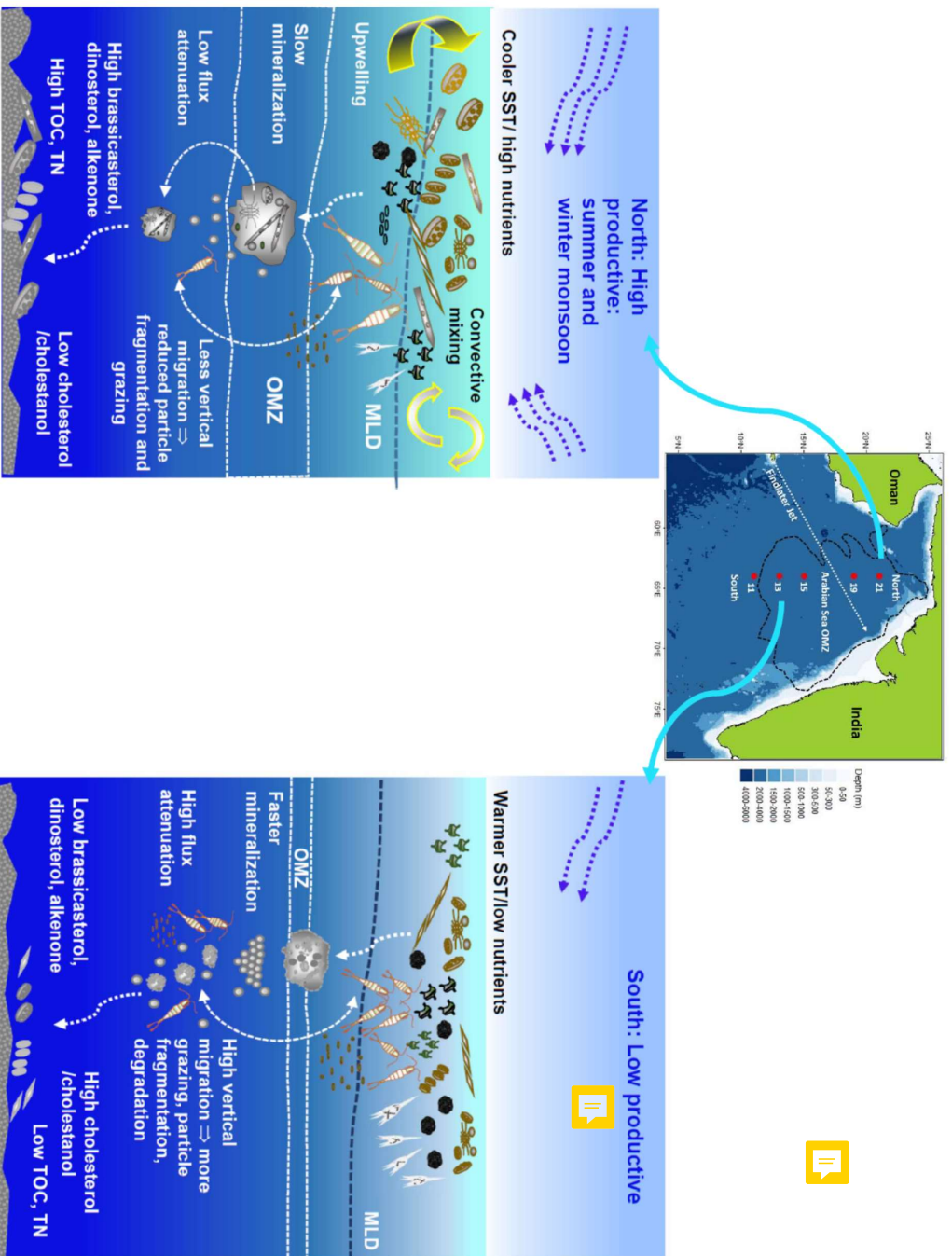
1037

1038

1039



1040  
1041  
1042  
1043  
1044  
1045  
1046  
1047  
1048  
1049  
1050  
1051  
1052  
1053  
1054  
1055  
1056  
1057  
1058  
1059



**Figure 5.** The schematic shows the spatial variability in particle flux along the 64° E transect in the central Arabian Sea.



1060 **Table 1.** Sedimentary characteristics, diatom frustules, and sterol concentrations in the surface sediments from the central Arabian Sea  
 1061 (n=2±SD). The values represent the average from 0.5 and 1 cm core slices.

Latitude (°N)	C%	TOC %	TN%	TOC: TN	Alkenone based SST (°C)	Diatom frustule (No.×10 <sup>4</sup> valves g <sup>-1</sup> )	Radiolarian (No.×10 <sup>4</sup> individuals g <sup>-1</sup> )	Brassicasterol (ng g <sup>-1</sup> )	Dinosterol (ng g <sup>-1</sup> )	Dinostanol (ng g <sup>-1</sup> )	C <sub>37</sub> alkenone (ng g <sup>-1</sup> )	Cholestrol (ng g <sup>-1</sup> )	Cholestanol (ng g <sup>-1</sup> )	Dinosterol: Brassicasterol	Brassicasterol: Alkenone
21	3.25±0.15	1.04±0.01	0.11±0.001	9.5±0.18	27.6±0.05	5.33±0.83	1.07±0.36	128.0±52.6	171.1±84.4	79.0±39.4	52.2±6.3	113.2±24.4	104.4±26.9	1.31	2.41
19	5.50±0.09	0.91±0.03	0.08±0.005	10.9±0.28	27.7±0.33	6.36±0.20	1.14±0.20	68.6±43.0	114.2±51.4	48.0±31.5	36.0±7.4	84.4±23.3	93.7±24.6	1.78	1.82
15	6.70±0.24	0.96±0.03	0.07±0.002	14±0.08	27.5±0.42	4.69±0.94	1.57±0.38	58.2±43.5	89.8±66.2	34.7±35.2	39.0±8.0	94.1±36.8	143.5±115.1	1.55	1.41
13	7.60±0.13	0.78±0.06	0.06±0.003	13.9±1.83	27.9±0.36	3.75±1.43	2.13±0.39	46.4±24.4	61.0±36.7	28.3±27.8	36.9±19.1	132.3±29.5	98.6±65.3	1.28	1.25
11	6.51±0.06	0.79±0.07	0.07±0.009	12.1±2.69	28.1±0.20	2.78±0.73	1.83±0.55	42.0±33.9	57.7±38.8	29.8±28.0	33.3±19.3	87.3±42.9	141.6±116.5	1.49	1.16
Average ±SD	5.91±1.66	0.90±0.11	0.08±0.02	12.1±1.9	27.8±0.2	4.58±1.39	1.54±0.45	68.62±34.77	98.76±46.53	43.95±21.05	39.47±7.39	102.27±20.21	116.37±24.22	1.5±0.2	1.6±0.5

1062  
1063



1064 **Table 2.** Average values of various parameters ( $n=2$ ,  $\pm$ SD) from the northern (21, 19, and 15° N) and southern stations (13 and 11° N)  
 1065 of the central Arabian Sea. The values shown in **bold** “*p*” represent the level of significance (single-factor ANOVA at 95% confidence  
 1066 level) between the northern and the southern stations.  
 1067

Parameter	North	South	<i>p</i> -value
Total Inorganic Carbon (TIC %)	5.15 $\pm$ 1.57	7.06 $\pm$ 0.63	<b>0.05</b>
Total Organic Carbon (TOC %)	0.97 $\pm$ 0.06	0.78 $\pm$ 0.05	<b>0.0009</b>
Total Nitrogen (TN %)	0.087 $\pm$ 0.018	0.061 $\pm$ 0.008	<b>0.03</b>
Alkenone derived SST (°C)	27.6 $\pm$ 0.25	28.0 $\pm$ 0.26	<b>0.043</b>
Diatom frustules (No. $\times$ 10 <sup>4</sup> valves g <sup>-1</sup> )	5.46 $\pm$ 0.95	3.26 $\pm$ 1.08	<b>0.009</b>
Radiolarian (No. $\times$ 10 <sup>4</sup> individuals g <sup>-1</sup> )	1.26 $\pm$ 0.35	1.98 $\pm$ 0.43	<b>0.019</b>
Brassicasterol ( $\mu$ g g <sup>-1</sup> TOC)	8.64 $\pm$ 4.75	5.81 $\pm$ 3.48	0.3
Dinosterol ( $\mu$ g g <sup>-1</sup> TOC)	12.81 $\pm$ 6.30	7.80 $\pm$ 4.47	0.2
Dinostanol ( $\mu$ g g <sup>-1</sup> TOC)	5.50 $\pm$ 3.35	3.87 $\pm$ 3.17	0.46
C <sub>37</sub> alkenone ( $\mu$ g g <sup>-1</sup> TOC)	4.34 $\pm$ 0.81	4.60 $\pm$ 2.33	0.8
Cholesterol ( $\mu$ g g <sup>-1</sup> TOC)	9.99 $\pm$ 2.50	14.26 $\pm$ 5.83	0.14
Cholestanol ( $\mu$ g g <sup>-1</sup> TOC)	11.80 $\pm$ 6.33	15.85 $\pm$ 11.39	0.49
Dinosterol: Brassicasterol	1.55 $\pm$ 0.27	1.39 $\pm$ 0.21	0.34
Brassicasterol: Alkenone	1.88 $\pm$ 0.76	1.21 $\pm$ 0.21	0.13

1068