

# **Light absorption by suspended particles in the Red Sea: effect of phytoplankton community size structure and pigment composition**

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## Abstract

The light absorption properties of phytoplankton ( $a_{ph}(\lambda)$ ) and non-algal particles ( $a_{nap}(\lambda)$ ) associated with phytoplankton pigments were analyzed across the Red Sea, in the upper 200 m depth, between October 2014 and August 2016. The contribution by non-algal particles to the total particulate light absorption ( $a_{ph}(\lambda) + a_{nap}(\lambda)$ ) was highly variable ( $23 \pm 17\%$  at 440 nm) and no relationship between  $a_{nap}(440)$  and chlorophyll *a* concentration, [TChl *a*], was observed. Phytoplankton specific phytoplankton absorption coefficients at 440 and 676 nm for a given [TChl *a*],  $a_{ph}^*(440)$  and  $a_{ph}^*(676)$ , were slightly higher than those derived from average relationships for open ocean waters within the surface layer as well as along the water column. Variations in the concentration of photosynthetic and photoprotective pigments were noticeable by changes in phytoplankton community size structure as well as in  $a_{ph}^*(\lambda)$ . This study revealed that a higher proportion of picophytoplankton and an increase in photoprotective pigments (mainly driven by zeaxanthin) tended to be responsible for the higher  $a_{ph}^*(\lambda)$  values found in the Red Sea as compared to other oligotrophic regions with similar [TChl *a*]. Understanding this variability across the Red Sea may help improve the accuracy of biogeochemical parameters, such as [TChl *a*], derived from *in situ* measurements and ocean color remote sensing at a regional scale.

## 1 **1. Introduction**

2 Light absorption coefficients by suspended particles,  $a_p(\lambda)$ , i.e., phytoplankton ( $a_{ph}(\lambda)$ ) plus  
3 non-algal particles ( $a_{nap}(\lambda)$ ), are key parameters that determine the optical signature of  
4 oceanic waters and affect the colour of the ocean. The natural variability of these coefficients  
5 in various oceanic regions has been studied to establish global bio-optical relationships.  
6 Based on these studies, algorithms for the retrieval of biogeochemical products (e.g., [TChl  
7  $a$ ]) from in situ or ocean colour remote sensing have been refined (Atlas & Bannister, 1980,  
8 Morel & Bricaud, 1981; Kiefer & Mitchell, 1983; Morel, 1991; Roesler & Perry, 1995;  
9 Garver & Siegel, 1997; Morel & Maritorena, 2001; Sathyendranath et al., 2001; Maritorena  
10 et al., 2002; Morel et al., 2006). Furthermore, these coefficients, and the phytoplankton  
11 specific phytoplankton absorption coefficient ( $a_{ph}^*(\lambda)$ ) in particular, are also relevant for  
12 primary production models and for inferring phytoplankton size and taxonomic composition  
13 (Platt & Sathyendranath, 1988; Sathyendranath & Platt, 1988; Ciotti & Bricaud, 2006; Uitz et  
14 al., 2010; Tilstone et al., 2014; Bracher et al., 2017). Indeed  $a_{ph}^*(\lambda)$  is, at the first order,  
15 driven by the concentration in phytoplankton biomass (Mitchell & Kiefer, 1988; Cleveland,  
16 1995; Bricaud et al., 1998, 2010) and, at the second order, by phytoplankton size and  
17 taxonomic structure as well as pigment composition and proportions (Bricaud et al., 1995,  
18 2004; Ciotti et al., 2002; Ciotti & Bricaud, 2006; Devred et al., 2006). Thus, understanding  
19 the variability of  $a_{ph}^*(\lambda)$  with respect to [TChl  $a$ ], phytoplankton community structure and  
20 pigment composition is of primary relevance for biogeochemical studies and ocean colour  
21 remote sensing applications (Morel & Bricaud, 1981; Roesler & Perry, 1995; Sathyendranath  
22 et al., 2001).

23 While the variations in  $a_{ph}(\lambda)$  and  $a_{nap}(\lambda)$  have been extensively studied in various area of the  
24 global ocean (Bricaud et al., 1995, 1998, 2010; Lutz et al., 1996; Suzuki et al., 1998; Devred

25 et al., 2006; Boss et al., 2013), few studies have been performed in the Red Sea (Brewin et  
26 al., 2015, Organelli et al., 2017) during the last three decades. Recently, Brewin et al. (2015)  
27 suggested that the Red Sea waters and their optical characteristics can be affected by its  
28 different hydrological, biological and environmental conditions (low precipitation, little  
29 riverine input, and desert dust events), giving rise to distinct bio-optical relationships in some  
30 subareas of this sea. Using field or ocean colour remote sensing observations to infer  
31 biogeochemical parameters (e.g.,  $a_{ph}(\lambda)$ , [TChl  $a$ ]) from previously established bio-optical  
32 models, therefore, may introduce uncertainties in the retrieved products (Organelli et al.,  
33 2017). When analyzing the bio-optical characteristics of the Red Sea, Brewin et al. (2015)  
34 observed that the relationship established between the particulate backscattering coefficient  
35 and [TChl  $a$ ] as well as the relationship between  $a_p(\lambda)$  and [TChl  $a$ ] were similar to those  
36 parameterized by Brewin et al. (2012) and Bricaud et al. (1998) for other clear waters,  
37 respectively. Thus, they suggested that the overestimation of remotely-sensed [TChl  $a$ ]  
38 concentrations in the Red Sea, as derived from standard bio-optical algorithms, could be due  
39 to an excess of colored dissolved organic matter (CDOM) absorption per unit of [TChl  $a$ ].  
40 However, Organelli et al. (2017) did not observe bio-optical anomalies in the Red Sea, when  
41 analyzing measurements of diffuse attenuation coefficient for downward irradiance at those  
42 wavelengths used as proxies of CDOM and phytoplankton light absorption coefficients  
43 (Morel et al., 2007). In these studies, measurements were only taken during a limited period  
44 of the year (fall-winter season), either restricted to the surface layer or in a given sub-region  
45 of the Red Sea. It is now well known that changes in optical properties can depend on  
46 modifications of proportions between the optically significant substances (CDOM, non-algal  
47 particles and phytoplankton) observed over seasons (Sathyendranath et al., 1999; Devred et  
48 al., 2006; Organelli et al., 2014). Therefore, further characterization of the bio-optical  
49 behavior of the Red Sea is required.

50 The Red Sea is one of the most saline and warmest deep seas in the world (Belkin, 2009;  
51 Longhurst, 2007; Raitzos et al., 2011, 2013) characterized by low precipitation, little riverine  
52 input (Patzert, 1974) and high evaporation rates (Sofianos & Johns, 2003). The Red Sea  
53 displays pronounced south-north latitudinal gradients in environmental conditions such as  
54 temperature, salinity, light intensity and nutrients (Neumann & McGill, 1962; Sofianos &  
55 Johns, 2002; Raitzos et al., 2013; Churchill et al., 2014; Sawall et al., 2014; Ismael, 2015).  
56 The Red Sea is considered as a large marine ecosystem (Belkin, 2009) and sustains coral  
57 reefs, mangroves and seagrass beds, which provide habitat for a large variety of marine  
58 organisms (Berumen et al., 2013; Almahasheer et al., 2016). The Red Sea is known as an  
59 oligotrophic basin given the depletion of nutrients in the surface layer (Raitzos et al., 2013,  
60 2015; Triantafyllou et al., 2014; Racault et al., 2015).

61 Several studies showed that the seasonal variability of phytoplankton biomass in the Red Sea  
62 appears to be controlled by physical processes (winter mixing, mesoscale eddies, horizontal  
63 advection and intrusion of water masses from Bab-el-Mandeb) that determine the availability  
64 of nutrients to the euphotic layer (Raitzos et al., 2013, 2015; Triantafyllou et al., 2014;  
65 Racault et al., 2015; Dreano et al. 2016; Wafar et al. 2016; Gittings et al. 2017). Recently,  
66 Pearman et al. (2016) and Kheireddine et al. (2017) showed that phytoplankton community  
67 structure (size and taxonomy) and its spatio-vertical distribution appear to adapt in response  
68 to changes in environmental conditions along the south-north latitudinal gradients. They  
69 observed that picophytoplankton were generally the most abundant group at the surface along  
70 the whole basin. Nanophytoplankton, such as pelagophytes and prymnesiophytes, mainly  
71 characterized the community structure below the surface down to a depth of 150 m. In the  
72 southern Red Sea, microphytoplankton (diatoms) were more prominent at the bottom of the  
73 euphotic layer. Pearman et al. (2016) suggested that this distribution correlated with increased  
74 nutrients found in this region, caused by the inflow of nutrient-rich water from the Gulf of

75 Aden. How this variability in phytoplankton size structure, and thus in photosynthetic and  
76 photoprotective pigment concentrations, influences both  $a_{ph}(\lambda)$  and  $a^*_{ph}(\lambda)$  along the water  
77 column remains unknown.

78 A unique dataset of High-Performance Liquid Chromatography-derived phytoplankton  
79 pigments and spectral light absorption coefficients of phytoplankton and non-algal particles  
80 has been compiled for the upper 200 m water column across the Red Sea basin. This dataset  
81 will increase the understanding of the bio-optical properties of this region and, with a focus  
82 on surface waters, evaluate the feasibility to retrieve biogeochemical quantities with better  
83 accuracy from ocean colour observations. In particular, this study aims to (1) examine the  
84 relationships linking  $a_p(\lambda)$ ,  $a_{ph}(\lambda)$  and  $a_{nap}(\lambda)$  to phytoplankton biomass ([TChl  $a$ ]), (2) assess  
85 the influences of phytoplankton cell size and pigment composition on the variability in light  
86 absorption properties and (3) identify presence/lack of consistency between the bio-optical  
87 relationships established in Red Sea waters and those parameterized for other oceanic areas  
88 around the world.

89

## 90 **2. Materials and methods**

91 *2.1 Oceanographic cruises and sampling---* Samples were collected during five research  
92 cruises performed across the Red Sea between October 2014 and January 2016 on board of  
93 the R/V Thuwal. Two cruises named as CRS-01, and CRS-04 took place in the central Red  
94 Sea (CRS) during fall and winter, specifically from 16 - 28 October 2014 and from 17 - 28  
95 January 2016, respectively. Two cruises, Duba-01 and Duba-02 were conducted in the  
96 northern Red Sea (NRS) in spring during the periods of 17 - 28 April 2015 and 21 March - 2  
97 April 2016, respectively. A cruise to Jazan took place in the southern Red Sea (SRS) in  
98 winter from 8 - 21 February 2015. A total of 40 stations were sampled: 18 in the NRS, 14 in  
99 the CRS and 8 in the SRS (Fig. 1) (Table 1).

100 Discrete seawater samples for determining phytoplankton pigment concentrations and  
101 particulate absorption spectra were collected using a rosette system equipped with 10 L  
102 Niskin bottles at typically 10 depths within the upper 200 m depth of the water column (5, 10,  
103 20, 40, 50, 60, 70, 80, 150 and 200 m). Temperature and salinity profiles were obtained using  
104 a SBE 9 (Sea-Bird Electronics) Conductivity-Temperature-Depth (CTD) probe. The dataset  
105 consisted of 297 measurements of absorption spectra and phytoplankton pigment  
106 concentrations. The first optical depth, that corresponds to the surface layer observed by  
107 satellite ocean color sensors (Gordon & McCluney, 1975), was obtained as the euphotic  
108 depth,  $Z_e$ , divided by 4.6 (Morel, 1988).  $Z_e$  is the depth at which PAR decreases to 1% of its  
109 value ( $\ln(1\%) = -4.6$ ) just below the sea surface, and was derived from [TChl *a*]  
110 concentration profiles (Morel & Maritorena, 2001).

111 *2.2 Phytoplankton pigment analysis*--- Seawater samples (with volume ranging from 2.3 L to  
112 2.8 L) were filtered through 25 mm diameter Whatman GF/F filters (0.7  $\mu\text{m}$  porosity), stored  
113 in liquid nitrogen during the cruise and subsequently at -80 °C in the laboratory until  
114 analysis. A total of 25 pigments were quantified using a High Performance Liquid  
115 Chromatography (HPLC) complete 1260 Agilent Technologies system according to the  
116 protocol described in Ras et al. (2008). Briefly, filters were ground in 3 ml of 100% methanol  
117 together with glass beads of 1 mm diameter by cell homogenizer. The extract was centrifuged  
118 for ten minutes at 7500 rpm and cooled at -5 °C. Then the supernatants were filtered through  
119 a Teflon syringe filter of 0.2  $\mu\text{m}$  and the extracts were analyzed.

120 In this study, the sum of concentrations of chlorophyll *a*, divinyl chlorophyll *a*,  
121 chlorophyllide *a*, and phaeo was used as an index of phytoplankton biomass and noted [TChl  
122 *a* + phaeo]. The term phaeo includes the sum of phaeophytin *a* and phaeophorbide *a*  
123 pigments. The total chlorophyll b concentration, noted [TChl b], and the total chlorophyll c  
124 concentration, noted [TChl c], were computed as the sum of the concentrations of chlorophyll

125 b and divinyl chlorophyll b and chlorophyll c1, c2 and c3, respectively. Photosynthetic  
126 carotenoids (PSC) correspond to the sum of fucoxanthin (Fuco), peridinin (Peri), 19'  
127 hexanoyloxyfucoxanthin (19'HF) and 19'-butanoyloxyfucoxanthin (19'BF), while  
128 nonphotosynthetic carotenoids (PPC) include zeaxanthin (Zea), alloxanthin (Allo),  
129 diadinoxanthin (Diadi), diatoxanthin (Diato),  $\beta$ -carotene, lutein (Lut), violaxanthin (Viola),  
130 and neoxanthin (Neo).

131 *2.2.1 Estimation of phytoplankton size based on pigments---* Diagnostic accessory pigments  
132 considered as biomarkers of specific phytoplankton taxonomic groups and size classes  
133 (Vidussi et al., 2001) were used to determine the relative proportions of pico- (< 2  $\mu$ m), nano-  
134 (2-20  $\mu$ m) and microphytoplankton (> 20  $\mu$ m). The biomass proportions associated with each  
135 size class were computed from pigment ratios following Uitz et al. (2006):

$$136 \quad \% \text{ micro} = 100 * (1.41 [\text{Fuco}] + 1.41 [\text{Peri}]) / \text{DP} \quad (1)$$

$$137 \quad \% \text{ nano} = 100 * (0.6 [\text{Allo}] + 1.27 [19'\text{HF-Fuco}] + 0.35 [19'\text{BF-Fuco}]) / \text{DP} \quad (2)$$

$$138 \quad \% \text{ pico} = 100 * (0.86 [\text{Zea}] + 1.01 [\text{TChl b}]) / \text{DP} \quad (3)$$

139 where DP is the sum of the seven diagnostic pigment concentrations:

$$140 \quad \text{DP} = 1.41 [\text{Fuco}] + 1.41 [\text{Peri}] + 0.6 [\text{Allo}] + 0.35 [19'\text{BF-Fuco}] + 1.27[19'\text{HF-Fuco}] \quad (4)$$

$$141 \quad + 0.86 [\text{Zea}] + 1.01 [\text{TChlb}]$$

142 This approach has notable limitations. Some diagnostic pigments are shared by several  
143 phytoplankton groups and some groups may cover a broad size range, such as zeaxanthin  
144 containing *Trichodesmium* (microphytoplankton), or 19'BF and 19'HF in some picoplankton  
145 prymnesiophytes. This approach is not compared with others techniques such as flow  
146 cytometry, microscopy and molecular analysis. However, several previous studies  
147 demonstrated good performances of this method in providing the dominant trends of the

148 phytoplankton community size structure in other oligotrophic regions of the world's oceans  
149 (Uitz et al., 2008, 2015; Ras et al., 2008; Organelli et al., 2013).

150 The size index (SI) was derived from the proportions of pico-, nano- and microphytoplankton  
151 to provide a single indicator of the dominant phytoplankton community size structure  
152 (Bricaud et al., 2004). SI was computed as follows:

$$153 \quad \text{SI} = (1*[\% \text{pico}] + 5*[\% \text{nano}] + 50*[\% \text{micro}]) / 100 \quad (5)$$

154 where 1  $\mu\text{m}$ , 5  $\mu\text{m}$  and 50  $\mu\text{m}$  are taken as central size values for each phytoplankton class  
155 (Bricaud et al., 2004).

156 *2.3 Particulate absorption measurements---* Particulate absorption spectra,  $a_p(\lambda)$ , were  
157 measured using a quantitative filter pad technique (Mitchell et al., 2003). Seawater samples  
158 (2.3 L to 2.8 L) were filtered on Whatman GF/F filters (0.7  $\mu\text{m}$  porosity) and stored in liquid  
159 nitrogen during the cruise and subsequently at -80 °C in the laboratory until analysis.  
160 Particulate absorption spectra were measured, with a Varian Cary 5000 double-beam  
161 Ultraviolet-Visible-Infrared spectrophotometer equipped with an integrating sphere, in the  
162 300-800 nm spectral range at 1 nm intervals. A blank wet filter (pure water) was used as a  
163 reference. We used this equipment with samples placed inside the integrating sphere, which  
164 allowed us to minimize the scattering error and to determine whether significant absorption  
165 exists in the near infrared. All spectra were converted into  $a_p(\lambda)$  (in  $\text{m}^{-1}$ ) and then corrected  
166 for the path-length amplification effect according to Stramski et al. (2015).

167 The respective contributions of phytoplankton ( $a_{ph}(\lambda)$ ) and non-algal particles ( $a_{nap}(\lambda)$ ) to total  
168 particulate absorption were determined by numerical decomposition (Bricaud & Stramski,  
169 1990).

170 A few samples ( $N=21$ ) were also analyzed using the method of Kishino et al. (1985), based  
171 on the pigment extraction in methanol. Absorption ratios derived from these  $a_{ph}(\lambda)$  spectra

172 were found to be very close to the standard ratios used in the numerical decomposition. In  
173 addition, the comparison between  $a_{ph}(\lambda)$  and  $a_{nap}(\lambda)$  spectra obtained using the method of  
174 Kishino et al. (1985) and those estimated from numerical decomposition was high ( $R^2=0.96$ ,  
175 slope=1.03;  $R^2=0.88$ , slope=1.08;  $N=21$ ,  $p<0.0001$ , respectively) confirming the validity of  
176 the method established by Bricaud and Stramski, (1990) for Red Sea waters.

177 Phytoplankton specific values of phytoplankton absorption coefficients,  $a_{ph}^*(\lambda)$ , were  
178 computed by dividing  $a_{ph}(\lambda)$  by [TChl  $a$ ].

179 *2.4 Estimation of phytoplankton size based on the phytoplankton absorption spectrum---* An  
180 estimation of the phytoplankton size factor,  $S_f$ , was computed based on the shape of the  
181 phytoplankton absorption spectrum as described by Ciotti et al. (2002). The model developed  
182 by Ciotti et al. (2002) reconstructs the shape of any phytoplankton absorption spectrum  
183 (normalized by the mean in the 400-700 nm range) using a linear combination of two spectra  
184 corresponding to pure picophytoplankton and microphytoplankton populations. Note that the  
185 picophytoplankton vector used here was provided by Ciotti and Bricaud, (2006). The values  
186 of  $S_f$  vary from 0 to 1.  $S_f$  tends to 0 for a population composed exclusively of  
187 microphytoplankton and to 1 for a pure picophytoplankton assemblage. Values of  $S_f$   
188 comprised between 0 and 1 represent all possible conditions between these two extremes. The  
189 accuracy of the spectral fit was assessed for each phytoplankton absorption spectrum by  
190 computing the coefficient of correlation,  $R^2$ , between all spectral values and those  
191 reconstructed by the model. Values of  $S_f$  corresponding to  $R^2 \geq 0.97$  (RMSE =  $0.073 \pm$   
192  $0.022$ ) between measured and reconstructed phytoplankton absorption spectra were retained  
193 (92% of the entire database).

### 194 **3. Results and Discussion**

195 *3.1 Particulate, phytoplankton and non-algal particles absorption coefficients as a function*  
196 *of [TChl a]---* Variations of  $a_p(\lambda)$ ,  $a_{ph}(\lambda)$  and  $a_{nap}(\lambda)$  as a function of [TChl a] are displayed in  
197 Figures 2 and 3 and are compared with the global relationships established for oligotrophic  
198 waters using in situ measurements in various regions of the global ocean. With reference to  
199 ocean colour remote sensing, the analyses of  $a_p(\lambda)$ ,  $a_{ph}(\lambda)$  and  $a_{nap}(\lambda)$  as a function of [TChl a]  
200 was also restricted to the first optical depth. The regression formula in the form of a power  
201 law for each relationships between the parameter of interest and [TChl a] are presented in  
202 Table 2.

203

204 *3.1.1 Particulate absorption coefficients as a function of [TChl a]---*The  $a_p$  values at 440 and  
205 676 nm within the surface layer are significantly correlated to [TChl a] ( $R^2=0.87$  and  $0.89$ ,  
206 respectively,  $N=108$ ,  $p<0.0001$ ) as well as when considering all samples from the upper 200  
207 m depth ( $R^2=0.85$  and  $0.88$ , respectively,  $N=297$ ,  $p<0.0001$ ) (Fig. 2A, B). The  $a_p(\lambda)$  versus  
208 [TChl a] relationships obtained using measurements limited to the first optical depth  
209 significantly differ from those established when all depths were considered ( $p < 0.05$  for all,  
210 ANCOVA test). We also found that our measurements, which were collected both within the  
211 surface layer and in all depths, were slightly higher for a given [TChl a] than those of Bricaud  
212 et al. (1998), for the global ocean, and Brewin et al. (2015), for the Red Sea, over the whole  
213 range of our measurements ([TChl a] =  $0.006$  to  $1 \text{ mg.m}^{-3}$ ) (Fig. 2A, B).

214 The relationships obtained using measurements limited to the surface layer differ statistically  
215 with those established when all depths were considered ( $p < 0.05$  for all, ANCOVA test). We  
216 found that our measurements, which have been collected both within the surface layer and in  
217 all depths, were slightly above those of Bricaud et al. (1998), for the global ocean, and  
218 Brewin et al. (2015), for the Red Sea, over the whole range of our measurements ([TChl  
219 a]= $0.006$  to  $1 \text{ mg.m}^{-3}$ ) (Fig. 2A, B).

220 Possible reasons for the differences between our results and those of Brewin et al. (2015) may  
221 be attributed to the use of HPLC-measured [TChl *a*] in this study. Brewin et al. (2015)  
222 obtained [TChl *a*] from  $a_p$  measurements at 650, 676 and 715 nm (Line Height method) in  
223 Red Sea waters. Although this method has been found to perform well in various areas of the  
224 global ocean (Boss et al., 2007, 2013b; Dall'Olmo et al., 2009, 2012; Westberry et al., 2010;  
225 Roesler & Barnard, 2013), our results show that a linear fit to our data of [TChl *a*] measured  
226 by HPLC versus [TChl *a*] retrieved from  $a_p(\lambda)$  provided the equation  $[TChl\ a]_{LH} = 1.17 * [TChl\ a]_{HPLC} + 0.0026$  ( $R^2 = 0.91$ ,  $N=297$ ,  $p<0.0001$ ) was not apparent, indicating significant  
227 overestimation of [TChl *a*]<sub>LH</sub> as compared with [TChl *a*]<sub>HPLC</sub>. Furthermore, Brewin et al.  
228 (2015) used a larger number of measurements of  $a_p(\lambda)$  below  $0.1\ mg.m^{-3}$  compared to our  
229 dataset, which could also affect the conclusions in our study.

231 *3.1.2 Phytoplankton absorption coefficients as a function of [TChl *a*]*---The relationships  
232 between  $a_{ph}$  and [TChl *a*] at 440 and 676 nm are shown in Figure 2C, D. A significantly high  
233 correlation is also found between  $a_{ph}(\lambda)$  and [TChl *a*] within the surface layer and among  
234 depths at 440 nm ( $R^2 = 0.89$  and  $0.91$ ,  $N=108$  and  $297$ , respectively,  $p<0.0001$ ) and at 676  
235 nm ( $R^2 = 0.91$  and  $0.92$ ,  $N=108$  and  $297$ , respectively,  $p<0.0001$ ). As for  $a_p(\lambda)$ , the  
236 relationships between  $a_{ph}(\lambda)$  and [TChl *a*] established within the surface waters significantly  
237 differ from those established considering all samples between 0 and 200 m depth ( $p < 0.05$   
238 for both, ANCOVA test).

239 The relationships obtained between  $a_{ph}(\lambda)$  and [TChl *a*] within the surface as well as along  
240 the water column are above the existing global relationships proposed by Bricaud et al.  
241 (1995), Devred et al. (2006) and Brewin et al. (2011) (Fig. 2C, D) ( $p < 0.05$  for all,  
242 ANCOVA test). Given the relationships established by Devred et al. (2006) and Brewin et al.  
243 (2011) are based on a two-population model and not on a power law function, this may affect  
244 our comparisons in this study. Indeed, these models relate  $a_{ph}(\lambda)$  to [TChl *a*], assuming that

245 the assemblages of phytoplankton comprise mixtures of two populations whose proportions  
246 vary as the total concentration of cells changes. On the other hand, the relationship obtained  
247 at 440 nm considering all depths is in relatively good agreement with the relationship  
248 determined by Bricaud et al. (2004) (Fig. 2C) ( $p \geq 0.05$ , ANCOVA test), although this  
249 relationship is only representative of measurements collected in the surface layer. The  
250 relationship of Bricaud et al. (2004) is based on a different dataset (measurements collected  
251 in various oceanic regions and trophic states) than the one used in Bricaud et al. (1995) and  
252 might explain why the relationship of Bricaud et al. (2004) is more closely aligned to the  
253 relationship revealed in this study.

254 *3.1.3 Non-algal particles absorption coefficients as a function of [TChl  $a$ ]*---No clear  
255 relationship between  $a_{\text{nap}}$  at 440 nm and [TChl  $a$ ] appears among depths (Fig. 3A). This is in  
256 agreement with previous studies performed in oligotrophic waters (Cleveland, 1995). The  
257  $a_{\text{nap}(440)}$  values are highly scattered around the relationship established by Bricaud et al.  
258 (2010) from data collected in the Pacific Ocean (BIOSOPE area), reflecting different trophic  
259 regimes. Furthermore, in the deep layer where [TChl  $a$ ] varies from 0.006 to 0.1  $\text{mg}\cdot\text{m}^{-3}$ ,  
260  $a_{\text{nap}(440)}$  values are higher than those predicted by this relationship (Fig. 3A). The ratio of  
261 non-algal absorption coefficient to particulate absorption at 440 nm,  $a_{\text{nap}(440)}/a_{\text{p}(440)}$ , as a  
262 function of [TChl  $a$ ] is displayed in Figure 3B. Deep Red Sea waters with low [TChl  $a$ ]  
263 concentrations (0.006-0.1  $\text{mg}\cdot\text{m}^{-3}$ ) are characterized by high values of  $a_{\text{nap}(440)}/a_{\text{p}(440)}$ ,  
264 between 0.45 and 1. This result suggests that the  $a_{\text{nap}(440)}/a_{\text{p}(440)}$  varies inversely to [TChl  
265  $a$ ] in clear Red Sea waters. This is consistent with the observations made in other oligotrophic  
266 regions, such as in the Pacific Ocean (Bricaud et al., 2010). Bricaud et al. (2010) suggested  
267 that the high contribution of the  $a_{\text{nap}(440)}/a_{\text{p}(440)}$  ratio could indicate the presence of a large  
268 amount (or more colored) of non-algal particles. The Red Sea is also known as a region  
269 where significant inputs from dust occur [Prospero et al., 2002; Ginoux et al., 2012; Al Taani

270 et al., 2015; Prakash et al., 2015]. Frequent dust outbreaks and dust storms have been  
271 observed in the Red Sea during our research cruises. Satellite observations  
272 ([http://neo.sci.gsfc.nasa.gov/view.php?datasetId=MODAL2\\_M\\_AER\\_OD](http://neo.sci.gsfc.nasa.gov/view.php?datasetId=MODAL2_M_AER_OD)) revealed that  
273 Saharan dust events occurred in the entire Red Sea during most of the cruises (CRS-04,  
274 Duba-01, Duba-02 and Jazan) performed for this study. The presence of these inorganic  
275 particles can partly explain the high contribution of the  $a_{\text{nap}}(440)/a_{\text{p}}(440)$  ratio in Red Sea  
276 deep waters by increasing the sinking velocity of non-algal particles (Ploug et al., 2008).  
277 When [TChl *a*] varies from 0.1 to 1 mg.m<sup>-3</sup>,  $a_{\text{nap}}(440)/a_{\text{p}}(440)$  is highly variable with values  
278 ranging from 0.028 to 0.45. This is consistent with the values observed in the Pacific Ocean,  
279 Mediterranean Sea and Atlantic Ocean (Bricaud et al., 2010). This large variability can be  
280 explained by varying contributions of non-algal particles (detritus, bacteria, viruses, inorganic  
281 particles) along the water column. Several studies also demonstrated that dust inputs have a  
282 positive effect on bacterial growth and abundance, diversity and composition of the  
283 indigenous bacterial assemblages (Reche et al., 2009; Lekunberri et al., 2010; Morales-  
284 Baquero et al., 2013). Dust deposition can thus affect the proportion of bacteria in Red Sea  
285 waters and partly explain the high variability observed in the  $a_{\text{nap}}(440)/a_{\text{p}}(440)$  ratio.

286 The above comparisons suggest that the high values of  $a_{\text{p}}(\lambda)$  observed within the surface Red  
287 Sea waters ([TChl *a*] below 0.1 mg.m<sup>-3</sup>) is mainly related to an important contribution of non-  
288 algal particles in these waters (Fig. 2A, B).

289

### 290 3.2 Phytoplankton size structure associated with phytoplankton absorption spectra---

291 Variability in  $a_{\text{ph}}(\lambda)$  is observed in this study (Fig. 2C, B). The variability observed around  
292 the relationship between  $a_{\text{ph}}(\lambda)$  and [TChl *a*] may be due to changes in phytoplankton  
293 community structure. It is generally known that variations in phytoplankton size structure and  
294 the intracellular concentrations of diverse phytoplankton pigments induce variations in  $a_{\text{ph}}(\lambda)$

295 at a given [TChl *a*] (Sathyendranath et al., 1996; Bricaud et al., 2004, 2010; Organelli et al.,  
296 2011; Ferreira et al., 2013).

297 The relative contributions of nano- and picophytoplankton to total algal biomass are high in  
298 Red Sea waters (Fig. 4). Based on phytoplankton pigments ratio, we found that  
299 picophytoplankton dominate the upper layer in the whole basin due to the presence of  
300 *Prochlorococcus sp* and *Synechococcus sp*, but it remains highest in the central part of the  
301 basin (>60% of the phytoplankton biomass). The nanophytoplankton group, mainly  
302 associated with prymnesiophytes and pelagophytes, is relatively abundant (40-60% of the  
303 phytoplankton biomass) below 25 m depth to 180 m depth along the whole basin. The  
304 microphytoplankton pool, primarily associated with diatoms, is mainly observed in the  
305 southern part (45-75% of phytoplankton biomass) of the basin and were present in low  
306 concentrations (5-30% of the total phytoplankton biomass) in the other bioregions (not  
307 shown). These observations are consistent with the phytoplankton community size structure  
308 generally found in oligotrophic areas of the ocean (Bricaud et al., 2004; Ras et al., 2008;  
309 Organelli et al., 2011) and in the Red Sea (Pearman et al., 2016; Kheireddine et al., 2017). As  
310 this trend has been discussed in details in Kheireddine et al. (2017) where they studied the  
311 spatio-vertical distribution of phytoplankton pigments during similar time periods (Jazan and  
312 Duba-01 cruises) or season of sampling, the reader is referred to Kheireddine et al. (2017)  
313 and references therein for more information regarding the phytoplankton community size  
314 structure distributions in the Red Sea.

315 To examine variations in the shape of the phytoplankton absorption spectra of each  
316 phytoplankton size class (micro-, nano- and picophytoplankton), spectra are normalized to its  
317 mean value computed on the basis of all spectral values between 400 and 700 nm (Ciotti et  
318 al., 2002), and then grouped into the three size classes according to dominance (> 50%).

319 Differences between the average spectra for each dominant community size of phytoplankton  
320 can be observed (Fig. 5). For the picophytoplankton dominated spectra, the blue-to-red ratio  
321 is higher (2.35) than in nanophytoplankton (2.21) or microphytoplankton (2.16) dominated  
322 spectra. This result reflects a stronger package effect for microphytoplankton cells. This is in  
323 agreement with previous studies showing that variability in the spectral shape of  
324 phytoplankton absorption can be mainly attributed to changes in phytoplankton cell size  
325 (Sathyendranath et al., 2001; Ciotti et al., 2002; Lohrenz et al., 2003; Devred et al., 2006;  
326 Brewin et al., 2011, Wang et al., 2015). Note that the variations around the mean spectra of  
327 picophytoplankton-dominated absorption coefficients reflect a larger variability in the  
328 contribution of accessory pigments associated with smaller cells in comparison to those  
329 dominated by microphytoplankton (Fig. 5).

330 Ciotti et al. (2002) showed that in the surface layer, the variability in the spectral shape of  
331 phytoplankton absorption could be mainly explained by variation in cell size of the major  
332 phytoplankton group, thus enabling the development of a model to estimate a cell size  
333 parameter for phytoplankton (i.e.,  $S_f$ ). In the present study we estimated  $S_f$  for each  
334 phytoplankton absorption spectrum. The model of Ciotti et al. (2002) provides estimates of  
335 the dominant size of the phytoplankton community that can be compared to the relative  
336 proportions of pico-and microphytoplankton that are derived from phytoplankton diagnostic  
337 pigments (see methods; Vidussi et al., 2001; Bricaud et al., 2004; Uitz et al., 2006). The  
338 values of  $S_f$  vary from 0.12 to 0.98 (Fig. 6).

339  $S_f$  decreases when the contribution of microphytoplankton tends to increase (Fig. 6A), and  
340 increases with the proportion of picophytoplankton (Fig. 6B).  $S_f$  values are in good  
341 agreement with the relative proportion of picophytoplankton ( $R^2 = 0.63$ ,  $N=297$ ,  $p<0.0001$ )  
342 and microphytoplankton ( $R^2 = 0.44$ ,  $N=297$ ,  $p<0.0001$ ) despite the scattering observed  
343 around these relationships due to the photoacclimation of phytoplankton cells in depth. It is

344 well established that the proportion in accessory pigments vary along the water column  
345 (Bricaud et al., 1995; Organelli et al., 2011). For example, photoprotective pigments tend to a  
346 continuously decrease from the surface to deeper waters (Bricaud et al., 1995; Organelli et  
347 al., 2011; Kheireddine et al., 2017). This can significantly impact the shape of the  
348 phytoplankton absorption spectrum. As the model of Ciotti et al. (2002) was established for  
349 surface waters, its use for samples collected in depth could reveal photoacclimation responses  
350 to the vertical light variation. For example, for the same dominant cell size, the  $S_f$  values will  
351 tend to decrease if the phytoplankton community shows an increase in the concentrations of  
352 intracellular pigments caused, for instance, by photoacclimation (Ciotti et al., 1999).

353 The scattering observed around these relationships could also be partly explained by the fact  
354 that the phytoplankton community size is inferred by phytoplankton pigments that may be  
355 shared by several phytoplankton size class as mentioned previously. Overall, considering the  
356 assumptions in each approach, these results suggest that the absorption-based method  
357 developed by Ciotti et al. (2002) is consistent with the approach based on phytoplankton  
358 pigments.

359

360 *3.3 Specific phytoplankton absorption variability associated with changes in phytoplankton*  
361 *cell size and pigment composition---* As reported in previous studies (Bricaud et al., 1995,  
362 2004; Sathyendranath et al., 1996; Allali et al., 1997; Organelli et al., 2011; Ferreira et al.,  
363 2013),  $a_{ph}^*$  values clearly decrease with increasing [TChl  $a$ ] at 440 nm within the surface  
364 layer and among depths ( $R^2 = 0.61$ ,  $N=108$  and 297, respectively  $p<0.0001$ ), and slightly  
365 decrease at 676 nm only when all depth are considered ( $R^2 = 0.44$ ,  $N=297$ ,  $p<0.0001$ ) (Fig.  
366 7). A broad range of variation in [TChl  $a$ ] ( $0.008-1 \text{ mg}\cdot\text{m}^{-3}$ ) is associated with a narrower  
367 variability in  $a_{ph}^*(676)$  values ( $0.011-0.036 \text{ m}^{-1}$ ), whereas  $a_{ph}^*(440)$  values vary widely  
368 ( $0.029-0.152 \text{ m}^{-1}$ ). This observation is consistent with anterior studies in other oligotrophic

369 environments (Bouman et al., 2003; Perez et al., 2007; Organelli et al., 2011, Vijayan et al.,  
370 2014). The large variability observed in  $a_{ph}^*(440)$  and  $a_{ph}^*(676)$  for a given [TChl  $a$ ] can be  
371 attributed to changes in phytoplankton community size structure and pigment composition.  
372 The estimations of  $S_f$  may help in explaining the variability observed around the relationship  
373 between  $a_{ph}^*(\lambda)$  and [TChl  $a$ ] (Fig. 7). In general, the highest  $a_{ph}^*(\lambda)$  correspond to higher  $S_f$   
374 values, (smaller phytoplankton cell size), and the lower  $a_{ph}^*(\lambda)$  to the lower  $S_f$  values (larger  
375 phytoplankton cell size) (Fig. 7). This is in agreement with the literature (Stuart et al., 1998,  
376 Sathyendranath et al., 1999; Roy et al., 2011; Lohrenz et al., 2003; Brunelle et al., 2012;  
377 Ferreira et al., 2013; Wang et al., 2015) and reflects an increasing pigment packaging effect  
378 with increasing [TChl  $a$ ] and the dominance of larger phytoplankton cell sizes (Bricaud et al.,  
379 1995; Morel et al., 2006; Barlow et al., 2008). Nevertheless, some  $S_f$  values ( $0.2 < S_f < 0.4$ )  
380 above the surface layer are not consistent with the general assumption of increasing  $S_f$  with  
381 increasing  $a_{ph}^*(\lambda)$  (Fig. 7). These  $S_f$  values are observed for a large variation in [TChl  $a$ ] that  
382 does not conform with the general assumption that  $S_f$  values decrease with increasing [TChl  
383  $a$ ] (Ciotti et al., 2002) in response to photoacclimation processes (Fig. 7). Indeed, such  
384 inconsistencies can occur because  $S_f$  does not depend only on cell size. It reflects changes in  
385 pigment composition and package effect in response to changes in phytoplankton cell size  
386 associated with variations in intracellular pigment content from surface to deep waters that  
387 affect the spectral shape of phytoplankton absorption (Morel and Bricaud, 1981; Ciotti et al.,  
388 2002). For example, Ferreira et al. (2013) have shown that, for the same phytoplankton cell  
389 size,  $S_f$  values tend to decrease if phytoplankton community shows an increase in the  
390 concentrations of intracellular pigments due to photoacclimation (Ciotti et al., 1999). Thus,  
391 the parameter  $S_f$  cannot be used solely to study changes in phytoplankton cell size as  
392 variations in intracellular pigment content will also affect this parameter at a given cell size  
393 (Ciotti et al., 1999). This result is not surprising because it is known that the shape of the

394 phytoplankton spectrum is affected both by the cell size of the major phytoplankton groups  
395 and also by the intracellular pigment content (Morel and Bricaud, 1981).

396 *3.3.1 Impact of phytoplankton cell size on  $a_{ph}^*(440)$* ---The importance of phytoplankton cell  
397 size in determining  $a_{ph}^*(440)$  is displayed in Figure 8, in which  $a_{ph}^*(440)$  is plotted as a  
398 function of the relative proportion in micro- (Fig. 8A), nano- (Fig. 8B), picophytoplankton  
399 (Fig. 8C) and  $S_f$  (Fig. 8D). These relationships clearly show that the highest values of  
400  $a_{ph}^*(440)$  are found within the surface layer and are associated with small phytoplankton cell  
401 size (Fig. 8). We show that only 18% of the variability in  $a_{ph}^*(440)$  could be attributed to the  
402 microphytoplankton pool (mainly diatoms). The nanophytoplankton pool (prymnesiophytes  
403 and pelagophytes) can explain 28% of the variability in  $a_{ph}^*(440)$  and the picophytoplankton  
404 pool (*Synechococcus sp.* and *Prochlorococcus sp.*) plays a significant role in changing  
405  $a_{ph}^*(440)$ , controlling 44 % of the variability (Fig. 8A, B, C). While we show that the  $S_f$   
406 parameter is not only dependent on the phytoplankton size but also on the intracellular  
407 pigment content, we observe that  $S_f$  can explain 46% of the variation observed in  $a_{ph}^*(440)$   
408 (Fig. 8D). It is well established that phytoplankton functional types (PFTs) correspond to  
409 phytoplankton species with similar biogeochemical roles and physiological traits and that the  
410 phytoplankton size distribution is a major defining trait of PFTs (Le Quéré et al., 2005). The  
411 size distribution is also known as a major factor determining particle sinking rates and thus  
412 their role in carbon export (Eppley et al., 1967; McCave, 1975; Stemmann et al., 2004;  
413 Buesseler et al., 2007). Therefore, in our study, we can considered that pico-, nano- and  
414 microphytoplankton are three PFTs according to their size distribution. Thus, our results  
415 confirm that variations in  $a_{ph}(\lambda)$  can induce information about PFTs.

416 *3.3.2 Influence of changes in phytoplankton pigment composition on  $a_{ph}^*(440)$* ---To examine  
417 the impact of changes in phytoplankton pigments composition on  $a_{ph}^*(440)$ , we chose to  
418 group the accessory phytoplankton pigments into four distinct categories: (1) [TChl b]; (2)

419 [TChl c]; (3) PSC and (4) PPC. The variability in  $a_{ph}^*(440)$  as a function of the ratio of the  
420 four categories of accessory pigments, relatively to [TChl *a*], is examined (Fig. 9). The [TChl  
421 b]/[TChl *a*] ratio within the surface layer mainly varies in a narrow range from 0 to 0.25  
422 while a broad range of variation in  $a_{ph}^*(440)$  at depth can be observed (Fig. 9A), suggesting  
423 that changes in proportion of chlorophyll b and divinyl chlorophyll b play no significant role  
424 in the variability of  $a_{ph}^*(440)$ . The [TChl c]/[TChl *a*] ratio values vary from 0.03 to 0.35  
425 (Fig. 9B) in all depths and from 0.03 to 0.18 within the surface layer. The increase in the  
426 [TChl c]/[TChl *a*] ratio from 0 to 0.2 is accompanied by decreasing  $a_{ph}^*(440)$  values (Fig.  
427 9B). Some [TChl c]/[TChl *a*] values deviate from this trend, notably measurements collected  
428 above the surface layer, for which the ratio is higher than 0.2. We show that only 24% of the  
429 variability in  $a_{ph}^*(440)$  could be associated with the [TChl c]/[TChl *a*] ratio (Fig. 9B). The  
430 [PSC]/[TChl *a*] ratio mainly varies from 0.2 to 0.5 within as well above the surface while  
431  $a_{ph}^*(440)$  show a more broad range of variations (Fig. 9C). The points where [PSC]/[TChl *a*]  
432 ratio values are higher than 0.5 are the samples collected in the deeper layer. In many studies,  
433 it has been shown that photosynthetic accessory pigment concentrations can increase with  
434 increasing depth in response to lower light levels in deep waters (Bricaud and Stramski,  
435 1990; Kirk, 1994; Majchrowski & Ostrowska, 2000). About 13% of the variability in  
436  $a_{ph}^*(440)$  is attributed to the [PSC]/[TChl *a*] ratio. Unlike the [PSC]/[TChl *a*] ratio, the  
437 [PPC]/[TChl *a*] ratio (mainly associated with zeaxanthin/[TChl *a*] in this study) varies in a  
438 broad range from 0 to 1.2 (Fig. 9D). The highest [PPC]/[TChl *a*] values associated with  
439 smaller phytoplankton cell size ( $S_f$  varying from 0.6 to 1) are observed within the surface  
440 (Fig. 9D), and this is consistent with those observed in other oligotrophic regions  
441 characterized by high light and low nutrient conditions (Bricaud et al., 1995, 2004; Stuart et  
442 al., 1998, 2004, Barlow et al., 2004; Sathyendranath et al., 2005; Organelli et al., 2011).  
443 Stuart et al. (2004) suggested that phytoplankton cells adapt to changes in light conditions

444 both by increasing their intracellular pigment content, and by changing the ratio of accessory  
445 pigments. They noted that high concentrations of photoprotective pigments are a  
446 characteristic feature of surface oligotrophic waters and can also be related to cell size. We  
447 observe that an increase in the  $[PPC]/[TChl\ a]$  ratio is accompanied by an increase in  
448  $a_{ph}^*(440)$ . About 51% of the variability in  $a_{ph}^*(440)$  is due to the direct combined effect of  
449 the  $[PPC]/[TChl\ a]$  ratio and phytoplankton cell size, with the strongest contribution coming  
450 from  $S_f$ , which explains 46% of the variability (Fig. 8D and 9D).

451 Summarizing the results in Figure 8 and 9, we notice that variations in phytoplankton cell  
452 size as well as variations in  $[PPC]/[TChl\ a]$  ratio are the main factors responsible for the  
453 variability in  $a_{ph}^*(440)$ .

454 Figure 10 displays variations of SI and  $[PPC]/[TChl\ a]$  ratio as a function of  $[TChl\ a]$  for  
455 diverse areas of the global ocean. As expected, the SI values increase with increasing  $[TChl\ a]$   
456 and are within the ranges of SI values found in various regions of the world's ocean,  
457 although these measurements were restricted to the surface layer (Bricaud et al., 2004, 2010)  
458 (Fig. 10A). On average, the phytoplankton community size structure seems to be slightly  
459 smaller than those in the Mediterranean Sea and slightly larger than those in the Atlantic  
460 Ocean (Fig. 10B). As reported in previous studies, the  $[PPC]/[TChl\ a]$  ratio decrease  
461 according to depth (higher values in surface water) in inverse relation to  $[TChl\ a]$  (Bricaud et  
462 al., 2004; Organelli et al., 2011). A group of low  $[PPC]/[TChl\ a]$  values ( $> 0.2$ ) is also  
463 identified in the deeper layer and appears to not be related to  $[TChl\ a]$  (Fig. 10C) as reported  
464 in the Mediterranean Sea by Organelli et al. (2011). As for SI values, the  $[PPC]/[TChl\ a]$   
465 values are within the range of those observed in the other areas of the global ocean (Bricaud  
466 et al., 2004, 2010). On average, the  $[PPC]/[TChl\ a]$  values are slightly higher than those  
467 observed in the Mediterranean Sea and in the Atlantic Ocean (Fig. 10D). Therefore, the  
468 differences in average phytoplankton cell size and  $[PPC]/[TChl\ a]$  values can affect the

469 variability in phytoplankton absorption and partially explain the higher  $a_{ph}(\lambda)$  values at a  
470 given [TChl *a*] observed in Red Sea waters compared to other areas of the global ocean.  
471 Indeed, our results indicate that phytoplankton cell size associated to changes in PPC  
472 pigments are rather well correlated to  $a_{ph}^*(\lambda)$ . The trend of decreasing cell size is associated  
473 to an increase in [PPC]/[TChl *a*] ratio and  $a_{ph}^*(\lambda)$  which is consistent with the expectation of  
474 higher relative proportions of accessory pigments when the proportion of smaller  
475 phytoplankton cells increases (Bricaud et al., 1995; Dupouy et al., 1997; Stuart et al., 1998,  
476 2004). These results reflect the changes in phytoplankton community size structure in  
477 response to the environmental conditions encountered in the Red Sea, which is characterized  
478 as an oligotrophic region with high light and low nutrient concentrations. *Prochlorococcus*  
479 and *Synechococcus* are known to be the most abundant organisms in highly stratified and  
480 nutrient depleted oceans between 45° N and 45° S (Olson et al., 1990; Partensky et al., 1999;  
481 Johnson et al., 2006; Al-Najjar et al., 2007; Shibl et al., 2014, 2016; Pearman et al., 2016;  
482 Kheireddine et al., 2017). They correspond to phytoplankton of small size associated to a  
483 high proportion in PPC pigments (mainly zeaxanthin pigment) which is consistent with our  
484 observations in this study.

485

486 *3.4 Influence of environmental parameters on  $a_{ph}^*(440)$* ---Recently, Kheireddine et al. (2017)  
487 have suggested that latitudinal changes in physico-chemical variables, such as temperature  
488 and salinity, may influence phytoplankton community size structure in Red Sea waters.  
489 Temperature and salinity are known to be important environmental parameters that influence  
490 phytoplankton community structure (Blanchot et al., 1992; Vaultot & Partensky, 1992;  
491 Campbell & Vaultot, 1993; Veldhuis & Kraay, 1993; Moore et al., 1995; Ahel et al., 1996;  
492 Graziano et al., 1996; Bouman et al., 2003, 2005; Lohrenz et al., 2003; Platt et al., 2005;  
493 Loureiro et al., 2006; Hulyal and Kaliwal, 2009; Fehling et al., 2012). Thus, the variability

494 around the relationship between  $a_{ph}^*(\lambda)$  and [TChl *a*] found in Red Sea waters might also be  
495 associated with changes in physico-chemical conditions within the basin. In Figure 11,  
496  $a_{ph}^*(440)$ , temperature (T °C) and salinity are plotted as a function of the latitude. The spatial  
497 distributions of  $a_{ph}^*(440)$  and T °C showed similar latitudinal variations (Fig. 11A, B)  
498 although no strong correlation is observed between  $a_{ph}^*(440)$  and T °C (not shown). Both  
499 parameters tend to increase from the SRS to the CRS and then to decrease from the CRS to  
500 the NRS (Fig. 11A, B). The highest values of  $a_{ph}^*(440)$  ( $> 0.10 \text{ m}^2.\text{mg}^{-1}$ ) are, generally,  
501 consistent with the highest values of T °C ( $> 30^\circ\text{C}$ ) and high values of salinity (39-40.5) in  
502 the CRS which is also the area where the abundance of picophytoplankton (mainly  
503 *Prochlorococcus* and *Synechococcus sp.*) is the highest ( $> 60 \%$  of the total phytoplankton  
504 biomass) (Fig. 11A, B, C). This finding is consistent with observations in the Red Sea [Shibl  
505 *et al.*, 2016; Kheiredine *et al.*, 2017] and from other oligotrophic regions (Partensky *et al.*,  
506 1999; Bouman *et al.*, 2006; Zinzer *et al.*, 2007) where variations in temperature and salinity  
507 influence the distribution of *Prochlorococcus* and *Synechococcus*. The lowest values of  
508  $a_{ph}^*(440)$  are found in the two extremities of the basin where the proportions in bigger cells  
509 to total phytoplankton biomass are higher than in the rest of the basin, as shown by  
510 Kheireddine *et al.* (2017) based on HPLC measurements collected at the same period or  
511 season (Fig. 11A).

512

#### 513 **4. Conclusion**

514 We have shown that the absorption coefficients of phytoplankton and non-algal particles  
515 measured in the Red Sea display a large variability associated with changes in environmental  
516 conditions. This variability can affect the proportion of non-algal particles and the  
517 phytoplankton community size structure. The cell size parameter and the proportion in the  
518 [PPC]/[TChl *a*] ratio (mainly associated with zeaxanthin pigment) both play a key role in the

519 variability observed in  $a_{ph}^*(440)$  (46 % and 51 %, respectively). Furthermore, values in  $a_{ph}(\lambda)$   
520 measured in this study are slightly higher for a given [TChl *a*] value than those estimated  
521 from existing global relationships established for oligotrophic waters (Bricaud et al., 1995,  
522 2004; Devred et al., 2006; Brewin et al., 2011), as well as for the Red Sea (Brewin et al.,  
523 2015) within the first optical depth and among depths. These higher coefficients are  
524 attributed to a higher relative proportion of PPC pigments, and smaller cell size. The  
525  $a_{nap}(440)$  coefficients are also higher than those previously observed in oligotrophic waters  
526 when [TChl *a*] < 0.1 mg.m<sup>-3</sup> and lower when [TChl *a*] > 0.1 mg.m<sup>-3</sup>. In the clearest waters  
527 ([TChl *a*] < 0.1 mg.m<sup>-3</sup>), the contribution of non-algal particles to total particulate absorption  
528 was found to be higher than expected, suggesting the presence of more numerous inorganic  
529 (dusts) and/or colored non-algal particles in these waters. Thus, in situ measurements to  
530 quantify and identify these particles in the Red Sea waters including all environmental  
531 conditions will be required.

532 It is known that some existing methods used to retrieve chlorophyll *a* needs to derive  $a_{ph}(\lambda)$   
533 from total light absorption and then estimate the chlorophyll *a* based on its relationship with  
534  $a_{ph}(\lambda)$  (Garver and Siegel, 1997; Morel and Maritorena, 2001; Maritorena et al., 2002; Morel  
535 et al., 2006). This relationship is essential for development of Red Sea algorithms for  
536 estimating the diffuse attenuation coefficient of downward irradiance and ocean primary  
537 production. Therefore, this study reveals the way to the refinement of ocean colour  
538 algorithms to more accurately retrieve biogeochemical parameters (chlorophyll *a*  
539 concentration, primary production, PFTs, etc.) in Red Sea waters.

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## Figures legends

**Figure 1:** Map showing the locations of stations sampled during 5 cruises between October 2014 and January 2016 in the Red Sea (see Table 1). The delineation of the Northern Red Sea (NRS), the Central Red Sea (CRS) and the Southern Red Sea (SRS) is indicated on the map.

Map Produced using ArcGIS.

**Figure 2:** Variations of the particulate absorption coefficients at 440 nm,  $a_p(440)$  (A), and at 676 nm,  $a_p(676)$  (B), as a function of [TChl  $a$ ]. The black and red solid lines represent the best fit (power law function) between  $a_p(\lambda)$  and [TChl  $a$ ] in all depth and within the first optical depth, respectively. The relationships from Bricaud et al. (1998) (dashed line) and Brewin et al. (2015) (dotted line) are displayed. Variations of the phytoplankton absorption coefficients at 440 nm,  $a_{ph}(440)$  (C), and at 676 nm,  $a_{ph}(676)$  (D), as a function of [TChl  $a$ ]. The black and red solid lines represent the best fit (power law function) between  $a_{ph}(\lambda)$  and [TChl  $a$ ] in all depth and within the first optical depth, respectively. The relationships from Bricaud et al. (1995) (dashed-dotted line), Bricaud et al. (2004) (dashed line), Devred et al. (2006) (red dashed line) and Brewin et al. (2011) (blue dashed line) are displayed. The version of  $a_{ph}(676)$  as a function of [TChl  $a$ ] was not provided by Bricaud et al. (2004). The relationships of Devred et al. (2006), Brewin et al. (2011, 2015) are for 443 nm and 670 nm rather than 440 and 676 nm.

**Figure 3:** Variations of the absorption coefficient of non-algal particles at 440 nm,  $a_{nap}(440)$ , as a function of [TChl  $a$ ] (A). The relationship provided by Bricaud et al. (2010) is displayed. Variations the non-algal to particulate absorption ratio,  $a_{nap}/a_p$  at 440 nm as a function of [TChl  $a$ ].

**Figure 4:** Relative proportions (%) of microphytoplankton, nanophytoplankton and picophytoplankton estimated from the relative concentrations of some diagnostic pigments (equations (1)-(3)). For each sample the relative contribution of a size class to total biomass can be read on the corresponding axis as indicated.

**Figure 5:** Average of phytoplankton absorption spectra normalized by the average value of absorption between 400 and 700 nm shown separately for picophytoplankton-dominated samples (blue solid line), nanophytoplankton-dominated samples (red solid line) and microphytoplankton-dominated samples (green solid line). For each group of data, the mean normalized spectrum (solid line) and the standard deviation (dashed area) are displayed.

**Figure 6:** Variations of the cell size parameter ( $S_f$ ) derived from the shape of the phytoplankton absorption spectrum as described by Ciotti et al. (2002) as a function of the proportions (%) of microphytoplankton (A) and picophytoplankton (B) estimated from the relative concentrations of some diagnostic pigments (equations (1)-(4)). The coefficient of determination was determined on the basis of all data in the form of a power law (A) and of a linear regression (B).

**Figure 7:** Variations of Chlorophyll specific phytoplankton absorption coefficients at 440 nm,  $a_{ph}(440)^*$  (A), and at 676 nm,  $a_{ph}(676)^*$  (B), as a function of [TChl *a*]. Samples are grouped for different ranges of cell size parameter ( $S_f$ ) as indicated in the legend. The coefficient of determination was determined on the basis of all data in the form of a power law.

**Figure 8:** Variations of Chlorophyll specific phytoplankton absorption coefficients at 440 nm,  $a_{ph}(440)^*$ , as a function of the proportions (%) of microphytoplankton (A), nanophytoplankton (B), picophytoplankton (C) estimated from the relative concentrations of some diagnostic pigments (equations (1)-(3)) and the cell size parameter ( $S_f$ ) (D) derived from the shape of the phytoplankton absorption spectrum as described by Ciotti et al. [2002]. Samples are grouped for different ranges of cell size parameter ( $S_f$ ) as indicated in the legend.

The coefficient of determination was determined on the basis of all data in the form of a power law (A, B) and of a linear regression (C, D).

**Figure 9:** Variations of Chlorophyll specific phytoplankton absorption coefficients at 440 nm,  $a_{ph(440)^*}$ , as a function of the accessory pigments to [TChl *a*] ratios: the ratio of total chlorophyll b [TChl b] to [TChl *a*] (A); the ratio of total chlorophyll c [TChl c] to [TChl *a*] (B); the ratio of photosynthetic carotenoids PSC to [TChl *a*] (C) and the ratio of photoprotective carotenoids PPC to [TChl *a*] (D). Samples are grouped for different ranges of cell size parameter ( $S_f$ ) as indicated in the legend. The coefficient of determination was determined on the basis of all data in the form of a power law (B, C) and of a linear regression (C, D).

**Figure 10:** Variations of the size index (SI) estimated from the relative concentrations of some diagnostic pigments (equations (1)-(5)) (A) as a function of [TChl *a*] and average (filled circle)  $\pm$  standard deviation (empty circle) SI values (B); variations of the PPC/ [TChl *a*] ratios as a function of [TChl *a*] (C) and average (filled circle)  $\pm$  standard deviation (empty circle) PPC/ [TChl *a*] values (F) for various areas of the global ocean. Data collected during cruises other than those performed in the Red Sea are taken from Bricaud et al. (2004, 2010).

**Figure 11:** Latitudinal variations of Chlorophyll specific phytoplankton absorption coefficients at 440 nm,  $a_{ph(440)^*}$  (A), Temperature (B) and salinity (C). The delineation of the Northern Red Sea (NRS), the Central Red Sea (CRS) and the Southern Red Sea (SRS) is indicated on each panel. Samples are grouped according to the phytoplankton dominated group (mico-, nano- or picophytoplankton) as indicated in the legend.



Figure 1

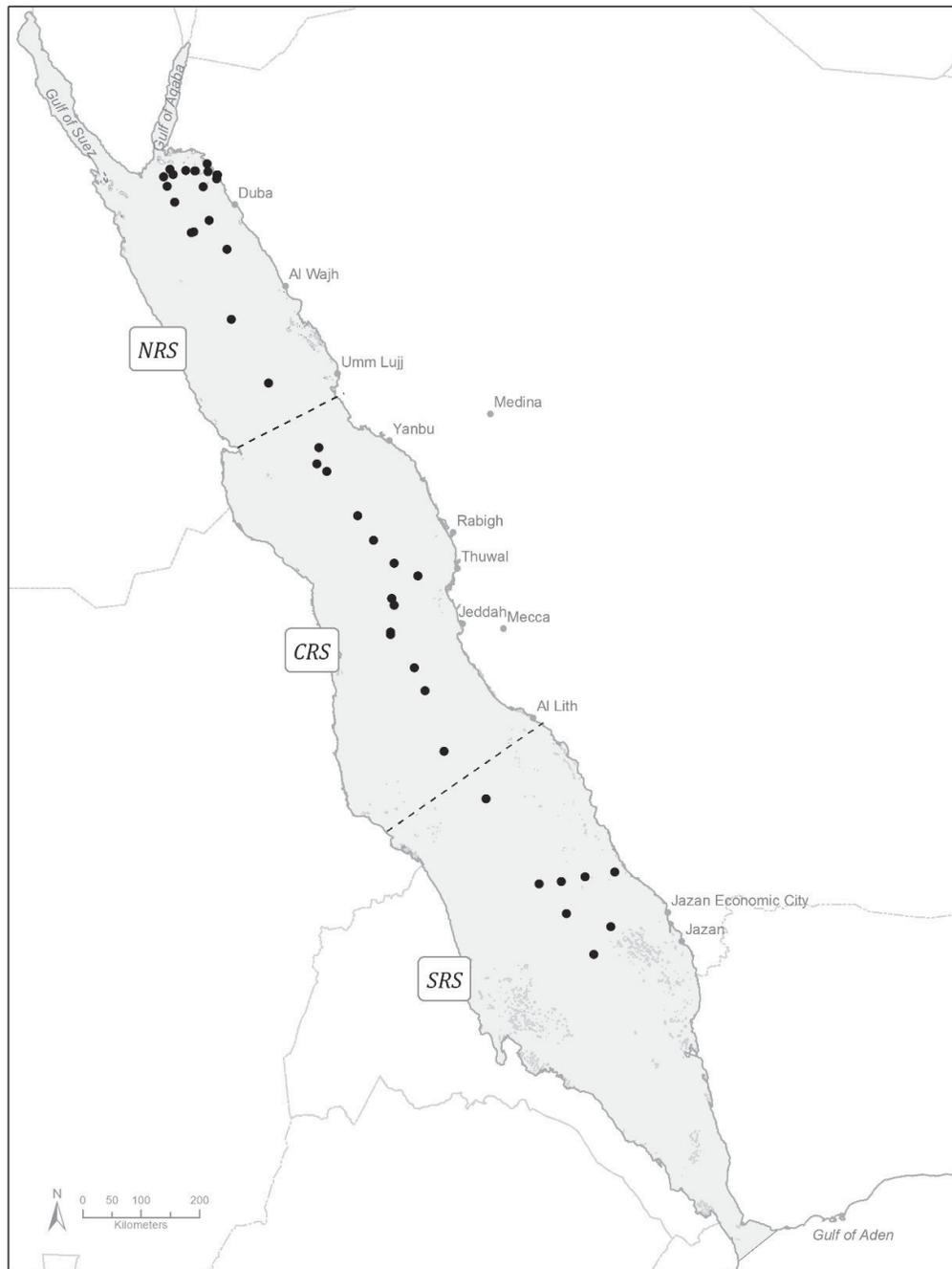


Figure 2

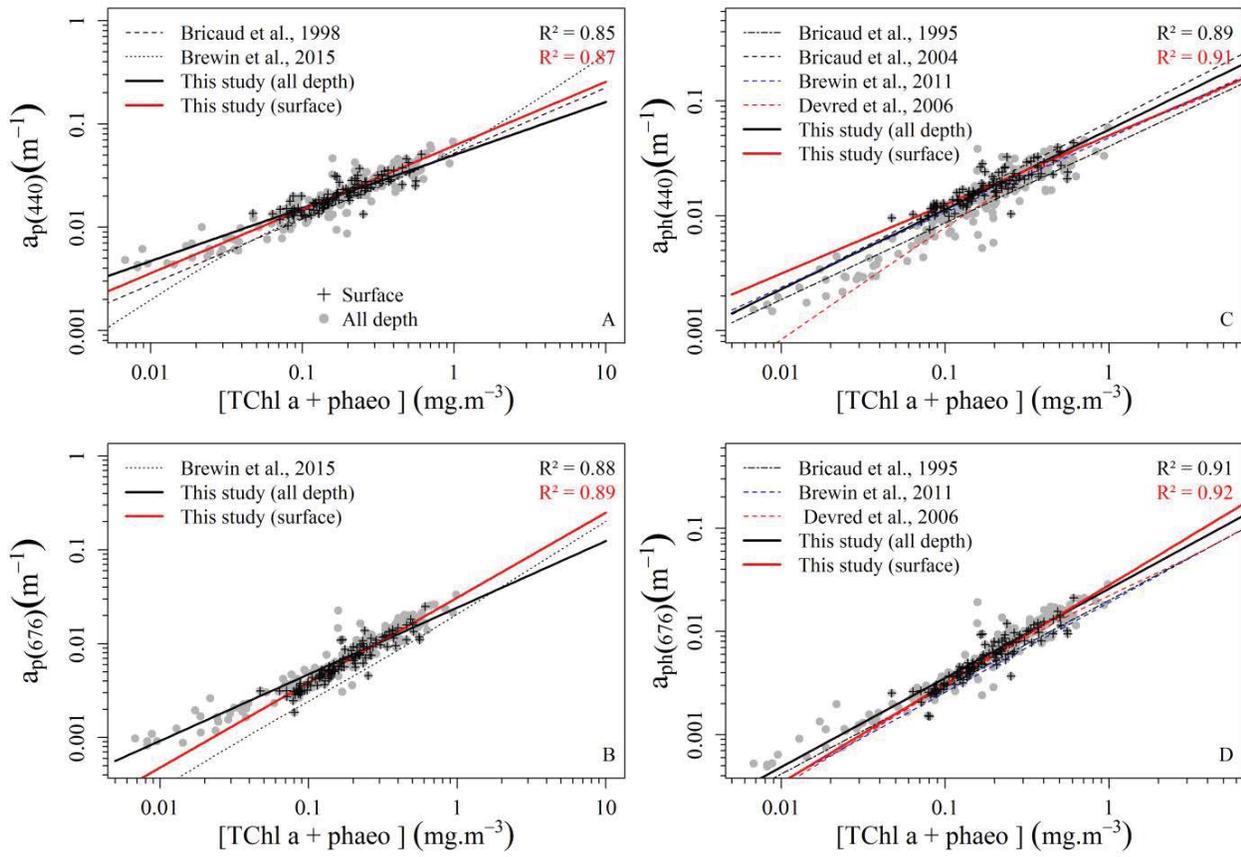


Figure 3

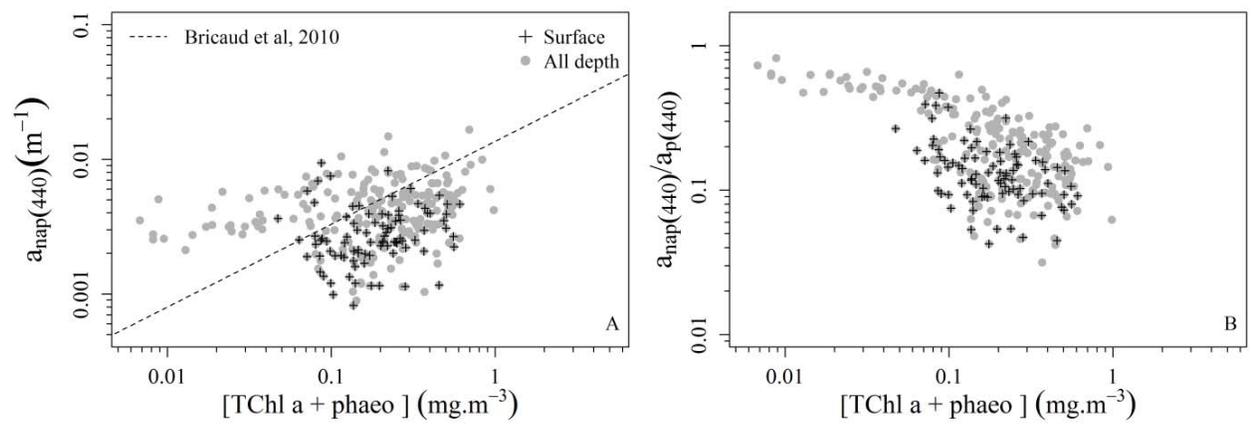


Figure 4

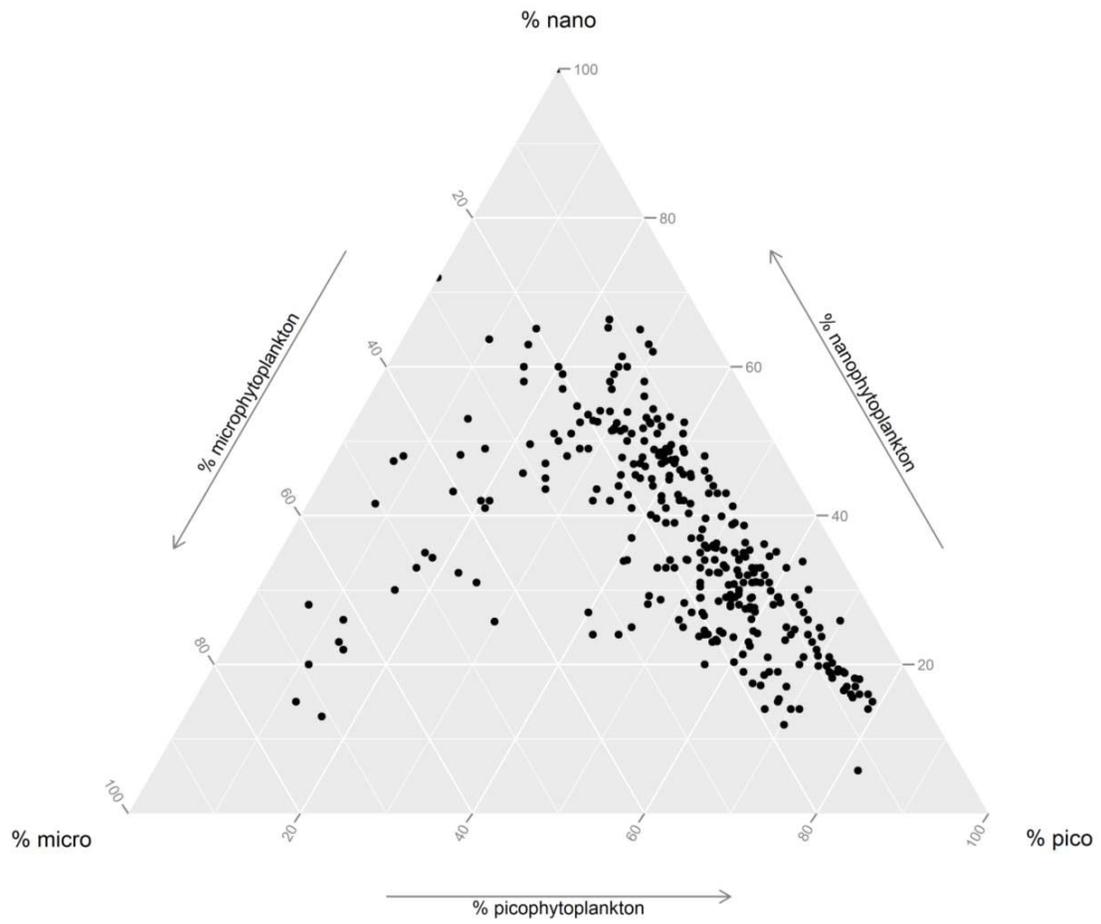


Figure 5

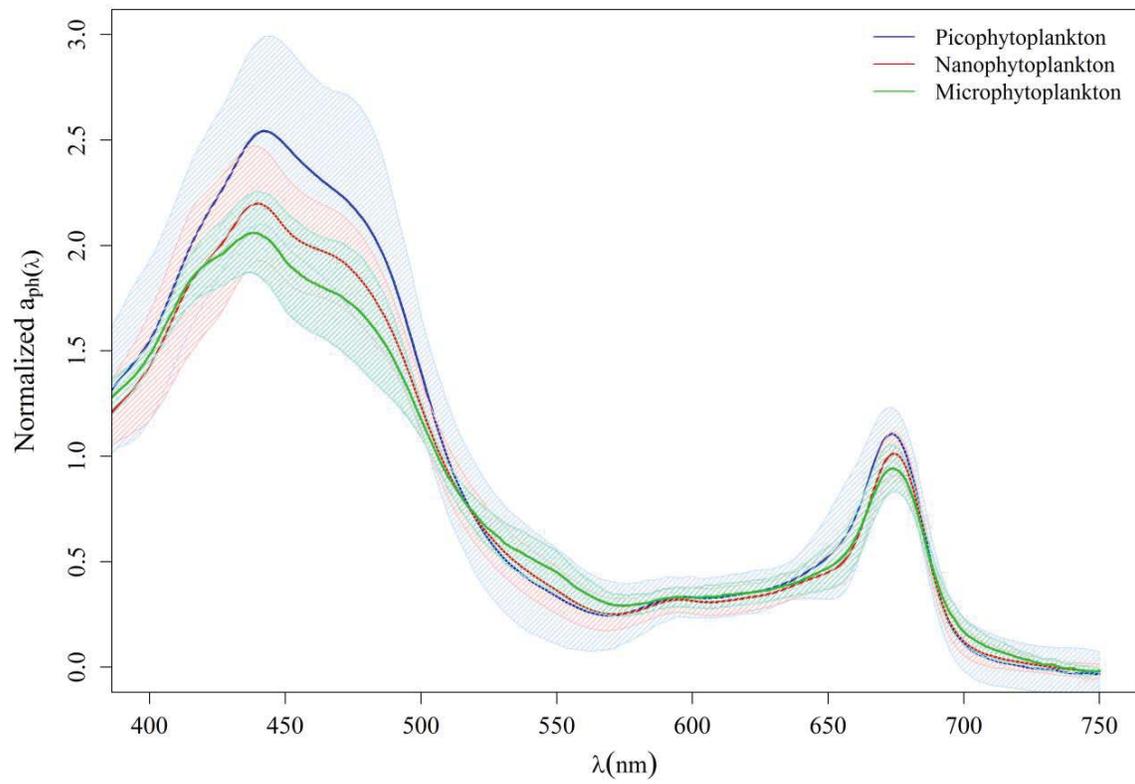


Figure 6

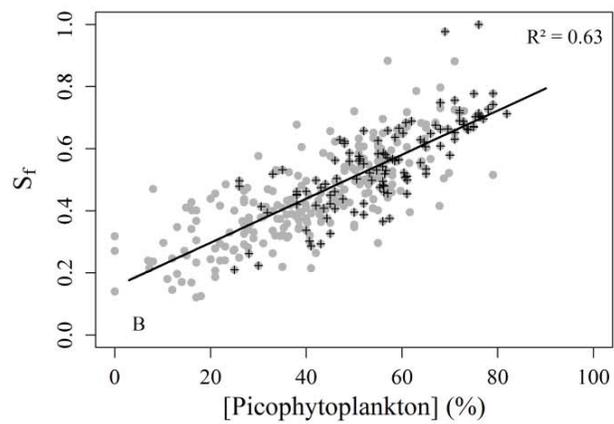
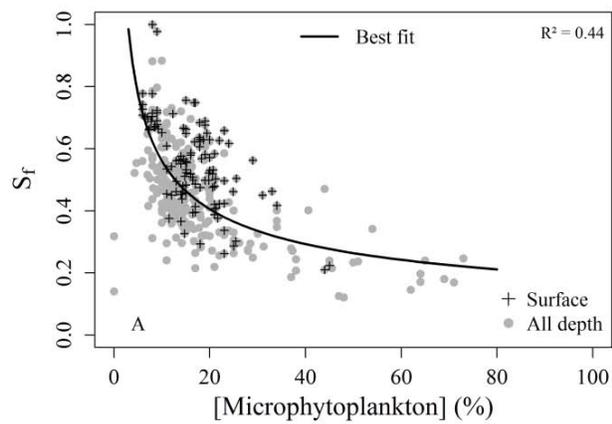


Figure 7

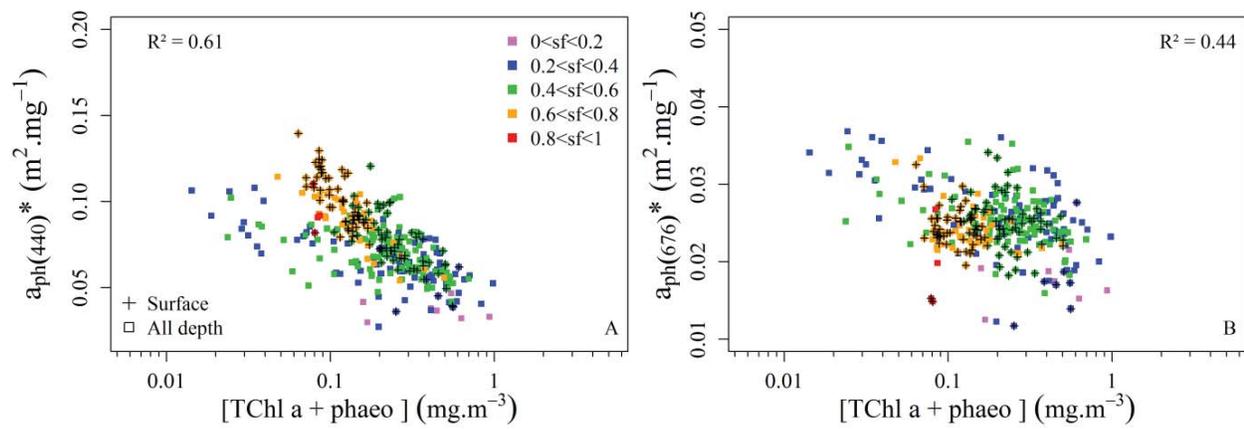


Figure 8

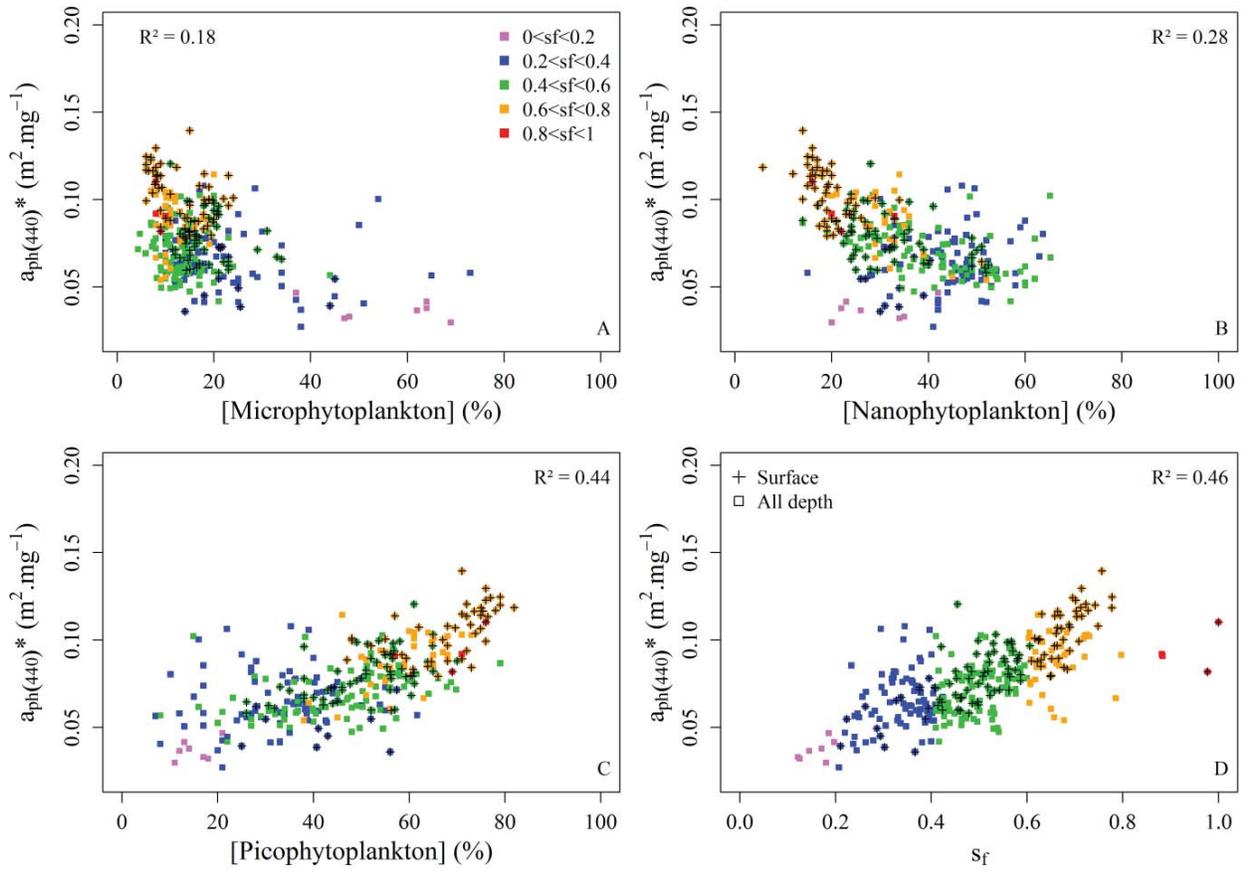


Figure 9

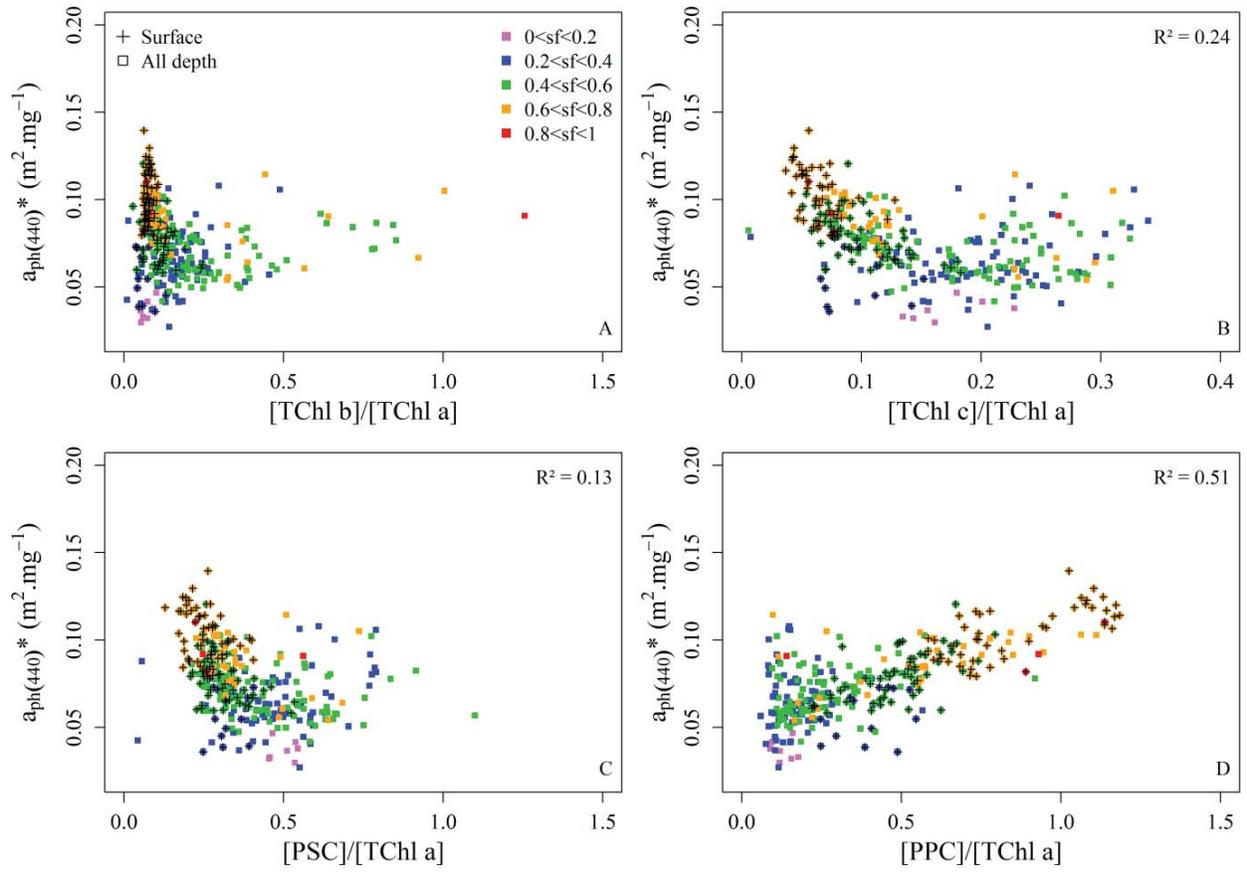


Figure 10

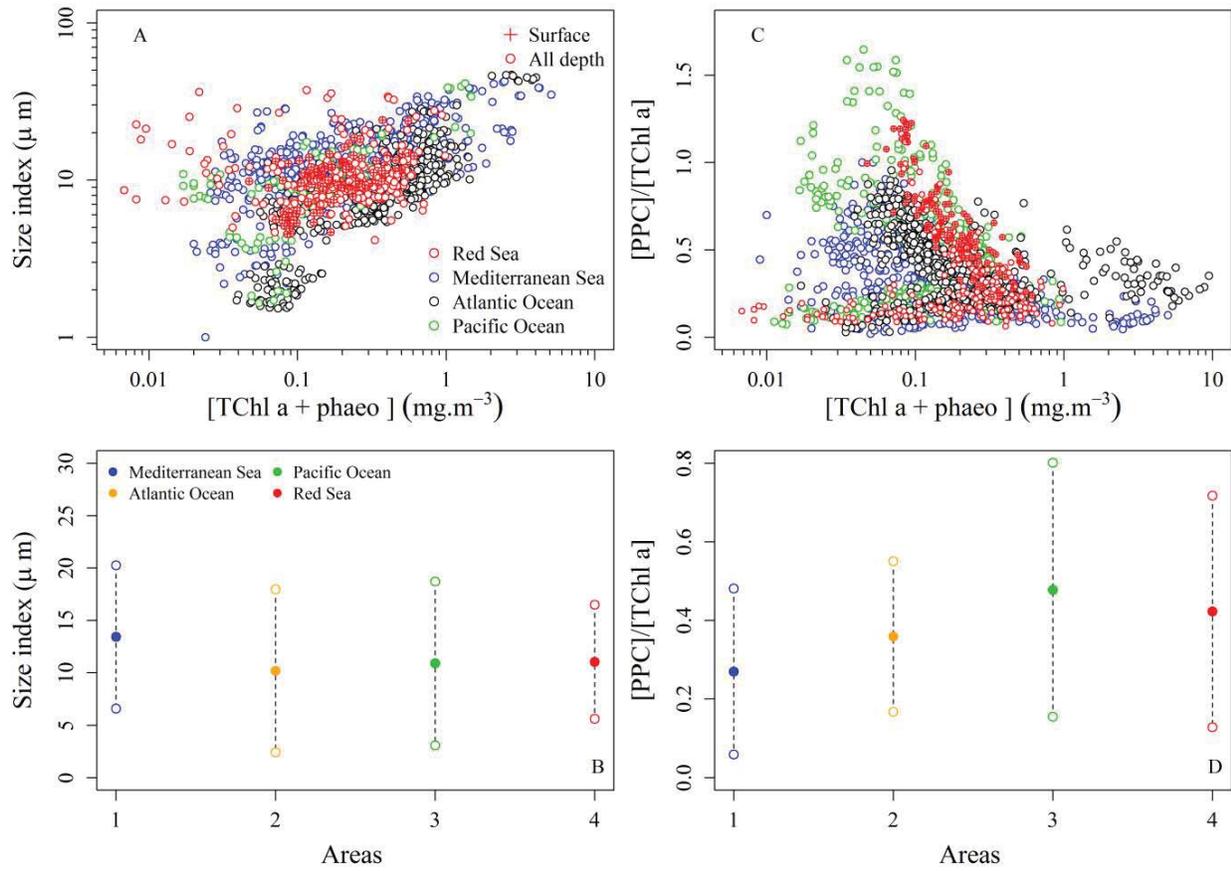
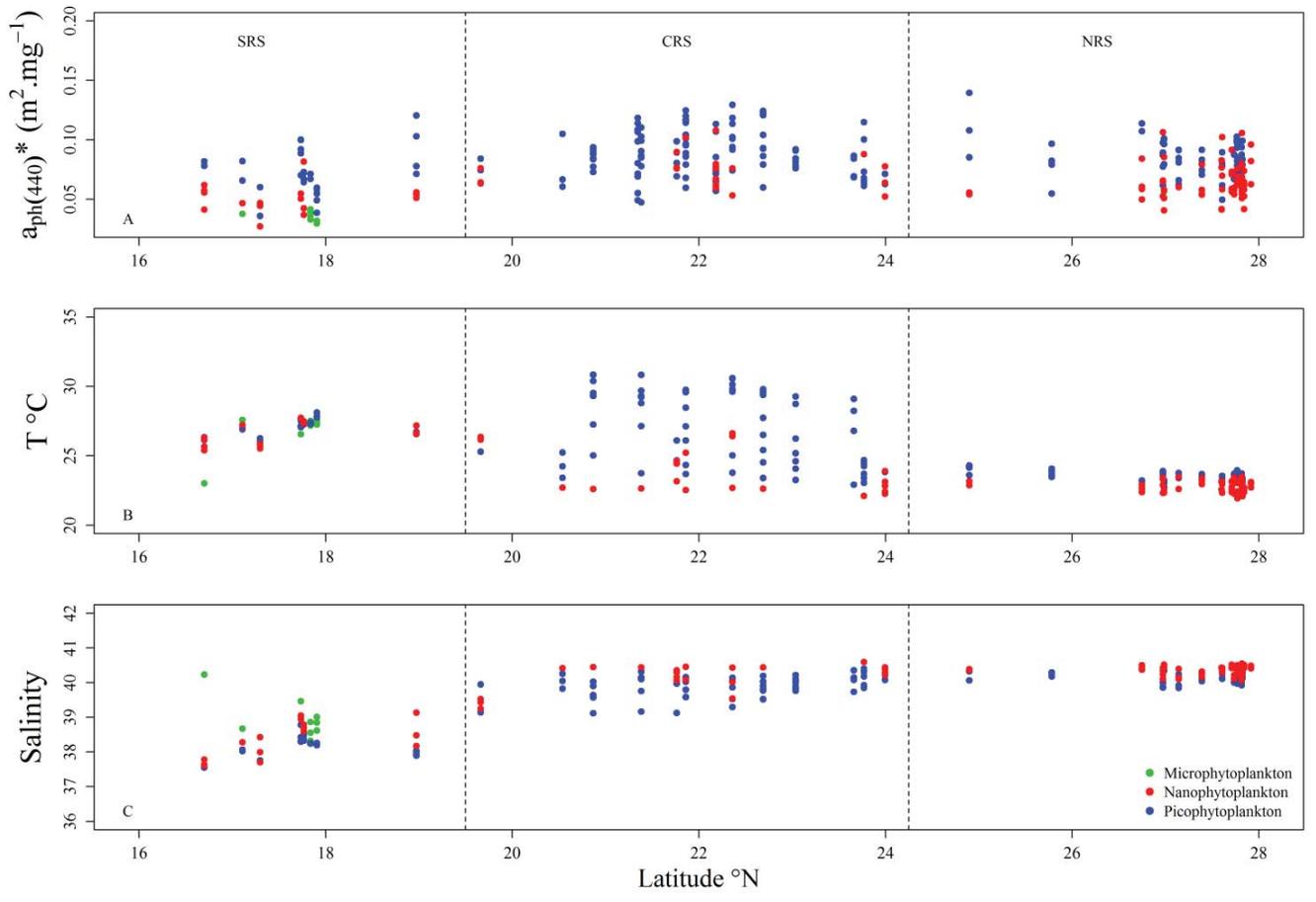


Figure 11



## Tables

Table 1: Location and dates of the 5 sampling cruises in the Red Sea.

Campaign	Platform	Location	Abbreviation	Period	Number of stations
Nutrient cycle cruise 1	RV <i>Thuwal</i>	Central Red Sea	CRS-01	16-28 Oct. 2014	8
Jazan cruise	RV <i>Thuwal</i>	Southern Red Sea	Jazan	8 -21 Feb. 2015	8
Duba cruise 1	RV <i>Thuwal</i>	Northern Red Sea	Duba-01	17- 28 Apr. 2015	10
Duba cruise 2	RV <i>Thuwal</i>	Northern Red Sea	Duba-02	21 Mar. to 02 Apr. 2016	8
Nutrient cycle cruise 4	RV <i>Thuwal</i>	Central Red Sea	CRS-04	17-28 Jan. 2016	6
Total					40

Table 2: Results from the regression<sup>a</sup> analysis between  $a_p(440)$ ,  $a_p(676)$ ,  $a_{ph}(440)$ ,  $a_{ph}(676)$  and [TChl *a*] among all depths and within the surface layer presented in Figure 2

		$a_p(440)$	$a_p(676)$	$a_{ph}(440)$	$a_{ph}(676)$
All depths	A	0.05	0.024	0.056	0.026
	B	0.51	0.71	0.70	0.87
	R <sup>2</sup>	0.85	0.88	0.89	0.91
	N			297	
Surface	A	0.062	0.031	0.050	0.028
	B	0.62	0.90	0.60	0.96
	R <sup>2</sup>	0.87	0.89	0.91	0.92
	N			108	

<sup>a</sup> The regression formula is in the form of a power law as  $X = A [TChl\ a]^B$  where A and B are the best fit parameters. The determination coefficient, R<sup>2</sup>, and the number of data, N, are also shown. All regressions are significant for  $p < 0.0001$ .

Figure 1.

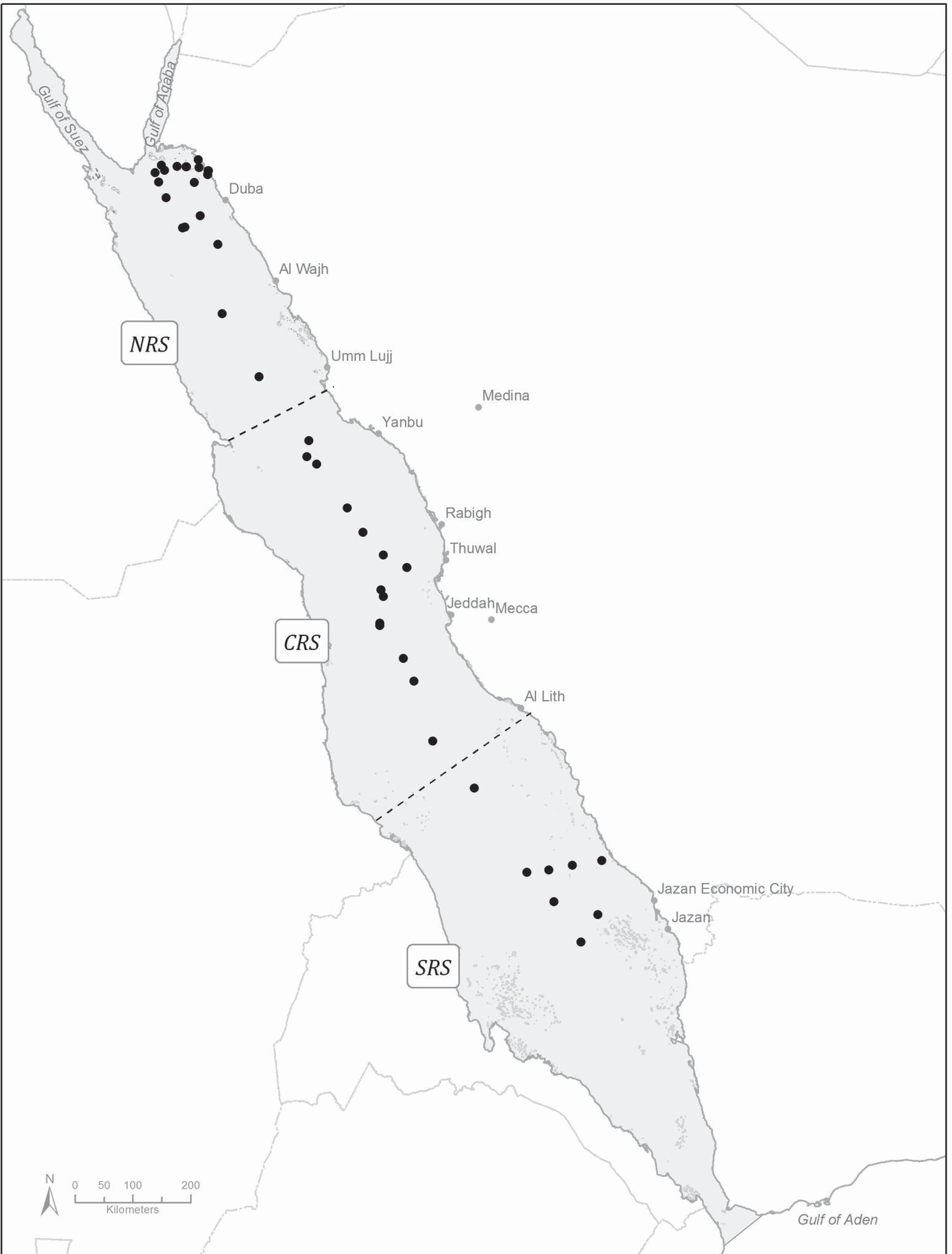


Figure 2.

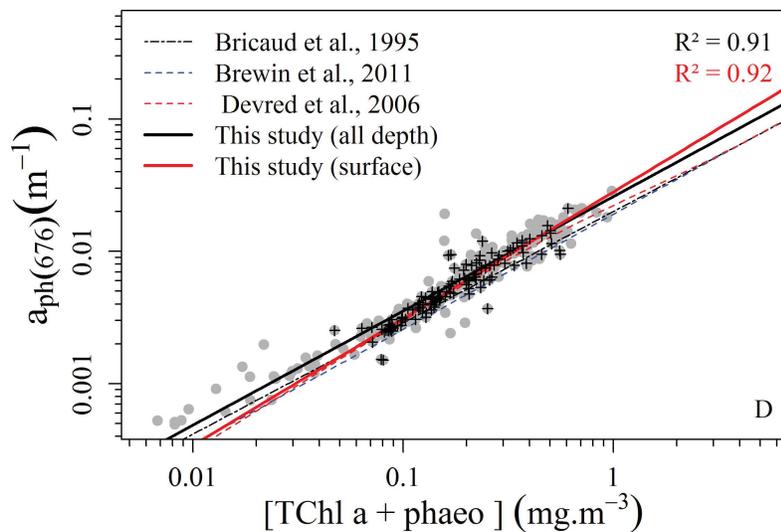
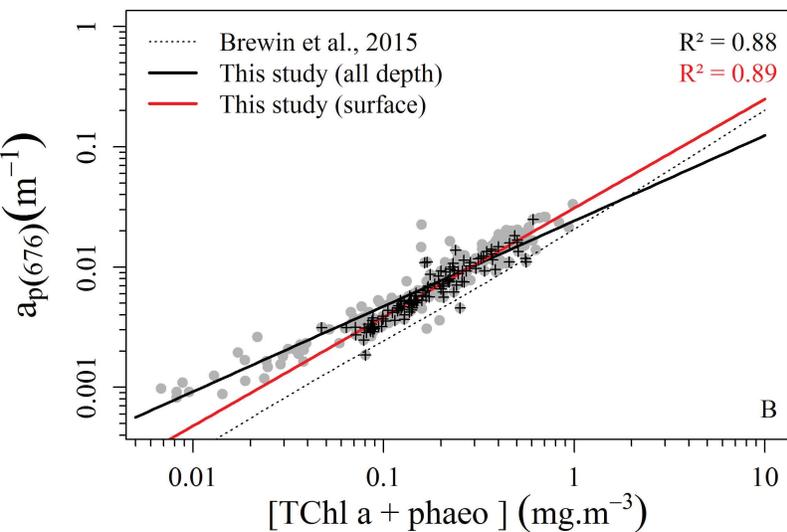
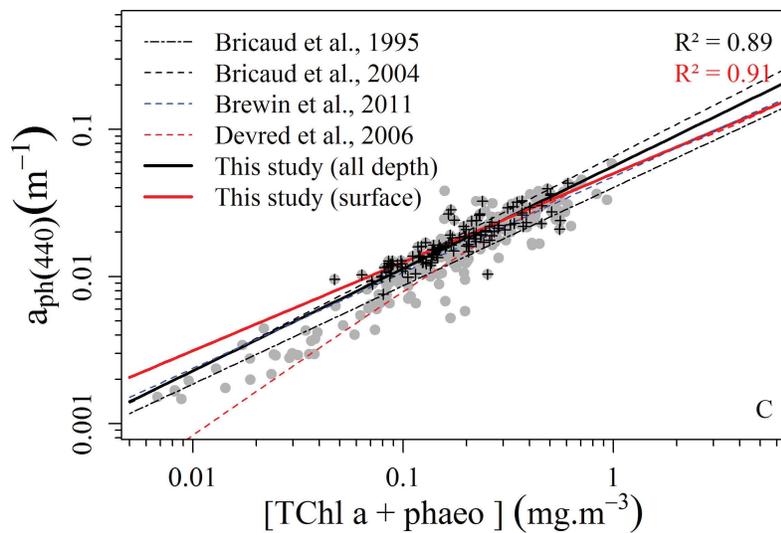
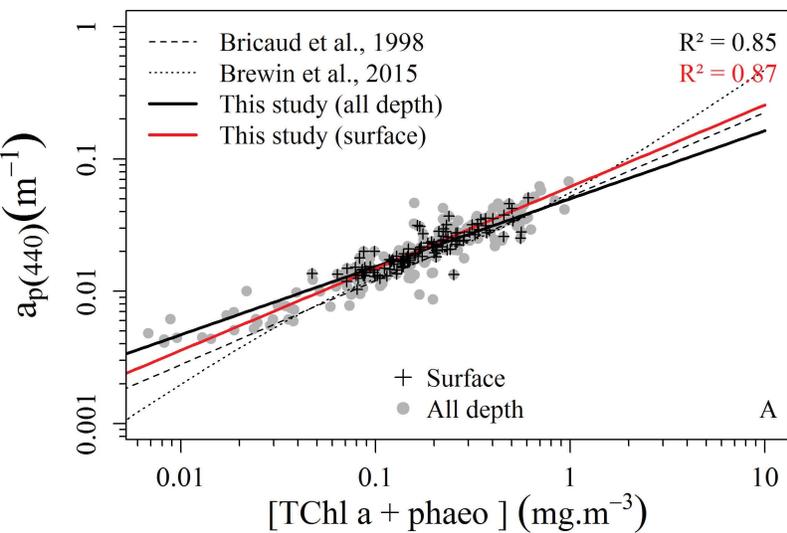


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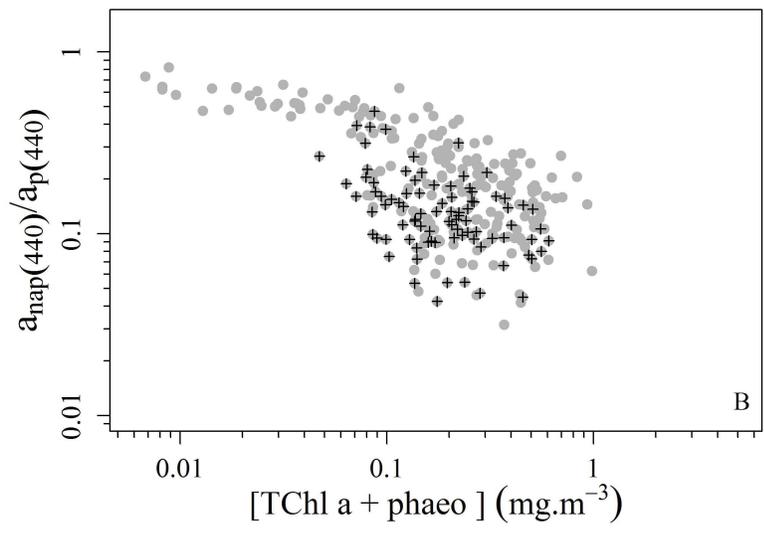
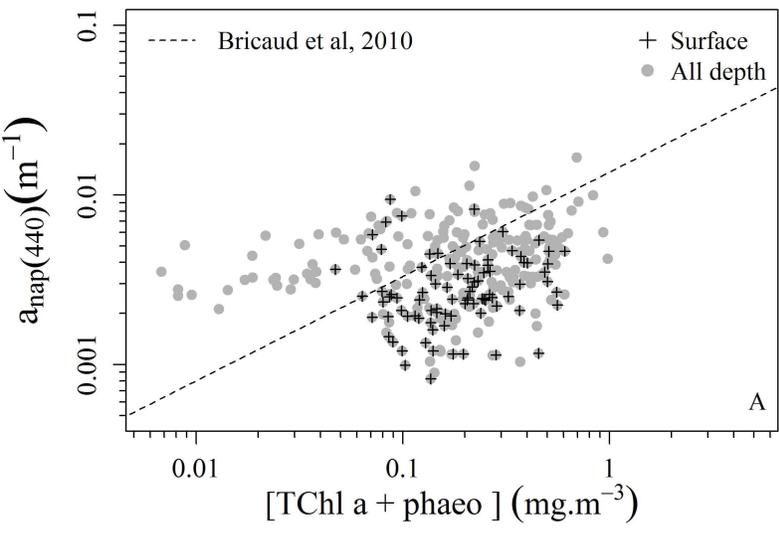


Figure 4.

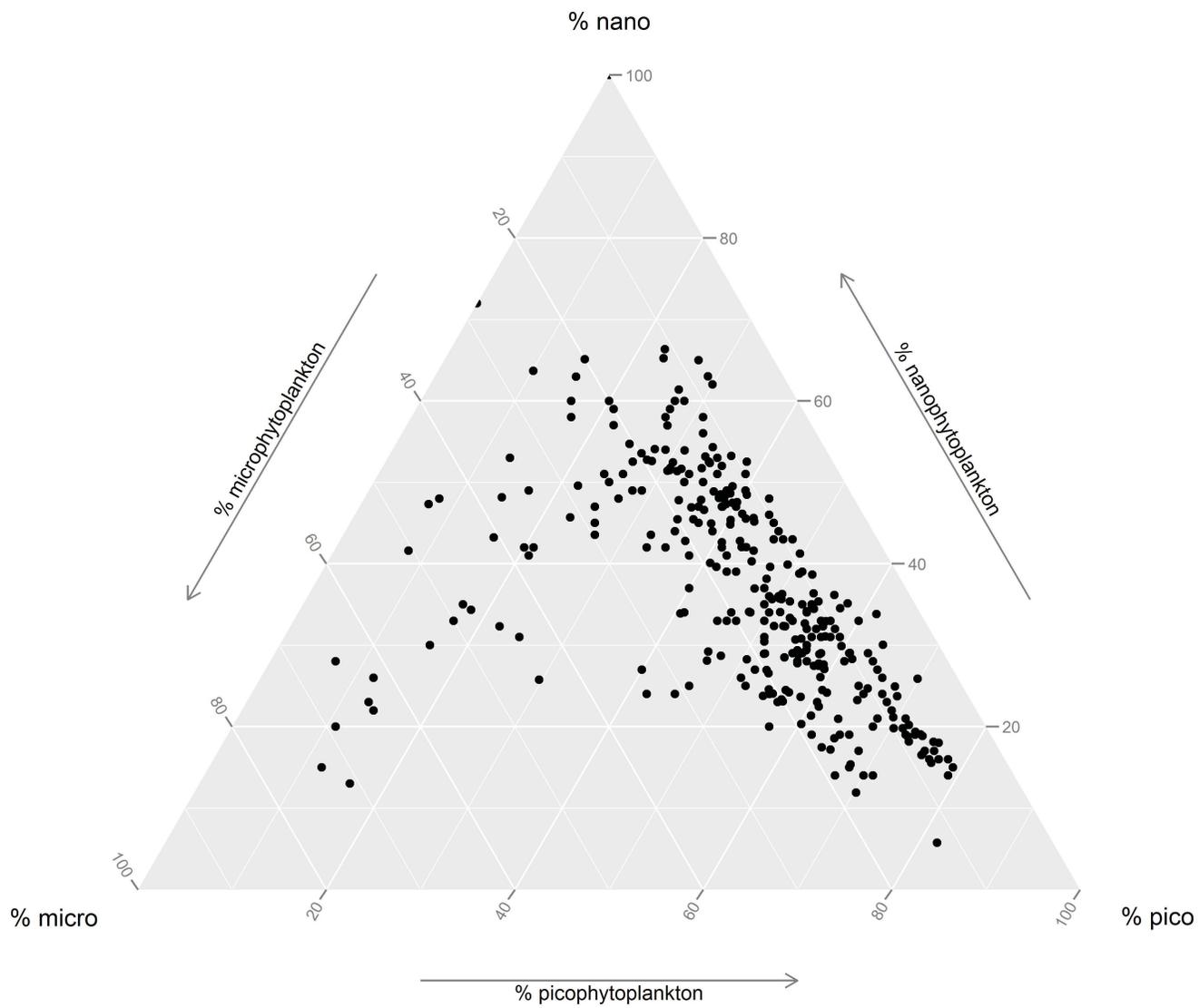


Figure 5.

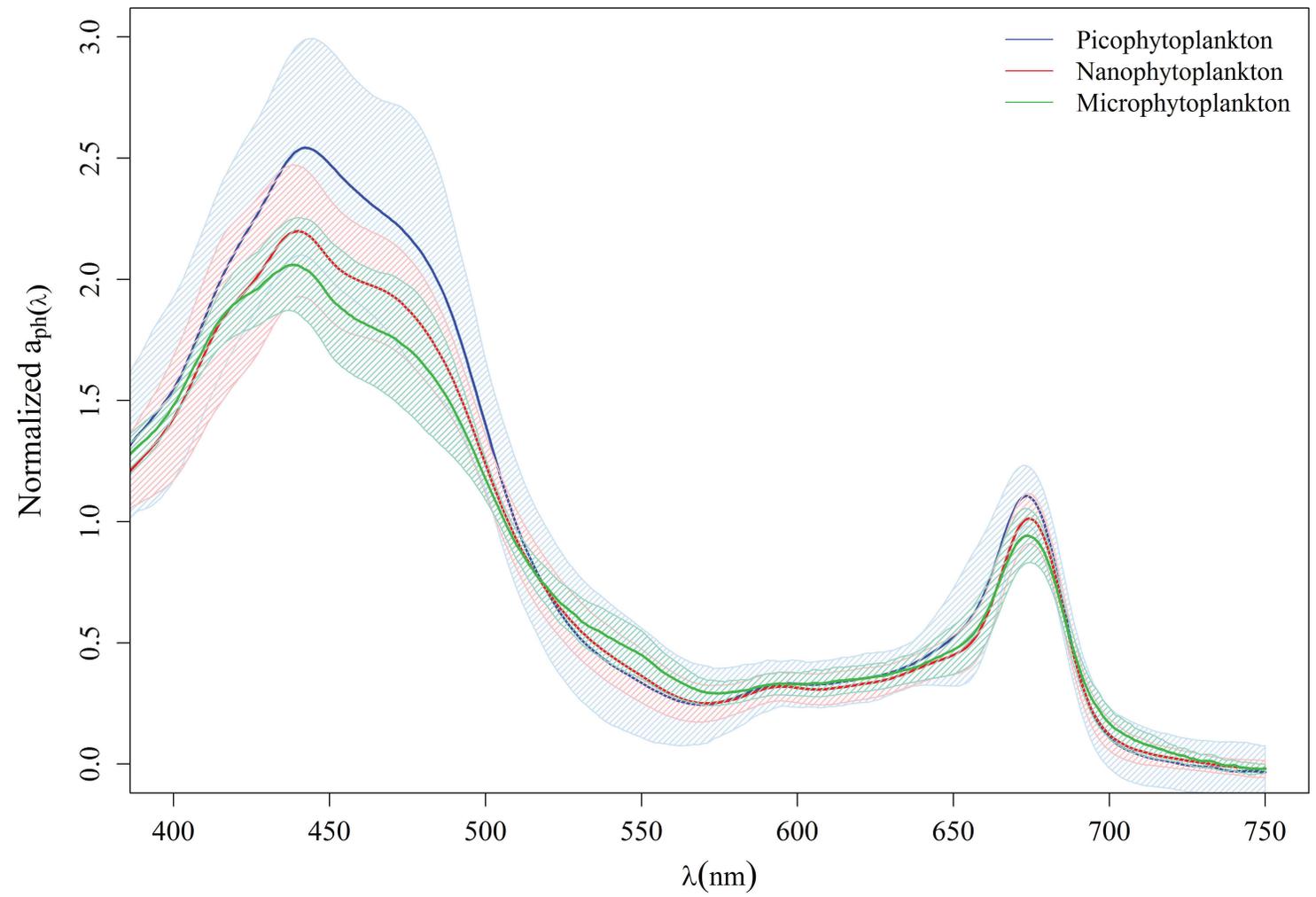
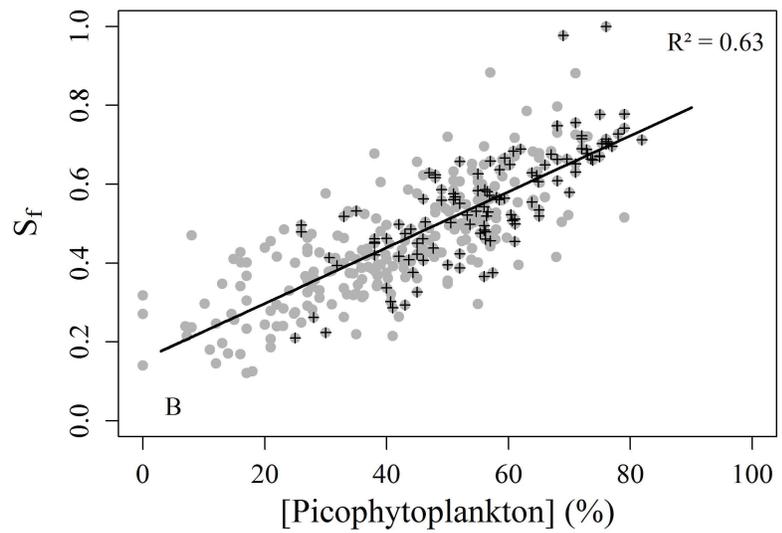
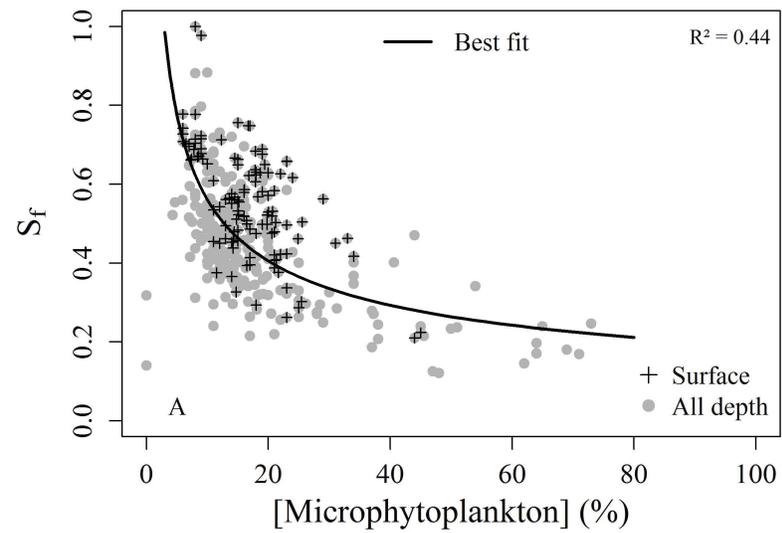


Figure 6.



**Figure 7.**

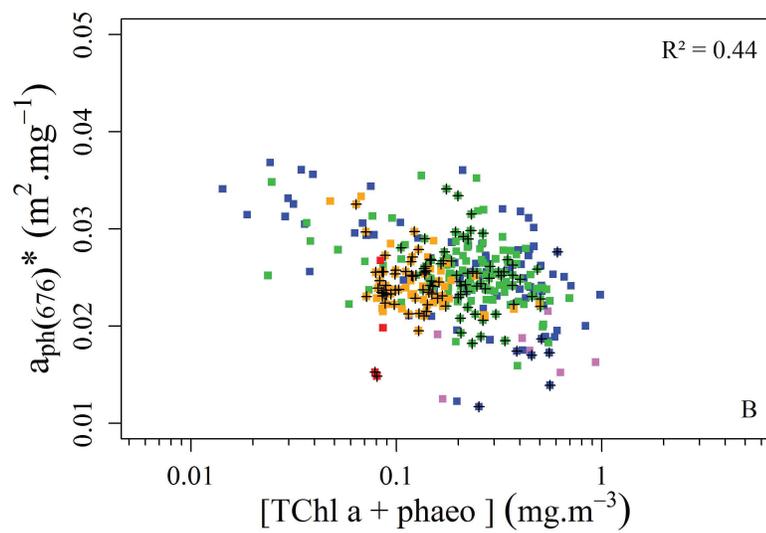
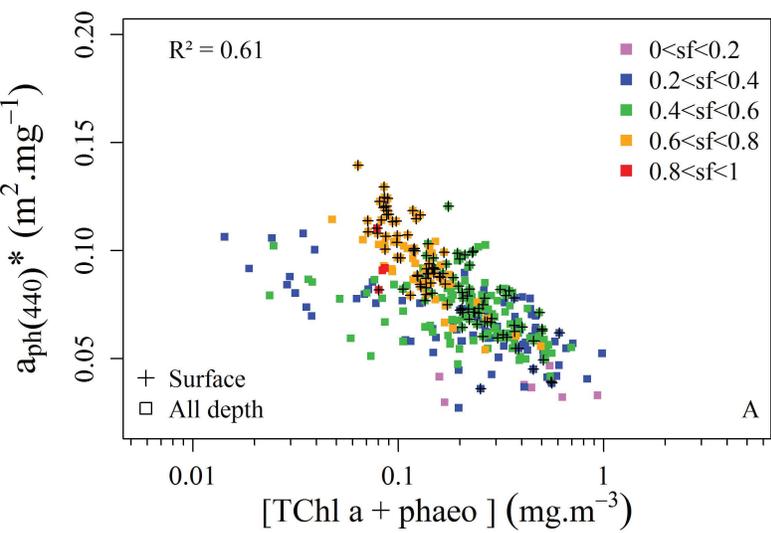


Figure 8.

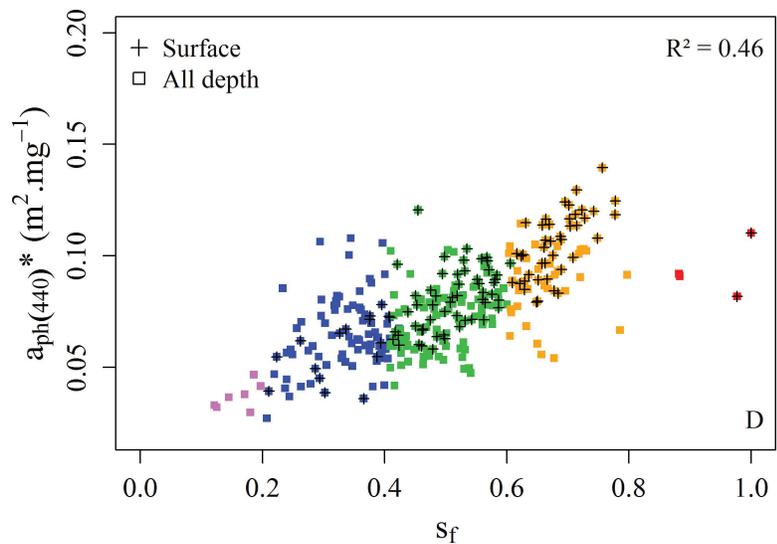
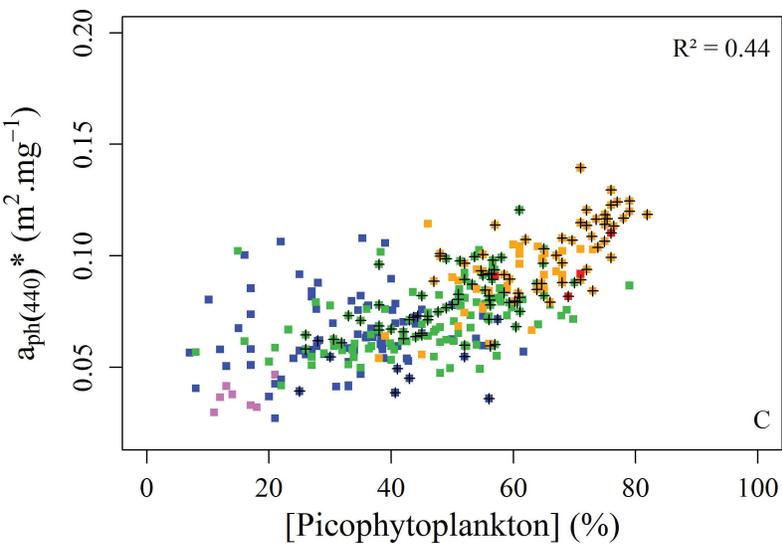
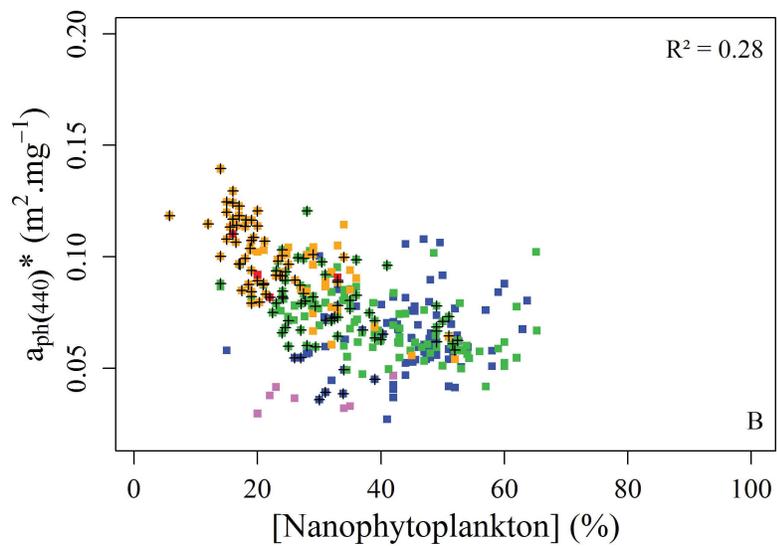
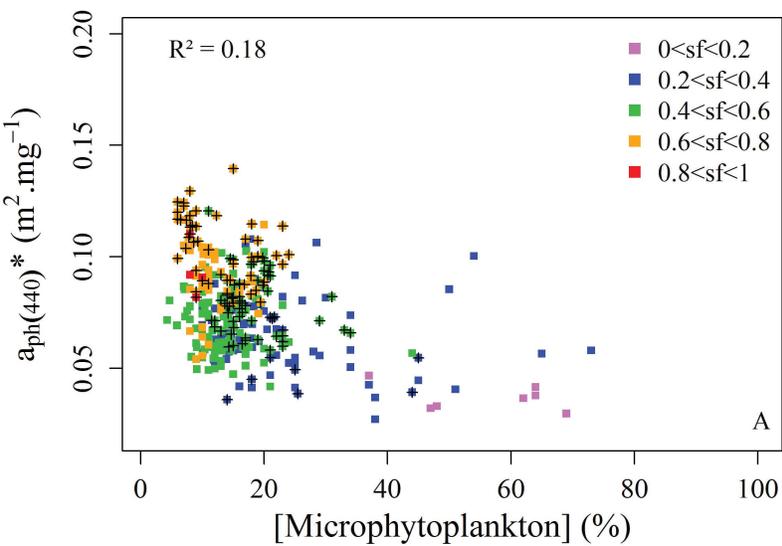


figure 9.

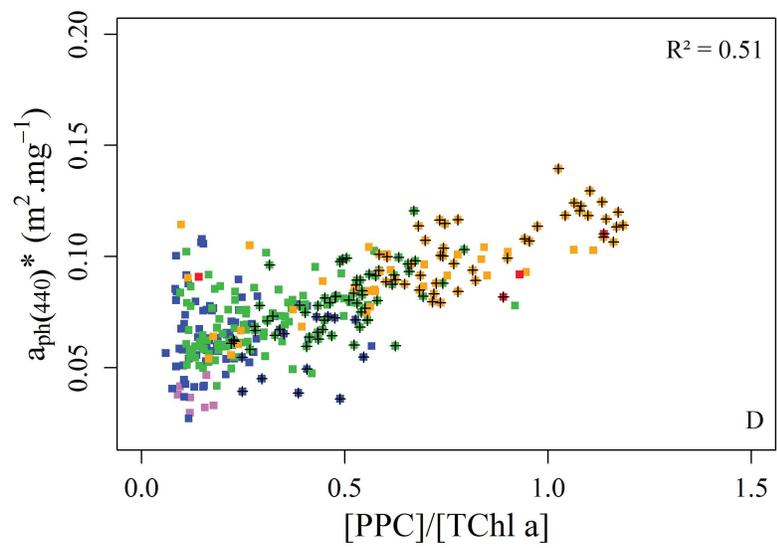
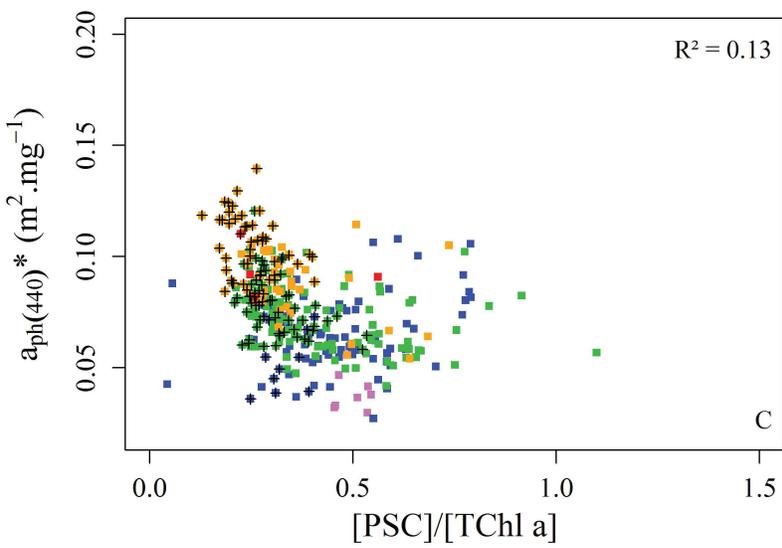
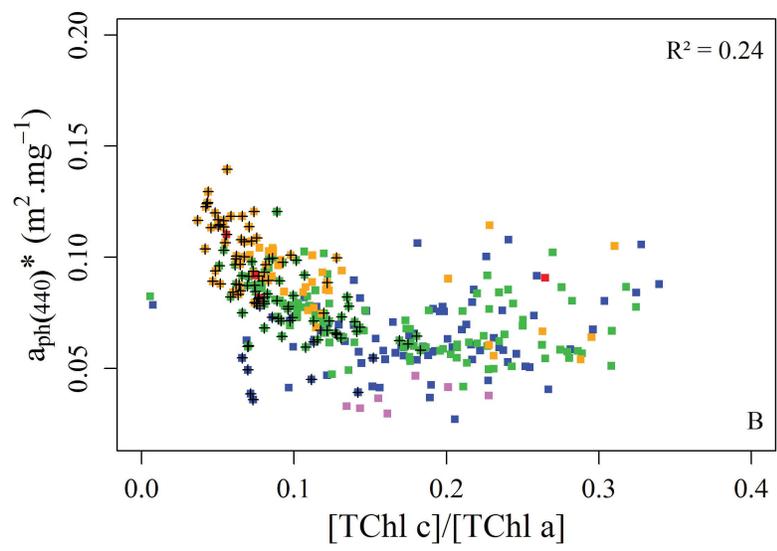
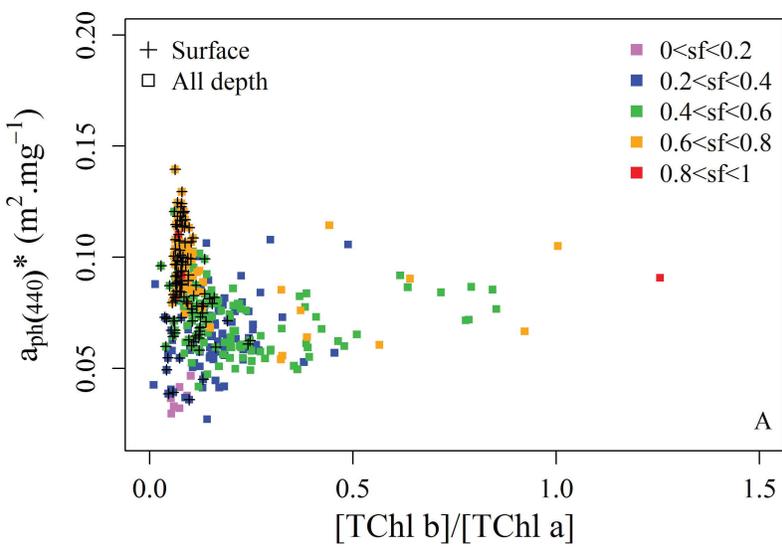


Figure 10.

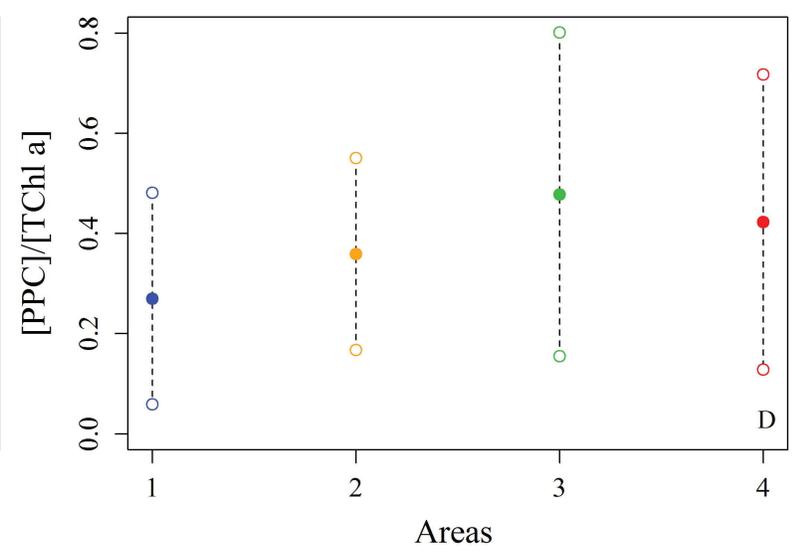
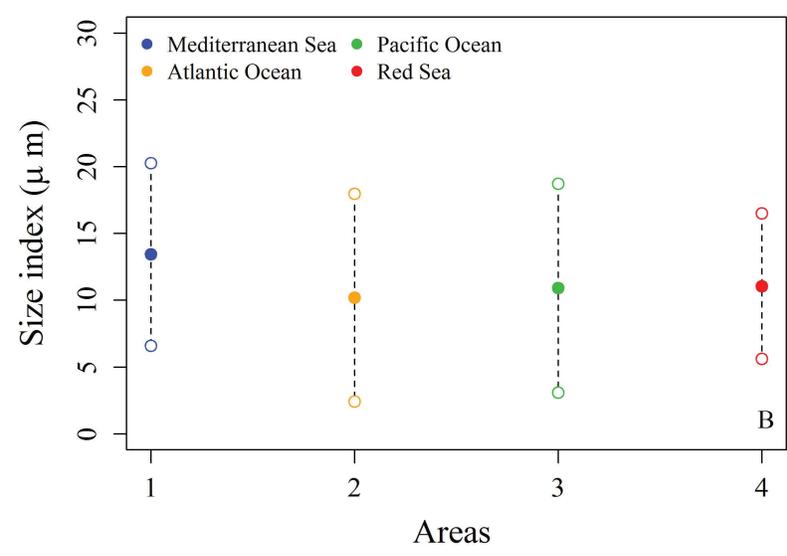
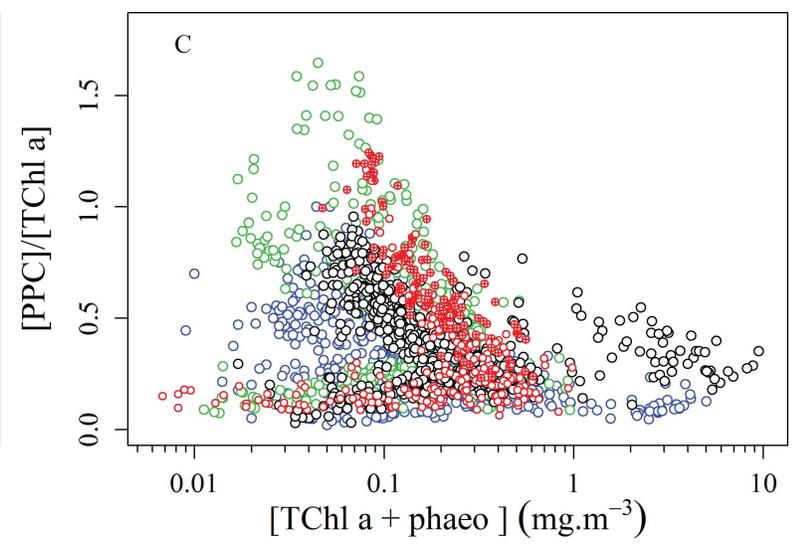
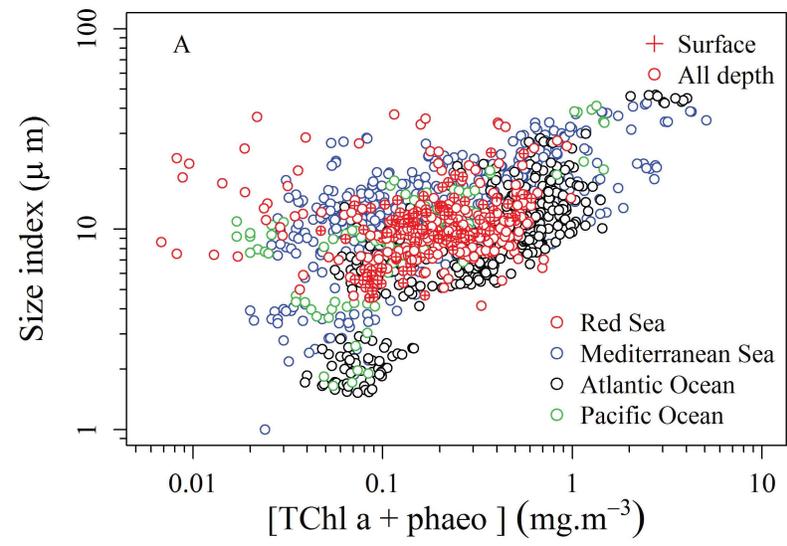


Figure 11.

