



1 **Transparent exopolymer particle binding of organic and inorganic**  
2 **particles in the Red Sea: Implications for downward transport of**  
3 **biogenic materials**

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20



21 **Abstract:** Binding of particulate and dissolved organic matter in the water column by marine  
22 gels allows sinking and cycling of organic matter into deeper water of the Red Sea and other  
23 marine water bodies. A series of four offshore profiles were made at which concentrations of  
24 bacteria, algae, particulate transparent exopolymer particles (p-TEP), colloidal transparent  
25 exopolymer particles (c-TEP), and the fractions of natural organic matter (NOM), including  
26 biopolymers, humic substances, low molecular weight neutrals, and low molecular weight acids  
27 were measured to depths ranging from 90 to 300 m. It was found that a statistically-significant  
28 relationship occurs between the concentrations of p-TEP and bacteria while a minimal, non-  
29 significant relationship between p-TEP and algae occurs. This likely reflects the low abundance  
30 of larger algal species in the study region. Variation in the biopolymer fraction of NOM in  
31 relationship to TEP and bacteria suggests that extracellular discharges of polysaccharides and  
32 proteins from the bacteria and algae are occurring without immediate abiotic assembly into p-  
33 TEP. In the water column below the photic zone, TOC, bacteria, and biopolymers show a  
34 generally common rate of reduction in concentration, but p-TEP decreases at a diminished rate,  
35 showing that it persists in moving organic carbon deeper into the water column despite  
36 consumption by bacteria.

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## 40 1 Introduction

41



42 Mechanisms that control the biogeochemical cycles influenced by microorganisms in the world  
43 's oceans are complex and poorly understood (Azam and Malfatti, 2007). The relationships  
44 between microalgal and bacterial abundance, total organic carbon (TOC), fractions of natural  
45 organic matter (NOM), polysaccharides, and transparent exopolymer particles (TEP) in seawater  
46 with depth play important roles in the transport and cycling of nutrients and sediments  
47 (Alldredge and Crocker, 1995; Passow, 2002; Azam and Malfatti, 2007). In particular, the  
48 binding of suspended sediments and particulate organic matter by TEP and other acidic  
49 polysaccharides, in addition to general aggradation, tends to increase particle size and weight,  
50 thus increasing settling rates in the water column (Passow et al., 2001; Wurl et al., 2011). It has  
51 been demonstrated that gel-type particles link particulate and dissolved organic matter in the  
52 ocean (Verdugo et al., 2004). The sinking of biogenic particles drives elemental cycling, which in  
53 turn controls primary and secondary productivity through the water column (Wurl et al., 2011).  
54 Particulate organic material is commonly occupied or influenced by bacteria which can reduce  
55 the biomass by consumption of some organic matter over various timeframes from days to  
56 weeks (Bižić-Ionescu et al., 2018).

57 TEP are ubiquitous in the oceans (Passow, 2002), likely caused by abiotic coagulation and  
58 aggradation of dissolved carbohydrates or primarily acidic polysaccharides, but also by biotic  
59 formation as extracellular secretions by algae or bacteria (Chin et al., 1998; Stoderegger and  
60 Herndl, 2001; Passow et al., 2001; Berman and Viner-Mozzini, 2001; Passow et al., 1994).

61 Particulate TEP (p-TEP) is in the size range 0.4–200  $\mu\text{m}$ , with a number of forms, including  
62 amorphous blobs, disseminated clouds, sheets, filaments or clumps (Zhou et al., 1998; Passow,  
63 2002; Mari et al., 2004). Colloidal TEP (c-TEP) consist of particles that are stained by Alcian blue



64 with a diameter range of 0.05 to 0.4  $\mu\text{m}$  (Villacorte et al., 2009). However, c-TEP is defined based  
65 solely on staining with Alcian blue, which is known to also stain other substances in seawater,  
66 including sulfated and carboxylated polysaccharides, glycoproteins, polyanions in general, and  
67 acidic polysaccharides not associated with TEP (Winters et al., 2016).

68 TEP are composed of acidic polysaccharides enriched with fucose and rhamnose, thus  
69 serving as a food source in the water column and commonly associated with layers of intense  
70 microbial and biochemical activity (Azam and Long, 2001). TEP generally decrease in  
71 concentration with depth in the sea (Engel et al., 2004), with a tendency to float to the sea  
72 surface if unballasted to contribute a gelatinous layer to the sea surface microlayer (Azetsu-  
73 Scott and Passow, 2004; Wurl and Holmes, 2008; Wurl et al., 2009). Bar-Zeev et al. (2015) have  
74 documented that p-TEP is mainly composed of polysaccharides, which can be dispersed in the  
75 presence of different types of chelators, be fractured to form colloids or reassemble abiotically.  
76 The trends in TEP concentrations in the seawater column have been previously examined  
77 (Jennings et al., 2017), and the relationship of TEP with TOC, DOC, and bacteria have also been  
78 investigated in many areas of the ocean (Engel, 2004; Simon et al., 2002; Ortega-Retuerta et al.,  
79 2009; Ortega-Retuerta et al., 2011; Bar-Zeev et al., 2011). However, these relationships have  
80 not been studied in the Red Sea.

81 Studies on TEP distribution in relation to other forms of organic matter in the Red Sea have  
82 focused mainly on assessing the links between TEP and phytoplankton and bacterial production  
83 (Bar-Zeev et al., 2009b) and the impacts of TEP and dissolved forms of NOM on biofouling in  
84 seawater desalination plants (Bar-Zeev et al., 2009a; Dehwah et al., 2015a; Dehwah et al.,  
85 2015b; Dehwah et al., 2015c; Dehwah and Missimer, 2016; Rachman et al., 2014; Rachman et



86 al., 2015). The intakes for reverse osmosis seawater desalination plants are located in shallow,  
87 nearshore areas of the Red Sea, so little consideration has been given to changes in TEP  
88 concentration with depth until it was suggested that deep-water intake systems may produce  
89 seawater quality with lower concentrations of algae, bacteria, and organic compounds, such as  
90 TEP, thus possibly lessening rates of membrane biofouling (Dehwah et al., 2015c).

91 The relationships between TEP concentrations and abundance of microalgae, bacteria, TOC,  
92 and dissolved fractions of NOM, including biopolymers, humic substances, building blocks, low  
93 molecular weight (LMW) acids, and LMW neutrals from the sea surface to 300 m depth are  
94 herein presented.

95 The present study provides the first data from the Red Sea, with initial insights into the  
96 vertical transport of organic carbon, including the fractions of natural organic matter from the  
97 surface to depths near or below the photic zone. The authors are keenly aware that the data  
98 presented herein have not been collected in a systematic manner with spatial and temporal  
99 comparisons to assess the biogeochemical cycles within the Red Sea comprehensively.  
100 However, the compiled data can be used to better characterize the biogeochemical cycles of  
101 the Red Sea as other researchers add new data. The reported datasets represent the first  
102 measured in the Red Sea wherein the fractions of organic matter, including biopolymers, humic  
103 substances, building blocks, low molecular weight neutrals, and low molecular weight acids  
104 (very expensive to measure), are linked with measurements of algae, bacteria, TOC, and TEP.

105

## 106 **2 Methods**

107



108 2.1 Compilation and comparison of available data

109

110 There have been several investigations on organic matter, including TEP, collected at depths  
111 near the sea surface along the Red Sea coast of Saudi Arabia, with the main focus to establish  
112 the relationships between seawater organic matter content and the potential for membrane  
113 biofouling in seawater desalination facilities. These shallow nearshore data were compiled and  
114 assessed to compare to the newly collected offshore data and to assess statistical relationships  
115 between various organic parameters. Note that these data have been collected at many  
116 different times of the year and were not used to attempt the characterize the natural seasonal  
117 variations and the overall biochemical activity in the nearshore area of the Red Sea.

118

119 2.2 Seawater vertical profiles in the Red Sea

120

121 Seawater properties of the water column were measured at four sites (A–D) north of Jeddah,  
122 along the Saudi coast of the Red Sea in deep water areas (> 1000 m) (Fig 1). In situ vertical  
123 profiles of temperature, salinity, dissolved oxygen (DO), pH, turbidity, chlorophyll-a  
124 (fluorescence), and photosynthetically active radiation (PAR) were determined with a multi-  
125 sensor assembly fitted to a Rosette carousel holding a set of Niskin water sampling bottles  
126 (General Oceanics, USA). Continuous vertical profiling was conducted from sea surface to 90 m  
127 depth at sites A–C, with seawater samples obtained at 10 m depth intervals for the analysis of  
128 organic parameters. At site D, continuous vertical profiles of physicochemical parameters were  
129 taken from 7 m below sea surface to 300 m depth, with seawater samples for organic



130 parameters obtained at 10 m intervals from the surface to 100 m depth and at 20 m intervals  
131 thereafter to 300 m depth. Sampling at sites A–C was conducted in April 2014, whereas at site  
132 D in February 2015. The sample timing was based on ship availability and the data collected  
133 cannot be used to fully characterize the Red Sea in deep water located far from the coast. Note  
134 that the water depth drops almost vertically to greater than 1000 m beginning in the nearshore  
135 at the 20 m contour (Dehwah et al., 2015c).

136 The multi-sensor assembly included the SBE 43 CTD device (Sea-Bird Scientific) for salinity,  
137 temperature and depth profiling, with a DO add-on sensor; Wet Labs ECO AFL/FL (Sea-Bird  
138 Scientific) was used for turbidity and fluorescence detection; and a biospherical light sensor (LI-  
139 COR) was used for PAR measurement. All sensors were pre-calibrated according to  
140 manufacturer specifications before actual use in field sampling and was normalized.

141

### 142 2.3 Quantification and characterization of microalgae and bacteria

143

144 Microalgal abundances in water samples were determined by flow cytometry, using a BD  
145 FACSVerse flow cytometer for counting and characterizing algal cells. An Accuri flow cytometer  
146 was used to measure bacterial abundance. Flow cytometry enables a rapid and accurate  
147 counting of microorganisms (VivesRego et al., 2000).

148 Light scattering properties and/or fluorescence intensity was determined by the flow  
149 cytometer to distinguish between different algal types, as described by van der Merwe et  
150 al. (2014). Lasers were used to excite both unstained autofluorescent organisms (algae) and  
151 stained bacterial cells. The red laser wavelength was set at 640 nm and the blue laser at 488 nm



152 for the Accuri flow cytometer. Algal cell counting was performed by combining 500  $\mu\text{L}$  of each  
153 sample with a 1  $\mu\text{L}$  volume of a standard containing 1  $\mu\text{m}$  beads to calibrate size in a 10 mL  
154 tube. The tube was then vortexed and measured at high flow rate with a 200  $\mu\text{L}$  injection  
155 volume for 2 min. The counting procedure was repeated three times to assess the precision of  
156 measurements. There different type of algae, cyanobacteria, *Prochlorococcus*, and  
157 pico/nanoplankton, were distinguished based on their autofluorescence as well as by the cell  
158 side-angle scatter, which was used to identify them by size (Radíć et al., 2009).

159 A comparative protocol employing SYBR<sup>®</sup>Green stain was used for bacteria counting. A  
160 volume of 500  $\mu\text{L}$  from each sample was transferred to a 10 mL tube, incubated in 35°C water  
161 bath for 10 min. SYBR<sup>®</sup> Green dye was added at a 5  $\mu\text{L}$  into a 500  $\mu\text{L}$  aliquot to stain the cells.  
162 The sample was vortexed and incubated for 10 min. The prepared samples were then analyzed  
163 at a medium flow setting with a 50  $\mu\text{L}$  injection volume for 1 min. For validation, 8-Peak  
164 calibration beads were used. Triplicate measurements were made on each sample to assess  
165 measurement precision.

166

#### 167 2.4 Measurement of TOC and NOM fractions

168

169 TOC concentration was measured with a Shimadzu TOC-VCSH. Fractions of dissolved organic  
170 carbon, including biopolymers, humic substances, building blocks, low molecular weight (LMW)  
171 neutrals, and low molecular weight (LMW) acids, were determined by Liquid Chromatography  
172 Organic Carbon Detector (LCOCD, DOC-Labor), using a size exclusion chromatography column  
173 Toyopearl HW-50S (TOSOH), following the methods by Huber et al. (2011). A calibration curve





174 was established for both molecular masses of humic substances and detector sensitivity before  
175 sample measurements. Humic acid and fulvic acid standards (Suwannee River Standard II) were  
176 used for the molecular mass calibration, whereas potassium hydrogen phthalate and potassium  
177 nitrate (KNO<sub>3</sub>) for sensitivity calibration based on Huber et al. (2011).

178 All seawater samples for LCOCD were manually pre-filtered using a 0.45 µm syringe filter to  
179 exclude the undissolved particulate organics. Before sample analysis, a system cleaning was  
180 performed by injection of 4,000 µL of 0.1mol/L NaOH through the column for 260 min. After  
181 cleaning, 2,000 µL of the sample was injected for analysis at 180 min retention time and 1.5  
182 mL/min flow rate. A mobile phase of phosphate buffer, with 28 mmol STD and 6.58 pH, was  
183 used to carry the sample through the system. The resulting chromatogram showed a plot of  
184 signal response of different organic fractions against retention time. Manual integration of the  
185 data, also following Huber et al. (2011), was performed to determine the concentrations of the  
186 different organic fractions, including biopolymers, humic substances, building blocks, LMW  
187 acids and LMW neutrals.

188

189 2.5 TEP measurement

190

191 Both p-TEP and c-TEP were simultaneously determined in each collected sample. The size range  
192 of p-TEP is between 0.4 and 200 µm, whereas c-TEP between 0.05 and 0.40 µm (Villacorte et  
193 al., 2009). TEP analysis was based on the method developed by Passow and Alldredge (1995),  
194 which involves sample filtration, membrane staining with Alcian blue, and then UV  
195 spectrometry. A staining solution was prepared from 0.06% (m/v) Alcian blue 8GX (Fluka) in



196 acetate buffer solution (pH 4) and freshly pre-filtered through a 0.2  $\mu\text{m}$  polycarbonate filter  
197 before usage. A 300 mL volume of seawater from each water sample was filtered through a 0.4  
198  $\mu\text{m}$  pore size polycarbonate membrane using an adjustable vacuum pump at low constant  
199 vacuum. After filtration, the membrane was rinsed with 10 mL of Milli-Q water to prevent the  
200 Alcian blue from coagulating, as salts may remain on the filter after seawater filtration, thus  
201 avoiding the likelihood of overestimating the TEP concentration. The retained TEP particles on  
202 the membrane surface were then stained with the Alcian blue dye for 10 seconds. After  
203 staining, the membrane was flushed with 10 mL of Milli-Q water to remove any excess dye. The  
204 flushed membrane was then placed into a small beaker, where it was soaked in 80% sulfuric  
205 acid for 6 hours to extract the dye that was bound to the p-TEP. Finally, the absorbance of the  
206 acid solution was measured by a UV spectrometer at 752 nm wavelength to determine the TEP  
207 concentration. The same methodology was applied to determine the colloidal TEP, except that  
208 a 250 ml volume of water sample from 0.4  $\mu\text{m}$  polycarbonate membrane permeate was filtered  
209 through a 0.1  $\mu\text{m}$  pore size to allow deposition of the c-TEP on the membrane surface.

210 To relate the measured UV absorbance values to TEP concentrations, a calibration curve  
211 was established. Xanthan gum solutions with different volumes (0, 0.5, 1, 2, 3 mL) were used to  
212 obtain the calibration curve (Fig. 2). The TOC concentrations of xanthan gum before and after  
213 0.4  $\mu\text{m}$  filtration were analyzed, and the TOC concentration difference was used to calculate  
214 the gum mass on each filter and the TEP concentration was estimated using the calibration  
215 curve. The same procedures were used for the 0.1  $\mu\text{m}$  membrane to establish the calibration  
216 curve for colloidal particles. Afterwards, the TEP concentration was expressed in terms of  
217 Xanthan Gum equivalent in  $\mu\text{g Xeq./L}$  by dividing the TEP mass by the corresponding volume of



218 TEP samples. Because particulate and colloidal TEP is determined indirectly, these values must  
219 be considered to be semi-quantitative. The new method developed by Villacorte et al. (2009)  
220 for TEP measurement was not used, as it would limit the comparability of the measured data  
221 with previous results.

222

### 223 2.6 Statistical methods used for data comparison

224 A series of scatter plots were constructed to test the statistical significance between various  
225 organic parameters. The  $R^2$  and p-values were calculated to assess the degree of fit to a curve  
226 and the statistical significance. When the p value was below 0.05, the null hypothesis was void  
227 and the relationship was deemed to be significant.

228

## 229 **3 Results**

230

231 3.1 Variations in salinity, temperature, fluorescence, pH, dissolved oxygen, PAR/irradiance,  
232 biospherical/licor, and turbidity

233

234 The thermocline in the three profiles (sites A-C) collected to a 90 m depth showed a slight  
235 decrease in temperature from near 29 °C to between 24 and 25 °C 90 m below surface (Fig. 3).  
236 The decline in temperature was relatively gradual at all three sites. In the deep profile, the  
237 temperature declined from about 26.5 °C at the surface to about 22 °C at 300 m. An inflection  
238 point occurred at about 115 m and the change in temperature below this depth to 300 m was  
239 only about 2.5 °C (Fig. 4). The difference in the temperature at the sea surface between profiles



240 was likely caused by the time of year of measurements, with the 90 m profiles occurring in April  
241 versus the 300 m profile in February which is the peak of winter in the study area.

242 The halocline showed similar salinity variations in the 90 m profiles with a slight, rather  
243 uniform increase from about 39 ppt at surface to 40 ppt at 90 m (Fig. 3). A slightly lower salinity  
244 gradient coinciding with a slightly higher temperature gradient occurred at site B. The salinity  
245 change in the 300 m profile showed a similar pattern from about 39 to 40 ppt in the upper 115  
246 m, but an inflection occurred at about 115 m wherein the rate of increase declined to a few  
247 tenths of a ppt over the lower 185 m. The inflection point showing a slope change for both  
248 temperature and salinity occurred at about the same depth (Figs. 3 and 4).

249 The vertical trends in pH also exhibited minimal variations down to 90 m at sites A–C (Fig.  
250 3), but with slightly lower pH values at site A (7.9–8.0) than at sites B and C (8.0–8.1). In the  
251 deep profile, pH was nearly stable at about 8.3 until 115 m and then steadily decreased to 8.1  
252 at 300 m (Fig. 4).

253 Dissolved oxygen (DO) concentrations in the shallow profiles at all three sites showed high  
254 variability (6–12.5 mg/L) in the top layer (unknown reason for variation), but with relative  
255 stability at about 5 mg/L from 20 to 90 m (Fig. 3). DO in the deep profile was at lower  
256 concentrations (0.8–1.5 mg/L) near the surface, increasing to around 2 mg/L at 115 m and then  
257 steadily declined to about 0.6 mg/L at 300 m with a saturation of only 10%.

258 The vertical pattern in chlorophyll *a* (chl-*a*) concentrations markedly differed between  
259 shallow and deep profiles (Figs. 3 and 4). At sites A–C, chl-*a* was slightly detected at the surface  
260 but abruptly increased from 0.3 to 1.2 mg/m<sup>3</sup> within 50–75 m and thereafter declined to near  
261 0.2 mg/m<sup>3</sup> at sites A and C and to about 0.5 mg/m<sup>3</sup> at site B. Chl-*a* concentrations were



262 relatively low in the deep profile, decreasing from about  $0.45 \text{ mg/m}^3$  at the surface to about  
263  $0.06 \text{ mg/m}^3$  at 100 m, from which it remained unchanged until 300 m. Note that these chl-*a*  
264 concentrations were based on *in situ* fluorescence detection using a sensor that was pre-  
265 calibrated with a chlorophyll standard from the manufacturer (Wet Labs). As chlorophyll  
266 fluorescence may vary with cell physiological condition, time of day, light regime, and other  
267 factors, and since the sensor was not field-validated after calibration, the present chl-*a* values  
268 should thus be considered semi-quantitative.

269 PAR levels at sites B and C were initially recorded at  $600\text{--}700 \mu\text{mol/m}^2/\text{s}$  at the surface and  
270 then steeply decreased to  $120\text{--}160 \mu\text{mol/m}^2/\text{s}$  at 20 m depth, from where it further decreased  
271 gradually until 90 m depth (Fig. 3). At site A, where the measurement was done at an earlier  
272 time, PAR varied between  $220\text{--}300 \mu\text{mol/m}^2/\text{s}$  within the top 10 m layer and then coincided  
273 with the same values at sites B and C. PAR in the deep profile steeply declined from about  $240$   
274  $\mu\text{mol/m}^2/\text{s}$  near the surface to about  $20 \mu\text{mol/m}^2/\text{s}$  at 40 m depth, after which it gradually  
275 decreased to near zero at about 75 m depth, which is generally similar to the trend in the  
276 shallow profiles (Figs. 3 and 4). The depths at which the PAR levels were at 1% of the surface  
277 values were in range of 38–54 m for all sites.

278 Turbidity was generally low in the vertical profiles at all sites. Turbidity varied in the narrow  
279 range of 0.2–0.3 NTU, with only a few spikes up to 0.4 NTU, in all three shallow profiles (Fig. 3).  
280 In the deep profile, most turbidity values were within 0.1–0.15 NTU, with intermittent spikes up  
281 to 0.2 NTU below 75 m depth (Fig. 4).

282

283 3.2 Algae and cyanobacteria concentrations



284

285 Total concentrations of algae and cyanobacteria (summed) with depth at the shallow and deep  
286 sampling stations are shown in Figs. 5 and 6, respectively. Previous results on total algal and  
287 cyanobacterial abundances, all collected from surface layers close to shore in the same study  
288 area, are compiled in Table 1, with a range of 1,677–137,363 cells/mL (mean 44,383 cells/mL  
289 out of 38 samples). Total algal and cyanobacterial concentrations from the surface at the  
290 shallow stations (A–C) during the present study were comparable to the mean of the previous  
291 data, while the surface concentration at the deep station (D) was close to the reported  
292 maximum (Figs. 5 and 6, Table 1).

293 The vertical profiles of algal and cyanobacteria concentrations by group (cyanobacteria,  
294 *Prochlorococcus* and pico/nanoplankton) are shown in Figs. 5 and 6 for the shallow (A–C) and  
295 deep sites, respectively. At sites A–C, cyanobacteria were more abundant near the surface (top  
296 10 m layer), below that *Prochlorococcus* was more predominant, with peak concentrations at  
297 about 50 m (Fig. 5). In general, algal and cyanobacterial concentrations showed a substantial  
298 decline below 80 m at all sites. The same compositional and abundance trends were exhibited  
299 in the deep profile, except that cyanobacteria had higher concentrations near the surface in the  
300 deep profile while *Prochlorococcus* was relatively denser at subsurface depths in the shallow  
301 profiles (Fig. 6). In addition, the concentrations of pico/nanoplankton in the upper layers were  
302 relatively higher at the deep site compared to the shallow sites (A–C) (Figs. 5 and 6).

303

304 3.3 Bacteria concentrations

305



306 The vertical trends in bacterial concentrations during the present study are shown in Figs. 7 and  
307 8, indicating higher cell densities in the upper 50 m layer at the deep site compared to sites  
308 A–C. Previous results on nearshore bacterial concentrations from the same study area ranged  
309 from  $1.13 \times 10^5$  to  $2.18 \times 10^6$  cells mL<sup>-1</sup> (mean  $5.26 \times 10^5$  cells mL<sup>-1</sup>; 40 samples) (Table 1). The  
310 new data on offshore surface concentrations of bacteria are comparable to the average of the  
311 nearshore results (Table 1, Figs. 7 and 8). Bacterial abundance generally declined with depth,  
312 with a decrement of about  $4.00 \times 10^5$  to  $9.00 \times 10^4$  cells mL<sup>-1</sup> from the surface to 90 m depth at  
313 sites A–C (Fig. 7) and from about  $5.00 \times 10^5$  cells mL<sup>-1</sup> at the surface to  $1.60 \times 10^5$  cells mL<sup>-1</sup> at  
314 160 m and to  $1.00 \times 10^5$  cells mL<sup>-1</sup> at 300 m (Fig. 8).

315

### 316 3.4 Total organic carbon (TOC)

317

318 TOC concentrations exhibited only minor differences between the sites, with fluctuations  
319 within a narrow range in the upper 50 m layer at both the shallow and deep sites (Figs. 7 and 8).  
320 Nearshore data on TOC ranged from 0.83 to 1.42 mg/L, with an average of 1.0 mg/L from 42  
321 measurements (Table 1). In the offshore near-surface profiles, the TOC ranged from 0.99 to  
322 1.35 mg/L.

323 TOC generally declined with depth at all sites, although only within a narrow range at sites  
324 A–C between 1.2 mg/L at surface and 0.9 mg/L at 90 m depth. The decline in the deeper profile  
325 was from 1.1 mg/L at surface to 1.0 mg/L at 120 m and then to 0.75 mg/L at 300 m.

326

### 327 3.5 Particulate and colloidal TEP concentrations



328

329 Nearshore p-TEP and c-TEP showed considerable variation in concentrations with ranges of  
330 53–347 (mean 191) and 36–287 (125)  $\mu\text{g Xeq./L}$ , respectively (Table 1). Comparable ranges of  
331 concentration for both parameters were found offshore, except for the markedly higher c-TEP  
332 concentrations in the vertical profile at site A (Figs. 7 and 8).

333 Both p-TEP and c-TEP generally declined with depth, although with fluctuations between  
334 50–100 m depth and an elevated value at 200 m depth in the deep profile. The difference in  
335 concentrations was more pronounced for c-TEP in the deep profile, from 265  $\mu\text{g Xeq./L}$  at 10 m  
336 to about 70  $\mu\text{g Xeq./L}$  at 300 m. The change in concentration of p-TEP with depth in the deep  
337 profile was relatively slight, from about 285  $\mu\text{g Xeq./L}$  at 40 m to 170  $\mu\text{g Xeq./L}$  at 300 m. At the  
338 shallow sites, both p-TEP and c-TEP trends with depth showed similar patterns between sites B  
339 and C, except that c-TEP was unusually low in the surface layer at site C (Fig. 7).

340

341 3.6 NOM fractions

342

343 There was considerable variability in concentrations of the NOM fractions in nearshore seawater  
344 The range in concentration, number of samples, and average of the concentrations are the  
345 following: biopolymers (28–164  $\mu\text{g/L}$ , 42, 62  $\mu\text{g/L}$ ), humic substances (159–442  $\mu\text{g/L}$ , 42, 248  
346  $\mu\text{g/L}$ ), building blocks (81–260  $\mu\text{g/L}$ , 42, 118  $\mu\text{g/L}$ ), LMW neutrals (16–477  $\mu\text{g/L}$ , 42, 271  $\mu\text{g/L}$ ),  
347 and LMW acids (10–130  $\mu\text{g/L}$ , 42, 40  $\mu\text{g/L}$ ). The range in biopolymer concentrations in the  
348 surface offshore samples are similar to the nearshore samples. All of the NOM fractions have  
349 higher concentrations at the A, B, and C profiles compared to the deep profile.





350 The biopolymer fraction of NOM shows a general reduction with depth in all offshore  
351 profiles. At sites A and B there is a spike in biopolymers at 10 m with minor variation between  
352 10 m to 90 m. In the deeper profile, there is considerable variation in the photic zone with the  
353 surface having the highest value and subsequent spikes occurring at 30 and 60 m. Beginning at  
354 about 90 m, there is a constant downward trend in concentration.

355 Humic acid concentrations showed only minor variations with depth in the shallow profiles,  
356 but the deep profile showed a reduction by about 29% from 90 to 300 m depth. There is a  
357 general decreasing trend in concentration of building blocks with depth at the deep site and  
358 only minimal differences throughout the depth profiles at sites A–C (Figs. 7 and 8). The  
359 concentrations of LMW neutrals at the shallow sites were the highest amongst NOM fractions,  
360 although with a wide range of variation. In contrast, LMW acids had the lowest concentrations  
361 without marked discrepancies in concentration in the vertical profiles between sites A–C, but a  
362 general reduction occurred below 120 m in the deep profile (Figs. 7 and 8).

363

#### 364 **4 Discussion**

365

##### 366 4.1 Algal and cyanobacterial concentrations

367

368 The flow cytometry approach used in this study was highly effective in characterizing and  
369 enumerating the small size classes of phytoplankton and cyanobacteria that are readily  
370 distinguishable on the basis of cell size and autofluorescence. Thus, cyanobacteria (presumably  
371 *Synechococcus* spp), *Prochlorococcus*, and the general class of pico/nanoplankton were



372 numerically dominant, with very few larger eukaryotic algal species detected. This is consistent  
373 with prior studies that reported that phytoplankton in the oligotrophic northern Red Sea and  
374 Gulf of Aqaba are dominated (>95%) by cells <5  $\mu\text{m}$  in size (Lindell and Post 1995; Yahel et al.  
375 1998). Only during the summer does the large macroalgae *Trichodesmium* sp. also become  
376 prominent. As reported here, algae ranging from 5 to several hundred  $\mu\text{m}$  are extremely scarce,  
377 although not totally absent (Sommer 2000; Kimor and Goldanski 1992).

378

379 4.2 Correlations between TEP, bacteria, algae, the biopolymer fraction of NOM, and TOC

380

381 TEP is composed of acidic polysaccharides and some large proteins that occur mostly in the  
382 biopolymer fraction of NOM and some of the proteins within the humic acid part of NOM (Bar-  
383 Zeev et al. 2015; Winters et al. 2016). TEP can be produced both abiotically and as extracellular  
384 discharges from bacteria and algae (Zhou et al. 1998; Passow et al. 2001; Passow 2002; Engel et  
385 al. 2004; Iuculano et al. 2017). Therefore, there should be some statistical relationship between  
386 TEP, the biopolymer fraction of NOM, bacterial concentration or algal concentration.

387 A series of statistical analyses were performed to test if there are significant relationships  
388 between the various organic properties (Table 2). In all cases there was no statistically-  
389 significant relationship between any of these parameters in the shallow, nearshore samples  
390 with the exception of bacteria and TOC. However, some important and statistically-significant  
391 relations were found between p-TEP and bacteria in the profiles measured at sites A, B, and C  
392 and in the 300 m profile. All of the offshore profiles showed a statistically significant  
393 relationship between c-TEP and bacteria with the exception of the site C profile. In comparison,



394 there was only one statically-significant relationship between p-TEP and algae at site B and for  
395 c-TEP the only profile showing statistical-significance was the deep profile. Based on these  
396 relationships, it appears that p-TEP may be produced by bacteria in greater amounts compared  
397 to algae at these locations. Consumption of the TEP by bacteria does not seem to be occurring  
398 in the water column at sites A, B, and C based on the p-TEP relationship, unless abiotically-  
399 generated p-TEP is replacing what is consumed. In the deep profile, the c-TEP concentration  
400 shows a statistically-significant relationship with bacteria which could indicate a breakdown of  
401 the p-TEP, particularly outside of the photic zone.

402 The relationship between the biopolymers and bacterial concentrations shows a significant  
403 statistical correlation in all offshore profiles while the correlation between biopolymers and  
404 algal concentrations is statistically significant only at site A and in the deep profile. These  
405 relationships suggest that extracellular discharges of polysaccharides and proteins from the  
406 bacteria and algae are occurring without immediate abiotic assembly into p-TEP. This  
407 suggestion is further supported by the statistical relationships between biopolymers and p-TEP  
408 and c-TEP which are statistically significant at several, but not all of the offshore profiles.

409 The offshore profiles show statistically-significant relationships between both p-TEP and c-  
410 TEP and TOC at sites A and the deep profile. Therefore, TEP in general is a significant part of  
411 TOC in the Red Sea at these locations, particularly below the photic zone.

412 There is usually no statistical relationship of significance between p-TEP and c-TEP.  
413 However, at site A the data produced an  $r^2$  value of 1 and with a corresponding p-value of 0  
414 (Table 2). This unusual relationship has no explanation but is noted.



415 A considerable amount of additional research will be required to better establish the  
416 processes occurring within the Red Sea water column that relate to NOM production and  
417 transport and how these processes relate to the measured TEP and NOM fraction  
418 concentrations. Since there are few data available in the literature that relate these parameters  
419 within the water column at other geographic locations, it is difficult to provide definitive  
420 conclusions. The data provided here appear to be the first published that relate the biopolymer  
421 fraction of NOM to TEP and provide all of the five fractions of NOM in the offshore marine  
422 environment throughout the water column. The carbon compounds that occur in p-TEP are  
423 largely contained within the biopolymer fraction of NOM with the exception of some proteins  
424 which occur in the size range found in the humic substances.

425 An assessment of the other fractions of NOM, humic substances, building blocks, LWM  
426 neutrals, and LMW acids, did not show any significant statistical relationships between these  
427 parameters, nor did it reveal potential relationships between them and the bacteria or algae.

428

#### 429 4.3 Comparison of the offshore and onshore TEP data in the Red Sea

430

431 All of the onshore measurements of p-TEP and c-TEP were collected between the sea surface  
432 and a depth of 10 m. Therefore, only the data in this depth range can be compared to the  
433 offshore data. The full range of p-TEP in the nearshore measurements is from 53 to 347  $\mu\text{g}$   
434  $\text{Xeq.}/\text{L}$  and the c-TEP range is between 36 and 287  $\mu\text{g}$   $\text{Xeq.}/\text{L}$ . The ranges in the offshore profiles  
435 in the same depth range for p-TEP and c-TEP are 135.4 to 279.4 and 0 to 340.7 respectively. In  
436 both locations there was considerable variation between sites and in different times of the year



437 which is expected based on production variations of TEP by algae and bacteria in the upper  
438 photic zone as well as the ability of TEP to have either negative or positive buoyancy at shallow  
439 depths (Zhou et al., 1998; Passow, 2002; Mari et al., 2004; Schuster and Herndl 1995; Ortega-  
440 Retuerta et al. 2017).

441

442 4.4 Comparison of TEP profiles in the Red Sea with other marine environments

443

444 Most TEP data profiles collected in the marine environment show an irregular variation in the  
445 upper 100 m of the water column (Schuster and Herndl 1995; Ortega-Retuerta et al. 2017), a  
446 general reduction of TEP with depth over 200 m (Busch et al. 2017; Jennings et al. 2017), but in  
447 some cases an increase at greater depths (Ramaiah et al., 2000). Also, the reported changes in  
448 TEP with depth are based mostly on p-TEP data and not both types of TEP which show differing  
449 trends in the water column. The TEP data collected from the profiles in this investigation within  
450 the photic zone (<100m) show differing concentrations with depth (Figs. 7 and 8). Within the  
451 upper 90, p-TEP declines between 31 and 39% at sites A, B, and C and shows no decline in the  
452 deep profile. The c-TEP concentration declines between 38 and 70% at sites A, B, and the deep  
453 profile, but increases by 150% at site C. For comparison, the TOC concentration reduction in the  
454 photic zone ranges between 10 and 32%. In the deep profile the difference between the  
455 surface and the 300 m depth showed a reduction in p-TEP of 20% and c-TEP of 69%. This may  
456 indicate that some abiotic assembly of p-TEP is occurring below the photic zone, particularly in  
457 the presence of bacteria which may feed upon the p-TEP. The TOC in the deep profile declines  
458 by about 32% comparing the surface to the 300 m depth.



459

460 4.5 Relationships between NOM fractions and other parameters

461

462 The primary fraction of NOM that shows a trend with depth is the biopolymers which track  
463 well to bacteria. Since the biopolymer fraction of NOM contains most of the polysaccharides,  
464 which are food for bacteria, the relationship with the bacteria is to be expected. In the upper  
465 100 m of the water column, the humic substances show a restricted range in concentrations  
466 with a small downward trend (Fig. 7), but below 100 m there is a lowering concentration  
467 following the same pattern as the biopolymers. The building blocks have a larger range in  
468 concentration changes in the upper 100 m of the water column compared to the humic  
469 substances (Fig. 7) and a similar downward trend in concentration similar to the humic  
470 substances below 100 m (Fig. 8). The LMW neutrals and acids show considerable variation in  
471 concentration in the upper 100 m and a slight downward change in concentration below 100 m.

472 There are some general suggestions made by these data related to the concentration  
473 changes. In the photic zone, the biochemical activity of algae and bacteria affect the NOM  
474 fraction concentrations. The LMW fractions are likely affected by the biochemical breakdown of  
475 large molecular weight organics and by selective, abiotic aggradation of larger organic particles  
476 suggested by the larger concentration of the neutrals over the acids. The reduction in  
477 concentrations in biopolymers, humic substances and building blocks below 100 m follows the  
478 reduction in bacteria below the photic zone. As bacteria feed on p-TEP, they may leave behind  
479 the LMW neutrals which could be compounds that cannot be used by the bacteria as food. The  
480 LMW acids may tend to occur within the context of c-TEP and may be subject to abiotic



481 aggradation during settling. Future research will be required to understand the complex  
482 relations between the NOM organic fractions and the biochemistry of the bacteria in the deep-  
483 water column.

484

## 485 **5 Conclusions**

486

487 Vertical changes in concentrations of TEP in the Red Sea tend to follow trends found in other  
488 locations of the world ocean in that there is a general reduction with depth. The changes in the  
489 photic zone tend to be quite irregular, as expected, because of variations in primary  
490 productivity and differing biochemical conditions. Although it was observed that no clear  
491 relationship between TEP and algae occurs in the Red Sea, this unusual result may be explained  
492 by the dominance of small algae and cyanobacteria. The measurement of the five fractions of  
493 NOM allows some preliminary conclusions to be made concerning the relationships between  
494 specific organic parameters and TEP variation with depth. These relationships suggest that  
495 extracellular discharges of polysaccharides and proteins from the bacteria and algae are  
496 occurring without immediate abiotic assembly into p-TEP in the photic zone of the water  
497 column. In the water column below the photic zone, TOC, bacteria, and biopolymers show a  
498 generally common rate of reduction in concentration, but p-TEP concentration changes at a  
499 reduced rate showing that it persists in moving organic carbon deeper into the water column  
500 despite consumption by bacteria. There may be some abiotic assembly of c-TEP into p-TEP to  
501 maintain the concentration without full bacterial removal.



502 The relationships between p-TEP and c-TEP and other organic parameters, especially the  
503 biopolymer fraction of NOM, is different when comparing the offshore water column to the  
504 nearshore area. The only statistically-significant relationship in the measured parameters in the  
505 nearshore was that between bacteria and TOC. Irregularity in local conditions in the nearshore  
506 zone causes large variations in the organic parameters measured, not allowing statistically-  
507 significant relationships to be established.

508

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634

635 Table 1. Compilation of related data from previous studies

636

Location	Date	Depth (m)	Total Algae (cells/mL)	Bacteria (cells/mL)	TOC (mg/L)	NOM ( $\mu\text{g/L}$ )			
						Biopoly.	Humic substances	Building Blocks	LMWN
<sup>1</sup> N. Obhor	1/8/2014	Surface	30,524	112,790	0.89	76	345	103	168
<sup>1</sup> Corniche	1/11/2014	Surface	3,603	196,377	0.94	90	360	91	192
<sup>1</sup> S. Jeddah	1/9/2014	Surface	1,677	264,728	1.02	116	351	139	197
<sup>1</sup> Buhayrat	-	Surface	30,395	320,870	1.053	47	343	82	16
<sup>2</sup> Site A (Buhayrat)	1/7/2014	Surface	14,956	179,837	0.88	63	367	131	230
<sup>2</sup> Site B (Saudia)	5/25/2013	Surface	23,773	317,174	0.83	84	289	101	45
<sup>3</sup> N. Obhor	10/25/2014	Surface	129,738	520,350	1.1	57	205	95	163
<sup>3</sup> Corniche	11/6/2014	Surface	89,033	254,450	1.0	44	201	86	249
<sup>3</sup> S. Jeddah	12/24/2014	Surface	42,923	216,400	0.9	32	196	95	276
<sup>4</sup> N. Obhor	6/7/2015	Surface	-	707,100	1.262	40	194	85	466
<sup>4</sup> N. Obhor	6/17/2015	Surface	-	-	1.034	42	185	99	231
<sup>4</sup> N. Obhor	7/1/2015	Surface	108,740	282,450	1.162	49	192	105	313
<sup>4</sup> N. Obhor	7/12/2015	Surface	87,615	252,233	1.036	50	188	105	477
<sup>4</sup> N. Obhor	8/3/2015	Surface	135,603	908,100	1.104	80	209	122	269
<sup>4</sup> N. Obhor	8/16/2015	Surface	49,770	1,764,850	1.118	71	184	111	284
<sup>4</sup> Saudia	6/7/2015	Surface	-	317,567	1.055	29	172	100	369
<sup>4</sup> Saudia	6/17/2015	Surface	-	-	1.233	46	189	84	183
<sup>4</sup> Saudia	7/1/2015	Surface	61,925	583,400	1.287	44	190	93	152
<sup>4</sup> Saudia	7/12/2015	Surface	137,363	1,070,400	1.294	40	159	82	188
<sup>4</sup> Saudia	8/3/2015	Surface	53,810	1,736,450	1.164	93	180	111	238
<sup>4</sup> Saudia	8/16/2015	Surface	43,060	2,182,550	1.181	83	208	103	276
<sup>5</sup> N. Obhor	2/4/2015	Surface	91,870	1,356,600	1.10	55	214	98	387
<sup>6</sup> KAUST SW	5/3/2014	Surface	4,766	273,400	1.42	29	217	119	315
<sup>6</sup> KAUST SW	5/22/2014	Surface	9,350	236,000	1.037	55	197	121	252
<sup>6</sup> KAUST SW	6/11/2014	Surface	3,140	287,850	0.992	36	246	81	319
<sup>6</sup> KAUST SW	7/3/2014	Surface	4,958	324,600	1.085	43	212	151	227
<sup>6</sup> KAUST SW	7/19/2014	Surface	11,080	389,450	0.97	53	212	91	233



<sup>6</sup> KAUST SW	8/18/2014	Surface	6,057	316,450	1.112	40	201	88	225
<sup>6</sup> KAUST SW	9/18/2014	Surface	52,453	321,250	0.923	35	193	93	171
<sup>6</sup> KAUST SW	10/21/2014	Surface	12,228	630,600	0.831	39	193	108	256
<sup>6</sup> KAUST SW	12/3/2-14	Surface	10,673	347,133	1.004	33	189	101	288
<sup>6</sup> KAUST SW	2/11/2015	Surface	12,890	292,500	1.275	36	200	102	343
<sup>6</sup> KAUST SW	5/21/2015	Surface	28,009	450,800	0.93	31	177	93	236
<sup>6</sup> KAUST SW	8/6/2015	Surface	44,153	336,900	1.041	42	184	86	229
<sup>6</sup> KAUST SW	9/17/2015	Surface	52,453	297,867	1.084	28	188	86	230
<sup>7</sup> KAUST SW	9/30/2016	Surface	11,955	369,300	1.073	112	429	213	385
<sup>7</sup> KAUST SW	10/2/2014	Surface	10,600	367,000	0.993	105	363	193	353
<sup>7</sup> KAUST SW	10/9/2014	Surface	17,777	368,463	0.944	140	373	218	335
<sup>7</sup> KAUST SW	10/16/2014	Surface	22,030	319,950	0.961	88	340	216	346
<sup>7</sup> KAUST SW	10/27/2014	Surface	42,550	297,700	0.917	164	348	260	468
<sup>7</sup> KAUST SW	11/6/2014	Surface	86,033	587,200	0.864	73	442	93	470
<sup>7</sup> KAUST SW	11/17/2014	Surface	107,030	673,700	0.897	71	374	221	352
No. Samples			38	40	42	42	42	42	42
Range in values			1,677-137,363	112,790-2,182,550	0.830-1.420	28-164	159-442	81-260	16-477
Average			44,383	525,820	1	62	248	118	271

637 <sup>1</sup> R. Rachman et al. 2015; <sup>2</sup> Dehwah et al. 2015; <sup>3</sup> Dehwah and Missimer 2016, <sup>4</sup> Alshari et al. 2017,

638 <sup>5</sup> Dehwah et al 2017; <sup>6</sup> Dehwah and Missimer 2017; <sup>7</sup> Dehwah and Missimer 2015d

639 Table 2. Regression analysis of selected organic parameters at the 0.05 significance level

640 0.05 level

Organic Parameters	Location	R <sup>2</sup>	p-value	Significant (?)
p-TEP v. Bacteria	Site A	0.6677	0.0039	Y
	Site B	0.7295	0.001656	Y
	Site C	0.6691	0.00383	Y
	Deep Profile (300 m)	0.3034	0.009661	Y
	Nearshore	0.0593	0.158757	N
p-TEP v. Algae	Site A	0.1011	0.37063	N
	Site B	0.5363	0.016017	Y
	Site C	0.2463	0.144607	N
	Deep Profile (300 m)	0.1495	0.083384	N
	Nearshore	0.0169	0.471436	N
c-TEP v. Bacteria	Site A	0.6677	0.0039	Y
	Site B	0.6430	0.005265	Y
	Site C	0.2474	0.143485	N
	Deep Profile (300 m)	0.5512	0.000116	N
	Nearshore	0.2622	0.006329	N
c-TEP v. Algae	Site A	0.1011	0.37063	N
	Site B	0.2900	0.108267	N



	Site C	0.0141	0.743804	N
	Deep Profile (300 m)	0.5713	7.4E-05	Y
	Nearshore	0.1476	0.057986	N
Biopolymers v. Bacteria	Site A	0.8166	0.000335	Y
	Site B	0.6726	0.003663	Y
	Site C	0.6868	0.003043	Y
	Deep Profile (300 m)	0.7814	1.08E-07	Y
	Nearshore	0.0123	0.495799	N
Biopolymers v. Algae	Site A	0.5801	0.010465273	Y
	Site B	0.2918	0.10701	N
	Site C	0.2996	0.101512	N
	Deep Profile (300 m)	0.7078	1.77E-06	Y
	Nearshore	0.0107	0.537011	N
Biopolymers v. p-TEP	Site A	0.4890	0.024407	Y
	Site B	0.4824	0.0258132	Y
	Site C	0.4020	0.049006	Y
	Deep Profile (300 m)	0.1551	0.077318	N
	Nearshore	0.0808	0.09790	N
Biopolymers v. c-TEP	Site A	0.4890	0.024407	Y
	Site B	0.3696	0.062253	N
	Site C	0.2590	0.13302	N
	Deep Profile (300 m)	0.5883	4.97E-05	Y
	Nearshore	0.0331	0.364097	N
p-TEP v. c-TEP	Site A	1	0	Y
	Site B	0.362578	0.065466	N
	Site C	0.3798	0.057758	N
	Deep Profile (300 m)	0.1660	0.066765	N
	Nearshore	0.0491	0.266597	N
p-TEP v. TOC	Site A	0.6591	0.00434	Y
	Site B	0.2760	0.118919	N
	Site C	0.0979	0.378796	N
	Deep Profile (300 m)	0.3156	0.008046	Y
	Nearshore	0.0284	0.332963	N
c-TEP vs. TOC	Site A	0.6591	0.0043396	Y
	Site B	0.0431	0.565154	N
	Site C	0.0165	0.723942	N
	Deep Profile (300 m)	0.6698	5.79E-06	Y
	Nearshore	0.1995	0.019513	N
Bacteria v. TOC	Site A	0.7717	0.000822	Y
	Site B	0.2994	0.101653	N
	Site C	0.1294	0.307187	N
	Deep Profile (300 m)	0.7812	1.08E-07	Y
	Nearshore	0.1144	0.032827	Y
Algae v. TOC	Site A	0.0928	0.3922134	N
	Site B	0.4907	0.024064	N
	Site C	0.3188	0.089015	N





	Deep Profile (300 m)	0.6220	2.16E-05	Y
	Nearshore	0.0388	0.236167	N

641

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643

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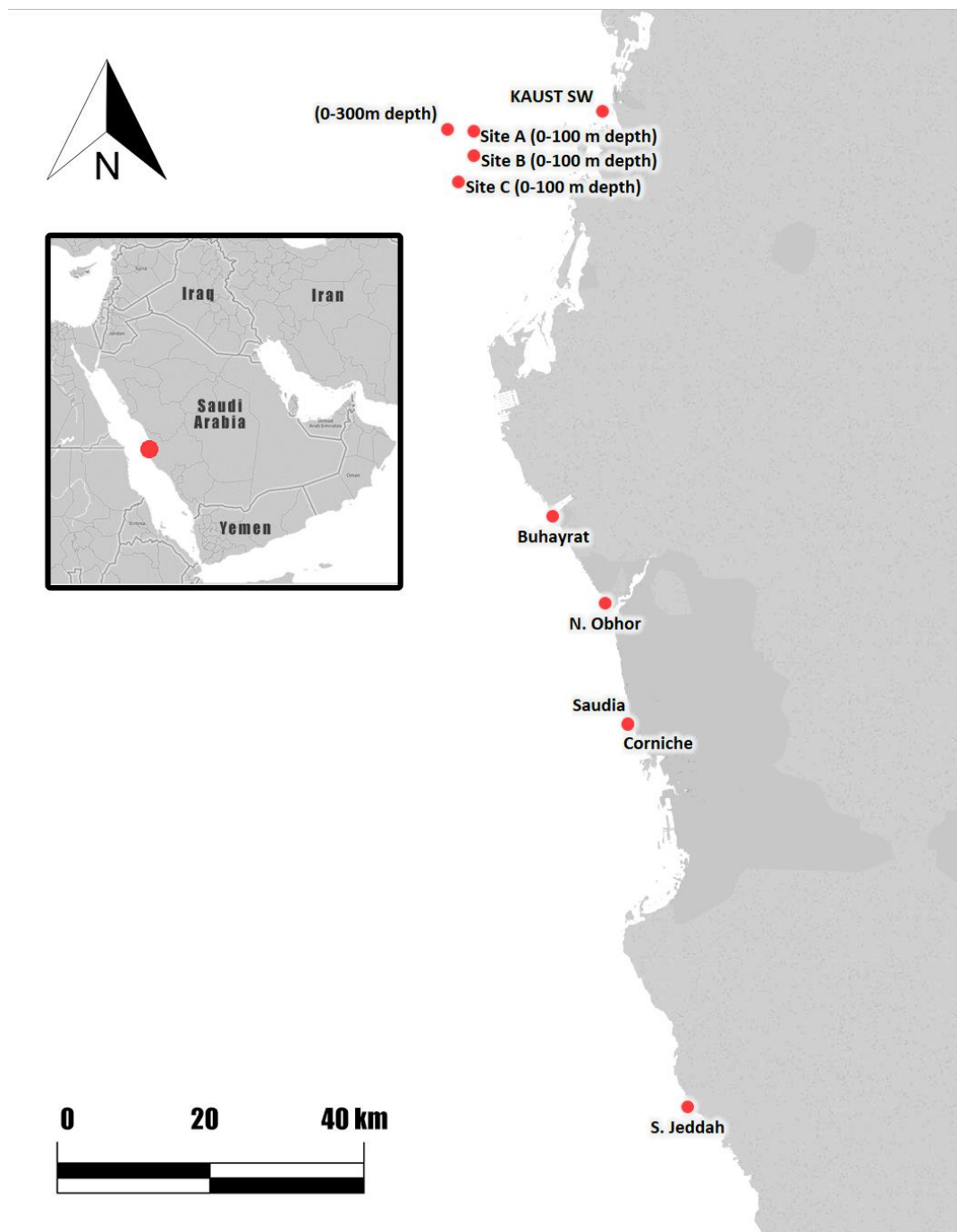
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651 **Conflicts of Interest**

652 None declared

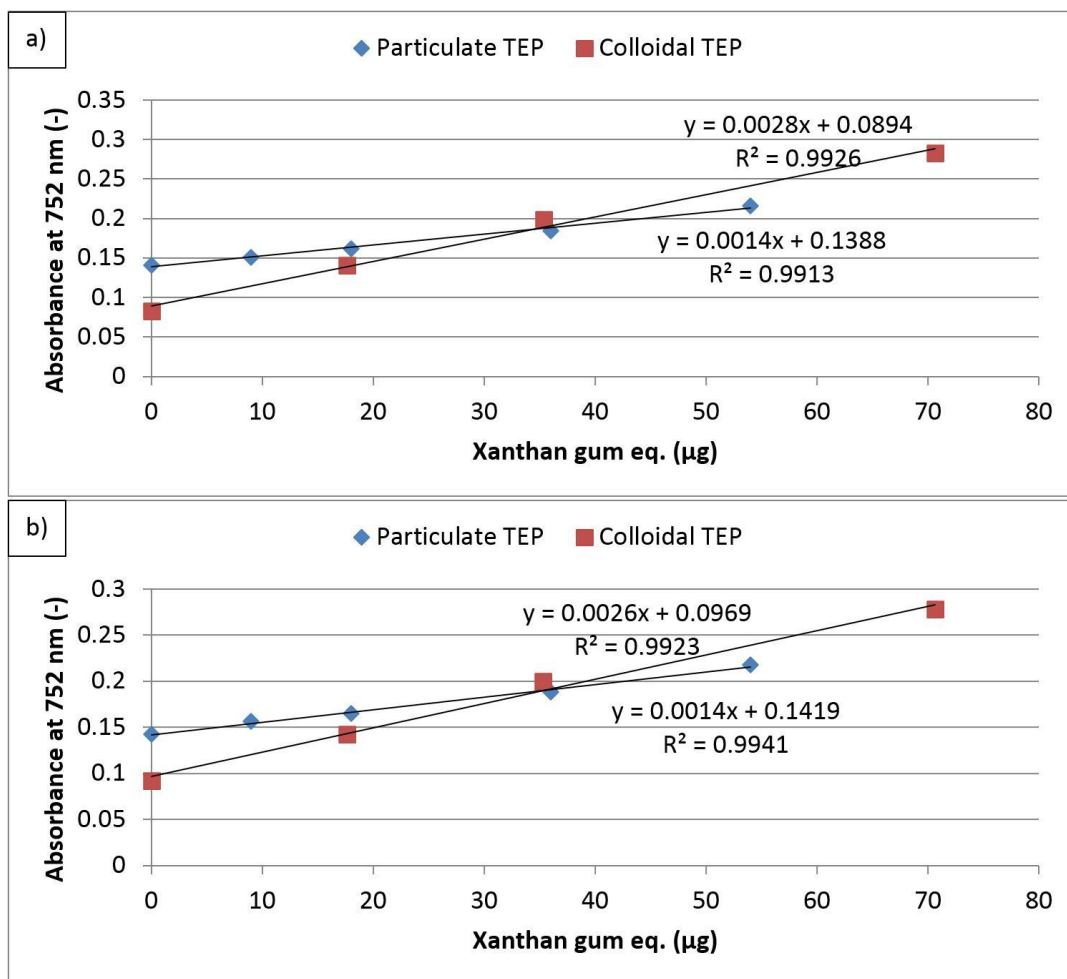
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654 Figure captions



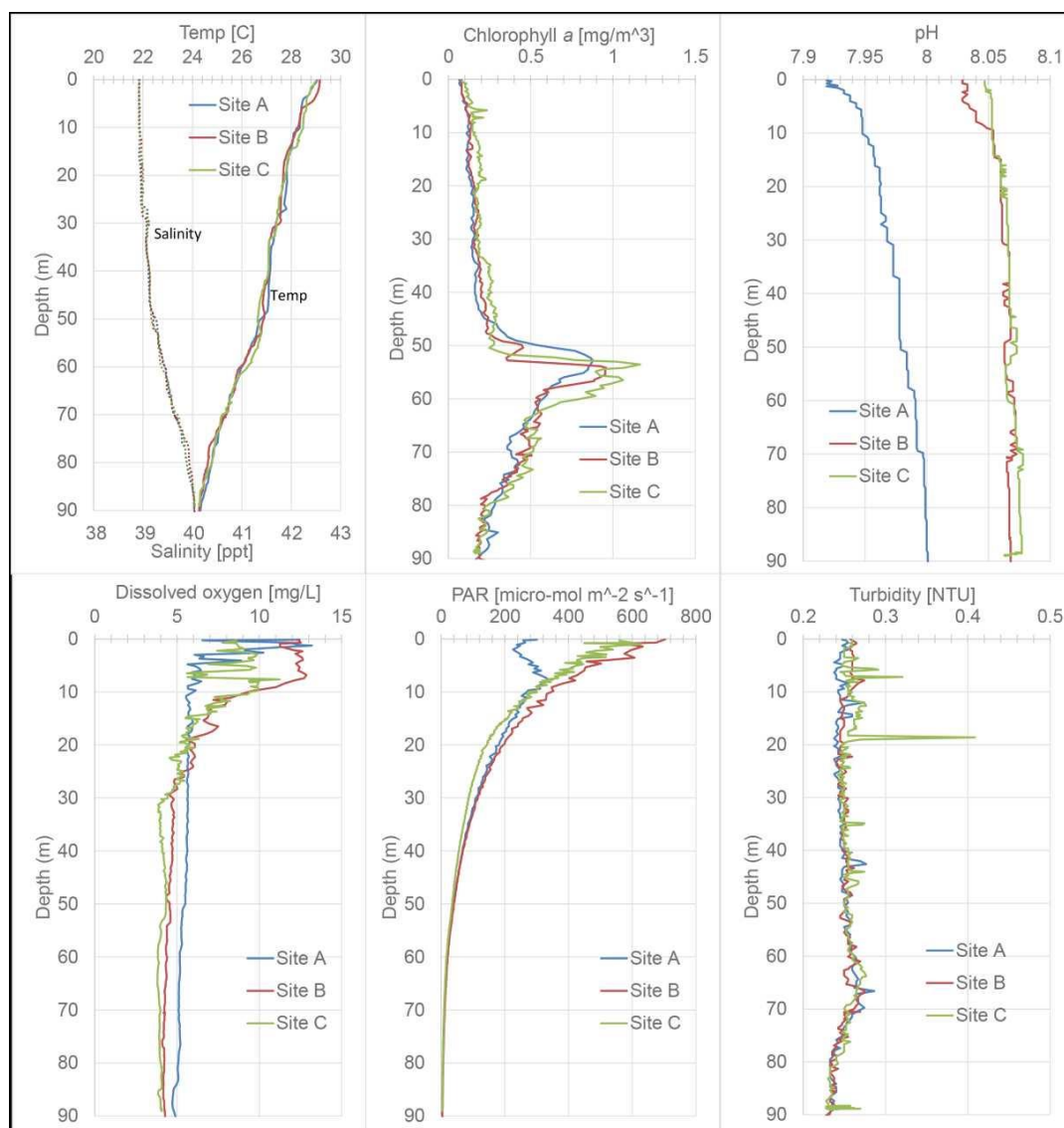
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656 Fig. 1. Map showing the sampling profile locations in the Red Sea



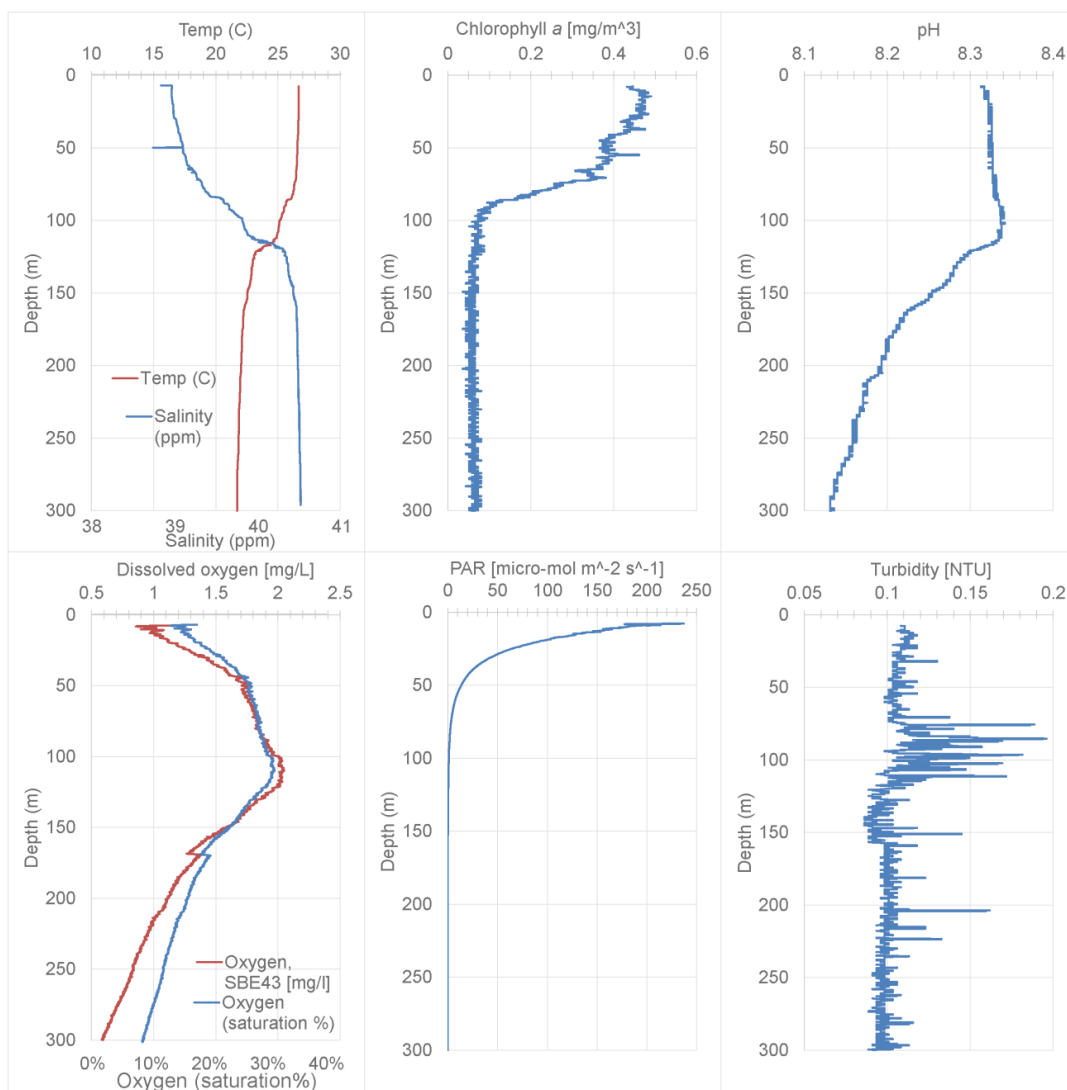
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658 Fig. 2. Xanthan gum standard calibration curves for determination of p-TEP and c-TEP



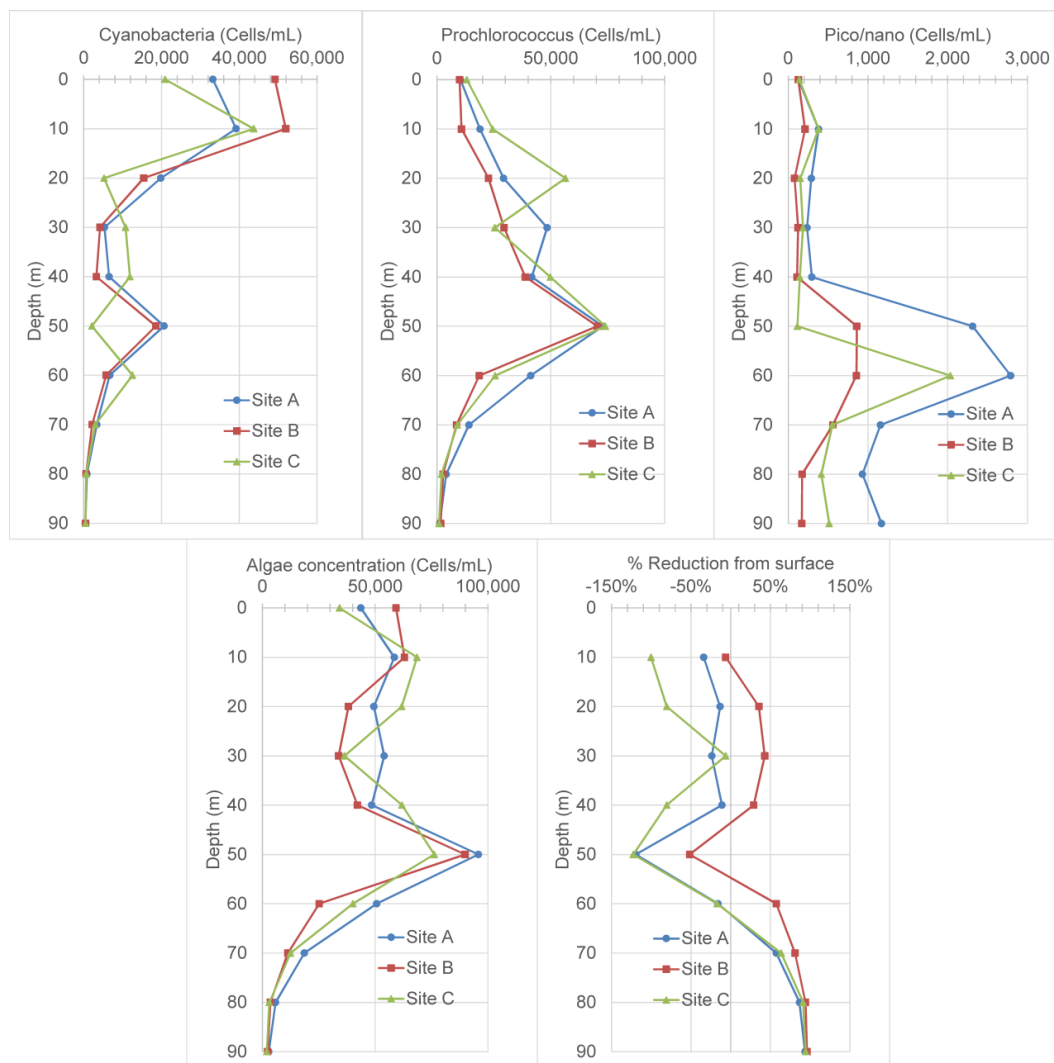
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660 Fig. 3. Physical data from the three 90 m profiles



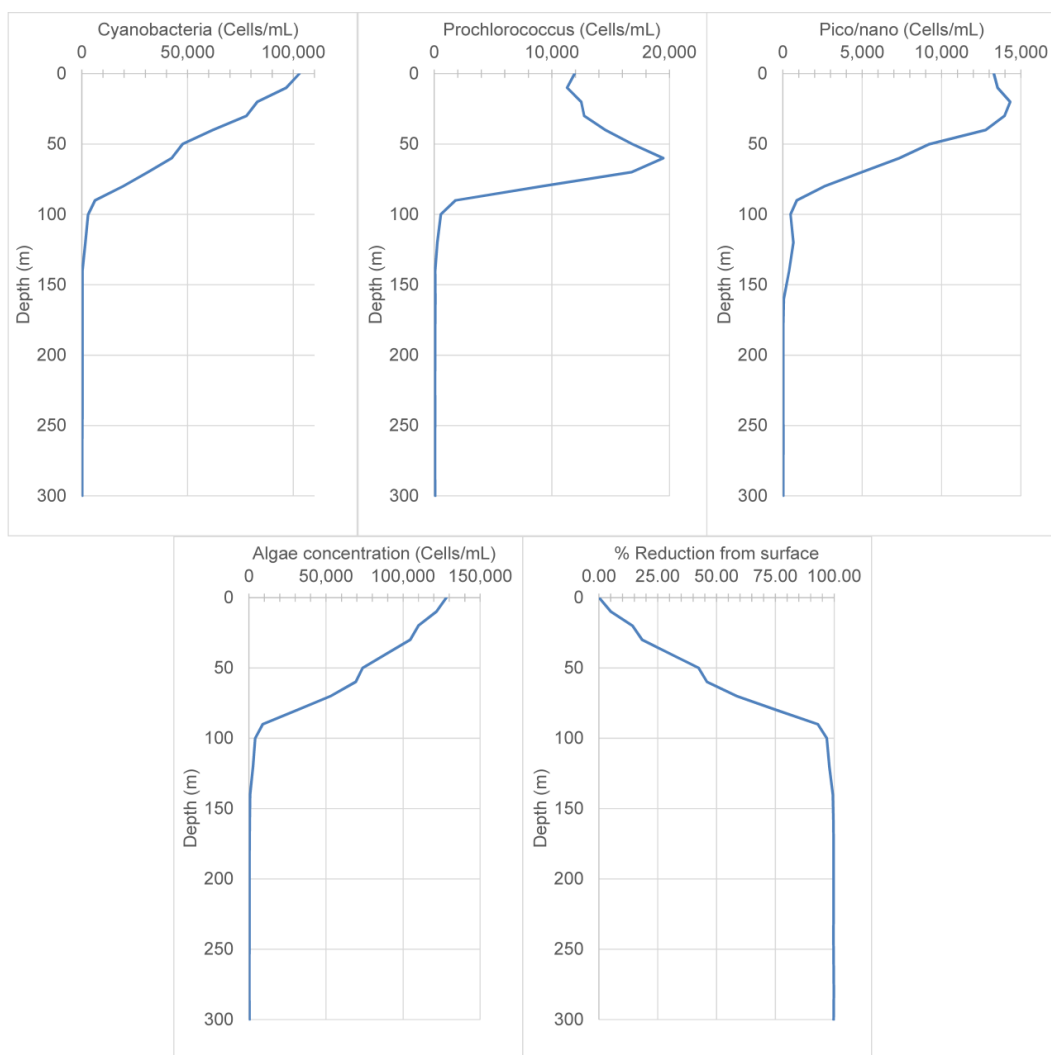
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662 Fig. 4. Physical data from the 300 m profile



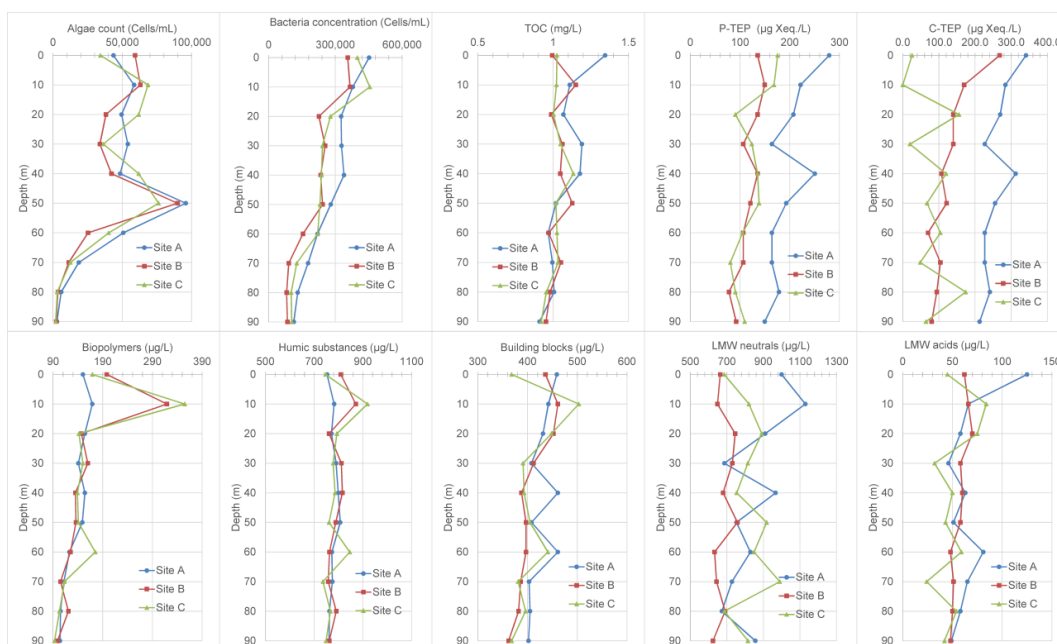
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664 Fig. 5. Algal composition and concentration data from the three 90 m profiles



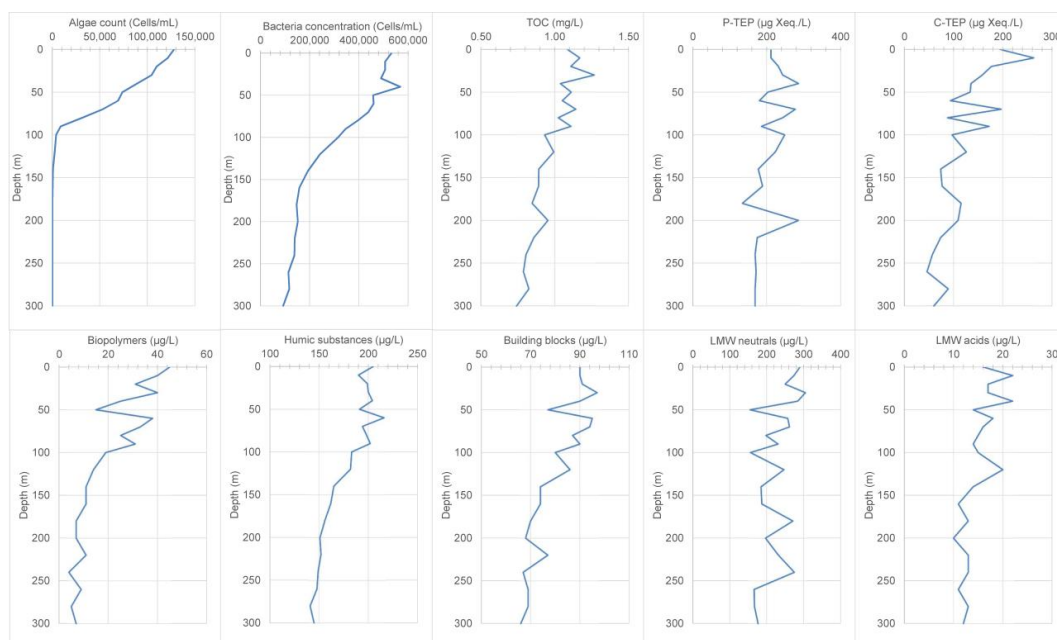
665

666 Fig. 6. Algal composition and concentration data from the 300 m profile



667

668 Fig. 7. Organic carbon concentrations for the three 90 m profiles



669

670 Fig. 8. Organic carbon concentrations from the 300 m profile