



1 **Sedimentary organic matter signature hints at the phytoplankton-driven Biological**
2 **Carbon Pump in the Central Arabian Sea**
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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 C₃₇ 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 C₃₇ 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**

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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 (CaCO₃) 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% H₂O₂, and
177 0.01 N anhydrous sodium diphosphate (Na₄P₂O₇) 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⁻¹ dry sediment. Radiolarians were also enumerated along
187 with diatom frustules and were represented as individuals g⁻¹.



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 ($10 \text{ ng } \mu\text{L}^{-1}$) 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 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 % H_2O , 60 μm 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 μL 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 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 μm). 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 $20^\circ\text{C minute}^{-1}$, then increased with $4.5^\circ\text{C minute}^{-1}$ to 260°C and finally
217 increased the temperature with $6^\circ\text{C minute}^{-1}$ 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 ($10 \text{ ng } \mu\text{L}^{-1}$) 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⁻¹. 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⁻¹ 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⁻¹ 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 C₃₇ 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_{37:2} and C_{37:3} alkenones as well as U_{37}^{kl} -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_{37}^{kl} 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 that the
271 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⁻¹) found in the surface sediment were the highest of
289 the biomarkers followed by brassicasterol (64 ± 44 ng g⁻¹) and C_{37} alkenones (39.4 ± 12 ng g⁻¹)
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⁻¹ TOC) at 21° N compared to other stations (19.96 ± 9.5
298 µg g⁻¹ TOC). The TOC normalized values of dinosterol (16.53 ± 8.3 µg g⁻¹ TOC) and
299 brassicasterol (12.37 ± 5.2 µg g⁻¹ 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⁻¹
301 TOC; south 7.8 ± 4.47 µg g⁻¹ TOC) and brassicasterol (north: 8.64 ± 4.75 µg g⁻¹ TOC; south
302 5.81 ± 3.48 µg g⁻¹ 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⁻¹ TOC (north) and 14.3 ± 5.8 µg g⁻¹ TOC (south) without any statistical significance. The
310 TOC normalized values of cholestanol are lower in the northern (11.8 ± 6.3 µg g⁻¹ TOC) than
311 in the southern part (15.9 ± 11.4 µg g⁻¹ 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 × 10⁴
314 individuals g⁻¹ 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 × 10⁴ individuals g⁻¹) compared to
316 northern stations (1.10 × 10⁴ individuals g⁻¹) 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 6.36×10^4 valves g^{-1} . The highest frustule abundance was
323 observed at $19\text{--}21^\circ$ N and the least at 11° N. At station 19° 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 ± 0.1 with the highest diversity at
328 21° 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 (2.46×10^4 valves g^{-1}) of *Coscinodiscus* sp. was
338 observed ($p < 0.05$) with the least abundance at 11° N (0.61×10^4 valves g^{-1}). In the south,
339 *Thalassiosira* seemed to dominate (1.59×10^4 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° 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° 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⁻¹. Conversely, in the south, these values increased to 0.24–0.72 mL L⁻¹.
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 C₃₇-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 C₃₇-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 well 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; Roubex 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.

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605

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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, 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 CO₂ 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 CO₂ changes, *The carbon cycle and*
940 *atmospheric CO₂: 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.

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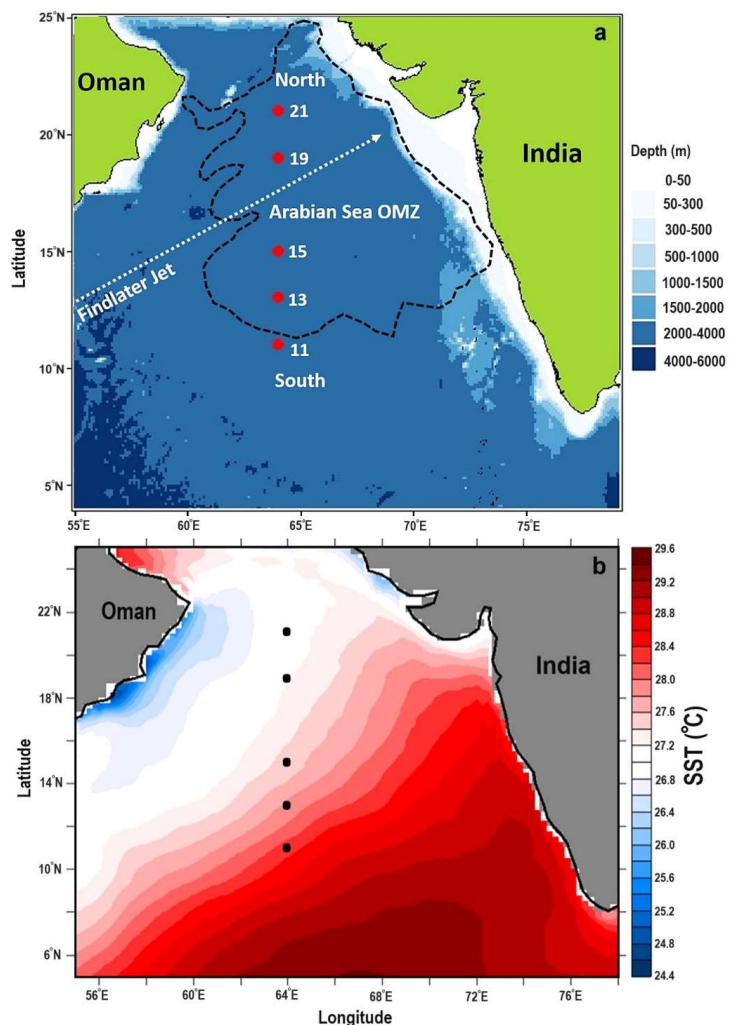
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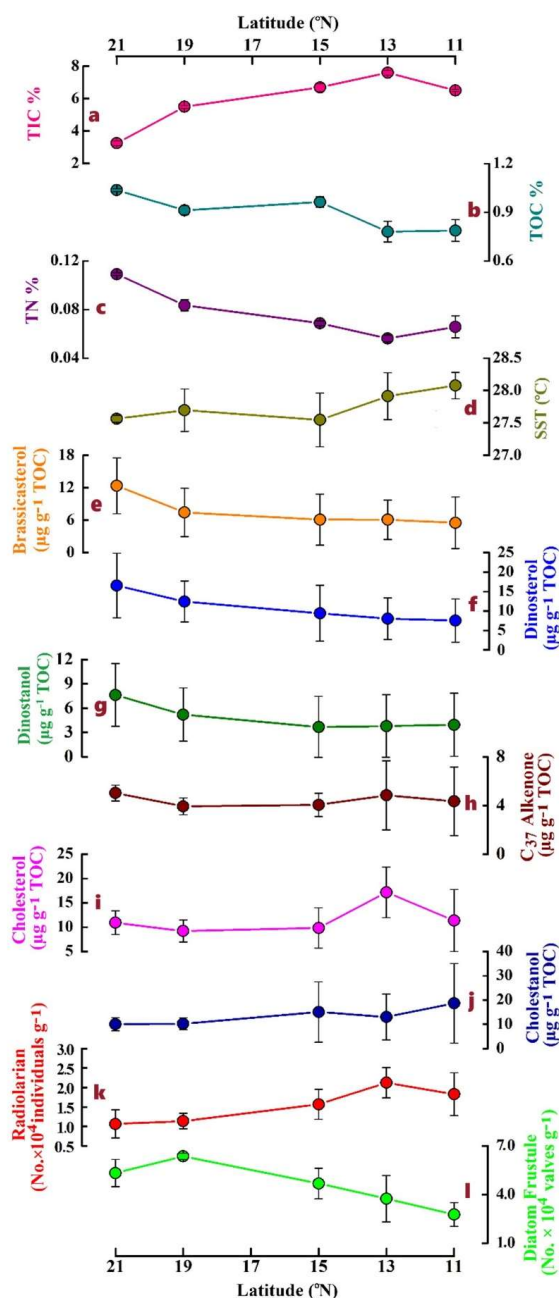
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977 **Figure 1.** Map showing the study location in the Central Arabian Sea along 64° E transect
978 during SSD-068 (Dec 2019) (a). The low-level atmospheric jet (Findlater Jet) is shown by a
979 white dashed arrow and the boundary of the Oxygen Minimum Zone (OMZ) (0.5 mmol L⁻¹ O₂
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).

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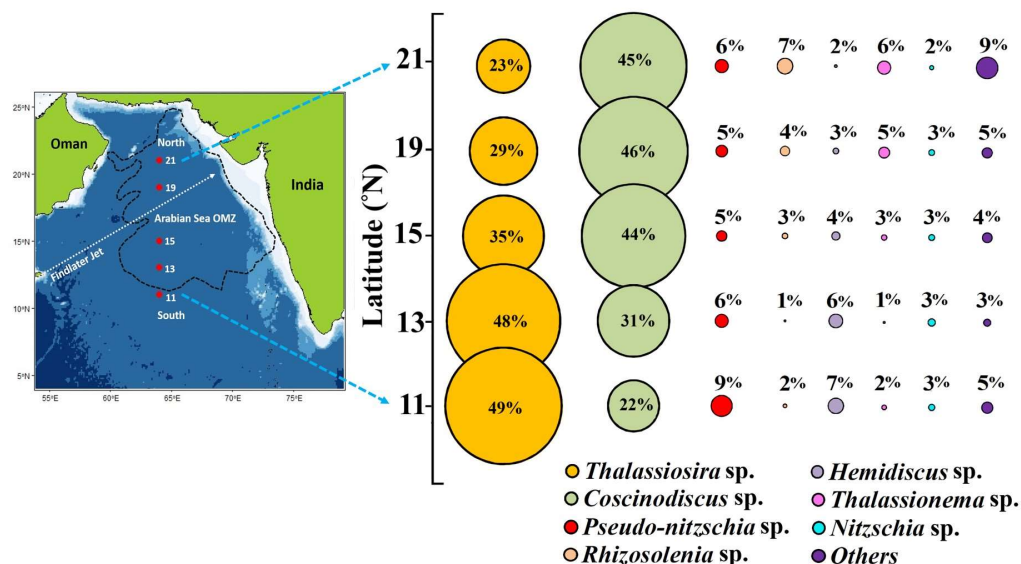
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1010 **Figure 2.** The distribution of total inorganic carbon (TIC %) (a), total organic carbon (TOC %) (b), total nitrogen (TN%) (c), sea surface temperature (SST °C) (d), brassicasterol (e), dinosterol (f), dinostanol (g), C₃₇ alkenones (h), cholesterol (i), cholestanol (j), radiolarians (k), and diatom frustules (l) along the 64° E transect in the central Arabian Sea.



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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”.

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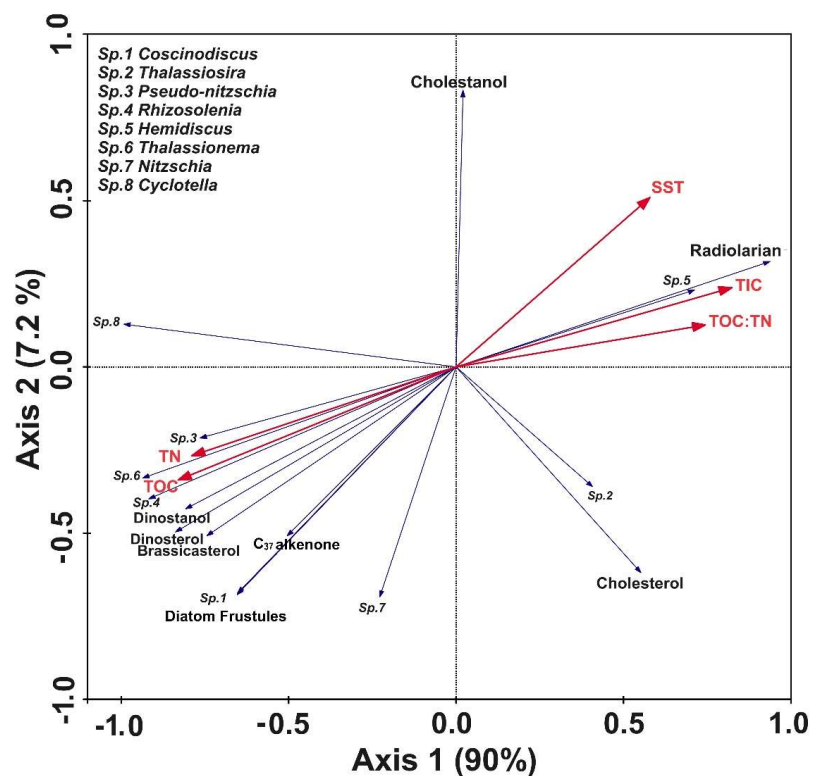
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1033 **Figure 4.** RDA biplot shows the interrelationship between the biotic and abiotic factors. The
1034 names of diatoms genera are marked as “Sp.” and are mentioned in the top left side of the
1035 panel. Axis 1 and axis 2 explained nearly 97.2%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

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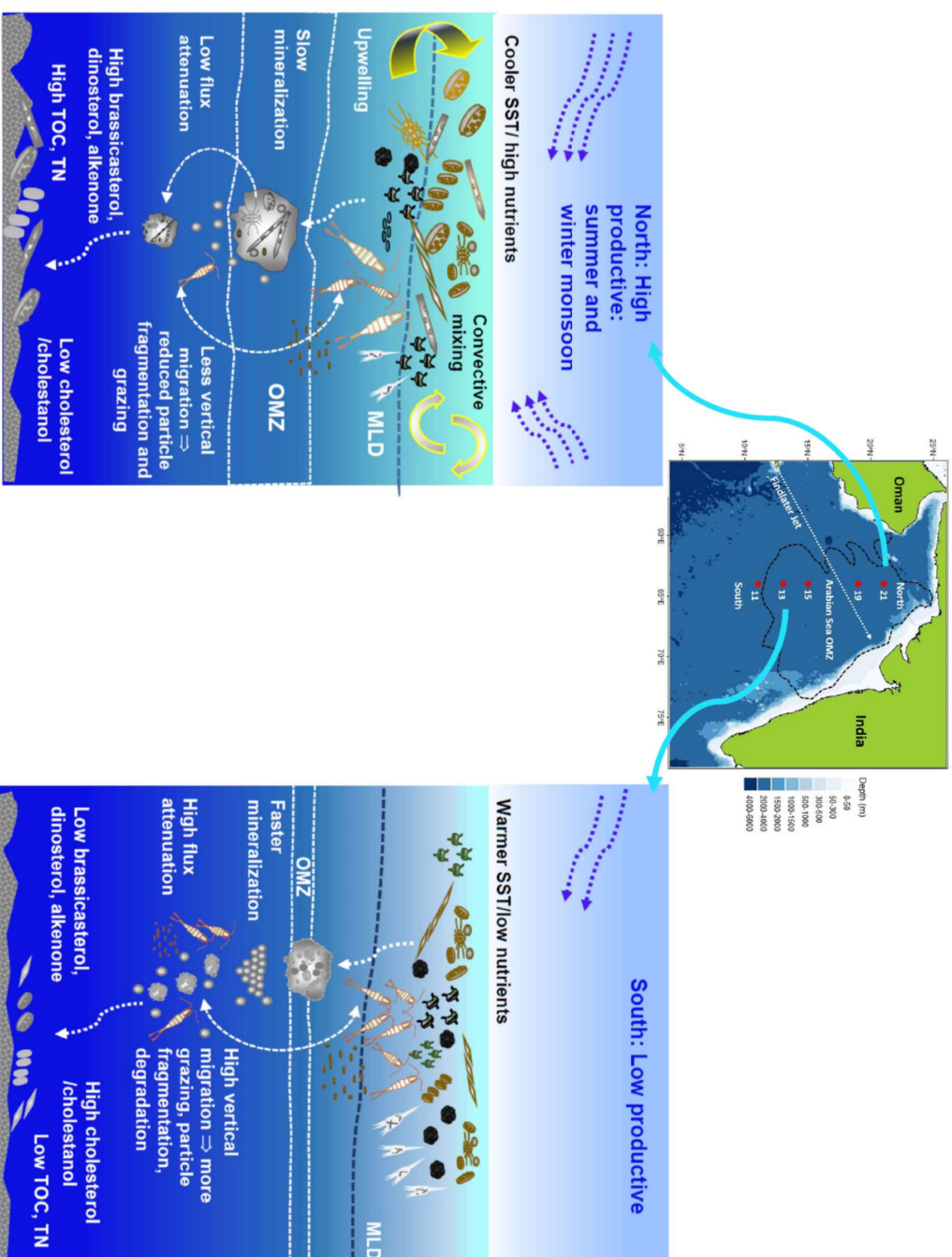


Figure 5. The schematic shows the spatial variability in particle flux along the 64° E transect in the central Arabian Sea.



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)	TIC %	TOC %	TN %	TOC: TN	Alkenone based SST (°C)	Diatom frustule (No.×10 ⁴ valves g ⁻¹)	Radiolarian (No.×10 ⁴ individuals g ⁻¹)	Brassicasterol (ng g ⁻¹)	Dinosterol (ng g ⁻¹)	Dinostanol (ng g ⁻¹)	C ₃₇ alkenone (ng g ⁻¹)	Cholesterol (ng g ⁻¹)	Cholestanol (ng g ⁻¹)	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

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

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