Main drivers of transparent exopolymer particle distribution across the surface Atlantic Ocean

Marina Zamanillo[1], Eva Ortega–Retuerta[1,2], Sdena Nunes[1], Pablo Rodríguez–Ros[1], Manuel Dall'Osto[1], Marta Estrada[1], Maria Montserrat Sala[1], Rafel Simó[1]

[1]Biologia Marina i Oceanografia, Institut de Ciències del Mar, CSIC, Barcelona, Catalonia, Spain
[2]CNRS, Sorbonne Université, UMR 7621, Laboratoire d'Océanographie Microbienne, Banyuls–sur–Mer, France

Correspondence to: Rafel Simó (rsimo@icm.csic.es)

36 **Abstract.** Transparent exopolymer particles (TEP) are a class of gel particles, produced mainly by microorganisms, which
37 play important roles in biogeochemical processes such as carbon cycling and export. TEP (a) are colonized by carbon-
38 consuming microbes; (b) mediate aggregation and sinking of organic matter and organisms, thereby contributing to the
39 biological carbon pump; and (c) accumulate in the surface microlayer (SML) and affect air–sea gas exchange. The first step
40 to evaluate the global influence of TEP in these processes is the prediction of TEP occurrence in the ocean. Yet, little is
41 known about the physical and biological variables that drive their abundance, particularly in the open ocean. Here we
42 describe the horizontal TEP distribution, along with physical and biological variables, in surface waters along a North–South
43 transect in the Atlantic Ocean during October–November 2014. Two main regions were separated due to remarkable
44 differences; the open Atlantic Ocean (OAO, n = 30), and the Southwestern Atlantic Shelf (SWAS, n = 10). TEP
45 concentration in the entire transect ranged 18.3–446.8 μg XG eq L^{-1} and averaged 117.1 ± 119.8 μg XG eq L^{-1}, with the
46 maximum concentrations in the SWAS and in a station located at the edge of the Canary Coastal Upwelling (CU), and the
47 highest TEP to chlorophyll *a* (TEP:Chl *a*) ratios in the OAO (183 ± 56) and CU (1760). TEP were significantly and
48 positively related to Chl *a* and phytoplankton biomass, expressed in terms of C, along the entire transect. In the OAO, TEP
49 were positively related to some phytoplankton groups, mainly *Synechococcus*. They were negatively related to the previous
50 24–hours–averaged solar irradiance, suggesting that sunlight, particularly UV radiation, is more a sink than a source for
51 TEP. Multiple regression analyses showed the combined positive effect of phytoplankton and heterotrophic prokaryotes
52 (HP) on TEP distribution in the OAO. In the SWAS, TEP were positively related to high nucleic acid–containing prokaryotic
53 cells and total phytoplankton biomass, but not to any particular phytoplankton group. Estimated TEP–carbon constituted an
54 important portion of the particulate organic carbon pool in the entire transect (28–110 %), generally higher than the
55 phytoplankton and HP carbon shares, which highlights the importance of TEP in the cycling of organic matter in the ocean.

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57

58 **1 Introduction**

59 Transparent exopolymer particles (TEP) are defined as a class of non–living organic particles in aqueous media, mainly
60 consisting of acidic polysaccharides, which are stainable with Alcian Blue (Alldredge et al., 1993). They are formed from
61 dissolved precursors that self–assemble to form TEP (operationally defined as particles > 0.4 µm) (Passow and Alldredge,
62 1994; Chin et al., 1998; Thuy et al., 2015). TEP are stabilized by covalent links or ionic strength (Cisternas-Novoa et al.,
63 2015) and therefore, the formation and fragmentation of TEP from/to dissolved precursor material spans the dissolved to
64 particulate continuum of organic matter in the sea. Due to their stickiness, TEP favour the formation of large aggregates of
65 organic matter and organisms (typically named marine snow), enhancing particle ballast and sinking and thereby
66 contributing to the biological carbon pump (Logan et al., 1995; Kumar et al., 1998; Passow et al., 2001; Burd and Jackson,
67 2009). The presence of TEP also affects the microbial food–web, as they can be used as a food source for zooplankton
68 (Decho and Moriarty, 1990; Dilling et al., 1998; Ling and Alldredge, 2003) and heterotrophic prokaryotes (HP) (Passow,
69 2002b) through microbial colonization of aggregates (Alldredge et al., 1986; Grossart et al., 2006; Azam and Malfatti, 2007).
70 On their way to aggregation, and due to their low density, TEP and TEP–rich microaggregates formed near the surface may
71 ascend and accumulate in the sea surface microlayer (SML) (Engel and Galgani, 2016), a process that is largely enhanced by
72 bubble–associated scavenging (Azetsu-Scott and Passow, 2004; Wurl et al., 2009; Wurl et al., 2011b). This accumulation in
73 the SML, also contributed by local TEP production (Wurl et al., 2011b), can supress the air–sea exchange of CO_2 and other
74 trace gases by acting as a physicochemical barrier or modifying sea surface hydrodynamics at low wind speeds (Calleja et
75 al., 2008; Cunliffe et al., 2013; Wurl et al., 2016). Sea surface TEP can also be released to the atmosphere by bubble bursting
76 (Zhou et al., 1998; Aller et al., 2005; Kuznetsova et al., 2005), contributing to organic aerosol and possibly acting as cloud
77 condensation nuclei and ice nucleating particles (Orellana et al., 2011; Leck et al., 2013; Wilson et al., 2015). All in all, TEP
78 play important roles in microbial diversity, carbon cycling and carbon exports to both the deep ocean and the atmosphere.

79 TEP distribution in marine systems depends on the complex balance between the sources and the sinks (Alldredge et al.,
80 1998; Passow, 2002a). TEP sinks include some of the above mentioned processes (sinking of aggregates to the deep ocean,
81 release to the atmosphere and consumption by organisms), and also photolysis by UV radiation (Ortega-Retuerta et al.,
82 2009b). Regarding the sources, TEP are produced by organisms, mainly microorganisms, during metabolic and
83 decomposition processes (Hong et al., 1997; Berman-Frank et al., 2007). Phytoplankton are major TEP producers in the
84 ocean, although also HP are able to produce TEP (Biddanda, 1986; Stoderegger and Herndl, 1998; Passow, 2002b; Ortega-
85 Retuerta et al., 2010). Some phytoplankton groups that have been shown to produce TEP include cyanobacteria (Grossart et
86 al., 1998; Mazuecos, 2015; Deng et al., 2016), diatoms (Passow and Alldredge, 1994; Mari and Kiorboe, 1996; Passow,
87 2002b), dinoflagellates (Passow and Alldredge, 1994), Prymnesiophyceae, coccolithophores included (Riebesell et al., 1995;
88 Engel, 2004; Leblanc et al., 2009), and Cryptomonads (Kozlowski and Vernet, 1995; Passow et al., 1995). Other organisms

89 such as *Posidonia oceanica* (Iuculano et al., 2017a), zooplankton (Passow and Alldredge, 1999; Prieto et al., 2001) and
90 benthic suspension feeders (Heinonen et al., 2007) have also been identified as TEP producers.

91 TEP sources and sinks in the ocean depend not only on the taxonomic composition of TEP producers, but they are also
92 influenced by other variables such as the organism's physiological state (Passow, 2002b), temperature (Nicolaus et al., 1999;
93 Claquin et al., 2008), light (Trabelsi et al., 2008; Ortega-Retuerta et al., 2009a; Iuculano et al., 2017b), carbon dioxide
94 concentration (Engel, 2002), nutrient availability (Guerrini et al., 1998; Radic et al., 2006), turbulence (Passow, 2000,
95 2002b), microbe–microbe interactions (Gärdes et al., 2011), or viral infection (Shibata et al., 1997; Vardi et al., 2012). For
96 example, limitation by nutrients often increases TEP production, due to dissolved inorganic carbon overconsumption (Corzo
97 et al., 2000; Engel et al., 2002a; Schartau et al., 2007), and also impedes prokaryotic consumption of TEP (Bar-Zeev and
98 Rahav, 2015). High solar radiation can stimulate TEP production by *Prochlorococcus* during cell decay (Iuculano et al.,
99 2017b), but also can limit TEP formation inhibiting the aggregation of the precursor polymers (Orellana and Verdugo, 2003).
100 HP have been found to stimulate TEP production by diatoms, suggesting that HP–diatom interaction is required for TEP
101 formation (Guerrini et al., 1998; Gärdes et al., 2011). HP may also facilitate the self–assembly of dissolved TEP precursors
102 (Sugimoto et al., 2007), e.g., through the release of amphiphilic exopolymers that induce microgel formation (Ding et al.,
103 2008).

104 The aforementioned importance of TEP in carbon fluxes in the pelagic ocean can be further stressed by considering the
105 following rough numbers: if the percentage of extracellular carbon release during planktonic primary production is generally
106 constrained within 10–20 % (Nagata, 2000; Mari et al., 2017), but can reach > 50 % (López-Sandoval et al., 2011), and half
107 of the extracellular release is in the form of reactive polysaccharides (Biddanda and Benner, 1997), then the production rate
108 of TEP precursors may represent 5–10 %, but can reach > 25% of planktonic primary production, without considering
109 production by heterotrophs. This calls for the need to quantify their occurrence across the oceans, elucidate their main
110 distribution drivers, and determine their contribution to the organic carbon reservoir. To date, large–scale studies of TEP
111 distributions in the ocean are scarce, particularly in the open ocean. In this study, we describe the horizontal distribution of
112 TEP (> 0.4 µm) in surface waters across a North–South transect in the Atlantic Ocean, including several biogeographical
113 provinces in the open ocean as well as the highly productive Southwestern Atlantic Shelf (SWAS). Our aims were (a) to
114 identify the main biological and abiotic drivers of TEP distribution across contrasting environmental conditions, and (b) to
115 quantify the TEP contribution to the total particulate organic carbon (POC) pool and compare it with those of phytoplankton
116 and heterotrophic prokaryote biomasses.

117 **2 Material and methods**

118 **2.1 Study site and sampling**

119 Sampling was conducted during the TransPEGASO cruise aboard the Spanish RV *Hespérides*, from 20 October to 21
120 November 2014. A total of 41 stations were sampled within a transit across the Atlantic Ocean from Cartagena (SE Spain) to
121 Punta Arenas (S Chile, Fig. 1). During the cruise, the ship crossed six biogeographical provinces (Longhurst, 1998): the
122 Northeastern Subtropical Gyre, the Canary Current Coastal, the North Atlantic Tropical Gyre, the Western Tropical Atlantic,
123 the South Tropical Gyre and the SWAS. Seawater was collected from 4 m depth using the ship's underway pump (BKMKC–
124 10.11, Tecnium, Manresa, Spain) and screened through a 150 μm Nylon mesh to remove large particles. Temperature and
125 salinity were measured continuously using a SBE21 Sea Cat Thermosalinograph. Solar irradiance was measured also
126 continuously using a LI–COR Biospherical PAR Sensor. The rest of the variables were collected twice a day (09:00:00 and
127 16:00:00 local time) with the ship moving at approximately 10 knots.

128 **2.2 Chemical and biological analysis**

129 **2.2.1 Particulate organic matter (TEP and POC)**

130 TEP concentrations were determined by spectrophotometry following Passow and Alldredge (1995). Duplicate samples
131 (100–500 mL each) were filtered through 25 mm diameter 0.4 μm pore size Polycarbonate filters (DHI) using a constant low
132 filtration pressure (~150 mmHg). The samples were immediately stained with 500 μL of Alcian Blue solution (0.02 %, pH
133 2.5) for 5 s and rinsed with Milli–Q water. The filters were stored frozen until further processing in the laboratory (within 8
134 months). Duplicate blanks (empty filters stained as stated earlier) were prepared twice a day to correct the interference of
135 stained particles in TEP estimates. Both the sample and blank filters were soaked in 5 mL of 80 % sulfuric acid for 3 h. The
136 filters were shaken intermittently during this period. The samples were then measured spectrophotometrically at 787 nm
137 (Varian Cary 100 Bio). The absorbance values of filter blanks did not change substantially between batches of samples,
138 suggesting stability in the staining capacity of the Alcian Blue solution throughout the cruise. The Alcian Blue dye solution
139 was calibrated just before the cruise using a standard solution of xanthan gum (XG) passed through a tissue grinder and
140 subsequently filtered through two sets of filters (four points in triplicate): pre–weighted filters to determine the actual
141 concentration of the XG solution, and filters that were subsequently stained, frozen and analysed in the spectrophotometer.
142 The detection limit was set to 0.034 absorbance units and the mean range between duplicates was 18.7 %. We estimated the
143 TEP carbon content (TEP–C) using the conversion factor of 0.51 μg TEP–C L^{-1} per μg XG eq L^{-1} (Engel and Passow, 2001).

144 POC was measured by filtering 1000 mL of seawater on pre–combusted (4 h, 450 ºC) GF/F glass fibre filters (Whatman).
145 The filters were stored frozen (-20 ºC) until processed. Prior to analysis, the filters were dried at 60 ºC for 24 h in an
146 atmosphere of HCl fumes to remove carbonates. Then filters were dried again and analysed by high–temperature (900 ºC)
147 combustion in an elemental analyzer (Perkin–Elmer 2400 CHN). No POC replicates were run, but replication in a previous
148 study yielded a coefficient of variation of around 5 %.

149 **2.2.2 Chlorophyll *a* (Chl *a*)**

150 Samples for fluorometric Chl *a* analyses were filtered (250 mL) on glass fibre filters (Whatman GF/F, 25 mm diameter) and
151 stored at -20 ºC until further processing in the ship's laboratory. Pigments were extracted with 90 % acetone at 4 ºC in the
152 dark for 24 hours. Fluorescence of extracts was measured according to the procedure described in Yentsch and Menzel
153 (1963), with a calibrated Turner Designs fluorometer. No "phaeophytin" correction was applied.

154 **2.2.3 Inorganic nutrients**

155 Samples for dissolved inorganic nutrients (nitrate, phosphate and silicate) were stored in 10 mL sterile polypropylene bottles
156 at -20 ºC until analysis. The samples were further processed in the laboratory using standard segmented flow analyses with
157 colorimetric detection (Hansen and Grasshoff, 1983), using a Skalar Autoanalyzer.

158 **2.2.4 Microscopic phytoplankton identification**

159 We quantified phytoplankton groups by microscopy. Water was fixed with hexamine–buffered formaldehyde solution (4 %
160 final formalin concentration) in a glass bottle, immediately after collection, and then was allowed to settle for 48 h in a 100
161 cm^3 composite chamber. An inverted microscope (Utermöhl, 1958) was used to enumerate the smaller phytoplankton cells
162 (< 20 µm, 312× magnification) and the larger phytoplankton cells (> 20 µm, 125× magnification). Micro–phytoplankton was
163 identified to the species level when possible, and finally classified into four groups: diatoms, dinoflagellates,
164 coccolithophores and other microplankton cells called from now on as "other microalgae". Cell C content was calculated
165 using conversion equations of Menden-Deuer and Lessard (2000), log pg C $cell^{-1}$ = log a (95 % confidence intervals) + b (95
166 % confidence intervals) × log volume (V; μm^3): one for diatoms (log pg C $cell^{-1}$ = log -0.541 (0.099) + 0.811 (0.028) × log
167 V) and one for the other algae groups (log pg C $cell^{-1}$ = log -0.665 (0.132) + 0.939 (0.041) × log V). Total carbon biomass
168 was calculated from cell C content and cell abundance. Uncertainty sources for micro–phytoplankton biomass estimates are
169 the conversion factors, biovolume estimates, and proper identification based on morphological characteristics, harder for
170 naked cells and those at the lower size edge (5–10 µm) (Kozlowski et al., 2011; Cassar et al., 2015).

171 **2.2.5 Picoplankton abundance**

172 To enumerate picoplankton cells, samples (4.5 mL) were fixed with 1 % paraformaldehyde plus 0.05 % glutaraldehyde (final
173 concentrations), let fix for 15 min. at room temperature, deep frozen in liquid nitrogen and stored frozen at -80 °C. Samples
174 were then analysed 6 months after the cruise end, using a FACS Calibur (Becton and Dickinson) flow cytometer equipped
175 with a 15 mW argon–ion laser emitting at 488 nm. Before analysis, samples were thawed and we added 10 µL per 600 µL
176 sample of a 10^5 mL^{-1} solution of yellow–green 0.92 µm Polysciences latex beads as an internal standard. Samples were then
177 run at high speed (approx. 75 µL min^{-1}) for 4 min. with Milli–Q water as a sheath fluid. Three groups of phytoplankton
178 (*Prochlorococcus*, *Synechococcus* and picoeukaryotic algae) were distinguished and enumerated on the basis of the
179 differences in their autofluorescence properties and scattering characteristics (Olson et al., 1993; Zubkov et al., 1998).
180 Abundances were converted to biomass (µg L^{-1}) using average C:cell conversion factors gathered in Simó et al. (2009): 51 ±
181 18 fg C $cell^{-1}$ for *Prochlorococcus*, 175 ± 73 fg C $cell^{-1}$ for *Synechococcus* and 1319 ± 813 fg C cell $^{-1}$ for picoeukaryotes.

182 **2.2.6 Heterotrophic prokaryotic abundance (HPA)**

183 HPA was determined by flow cytometry using the same fixing protocol and instrument as for picoplankton. Before analyses,
184 samples were thawed, stained with SYBRGreen I (Molecular Probes) at a final concentration of 10 µM and left in the dark
185 for about 15 min. Samples were run at a low flow rate (approximately 15 µL min^{-1}) for 2 min with Milli–Q water as a sheath
186 fluid. We added 10 µL per sample of a 10^5 mL^{-1} solution of yellow–green 0.92 µm Polysciences latex beads as an internal
187 standard. Heterotrophic prokaryotes (HP) were detected by their signature in a plot of side scatter versus FL1 (green
188 fluorescence). HP were enumerated separately as high–nucleic–acid–containing (HNA) and low–nucleic–acid–containing
189 cells (LNA), and the prokaryote counts presented are the sum of these 2 types. Data were gated and counted in the SSC vs
190 FL1 plot using the BD CellQuest™ software. HPA was expressed in cells mL^{-1}. Only one replicate was analysed since
191 standard errors of duplicates are usually very low (around 1.5 % at Pernice et al. (2015)). In order to estimate the number of
192 HP, cyanobacteria abundance (*Prochlorococcus* and *Synechococcus*) measured in the same but non–stained samples were
193 subtracted from the total number of prokaryotes counted. HPA was converted into carbon unit (HP–C) using the conversion
194 factor of 12 fg C $cell^{-1}$. Ducklow (2000) summarized the carbon contents of free–living marine bacteria reported in the
195 literature for a number of oceanic regions, bays and estuaries. The average ± standard deviation for open ocean regions was
196 12.3 ± 2.5 fg C $cell^{-1}$. A factor of 12 fg C $cell^{-1}$ is equivalent to use the empirical equation proposed by Norland (1993), fg C
197 $cell^{-1}$ = 0.12 (µm^3 cell volume)$^{0.72}$, for an average bacterial biovolume of 0.04 µm^3.

198 **2.3 Statistical analyses**

199 We used the R software package (RStudio Team, 2016) to test for covariations and to explore the potential controlling
200 variables of TEP distribution across the Atlantic Ocean. We performed pairwise Spearman correlation analyses between TEP
201 and POC concentrations. We performed bivariate and multiple regression analyses (ordinary least squares, OLS) between
202 TEP concentrations and several physical, chemical and biological variables. Data were log transformed to fulfil the
203 requirements of parametric tests. Ranged major axis (RMA) regression would have been more suitable since there were
204 errors in both our dependent and independent variables. However, we decided to perform OLS regressions for a better
205 comparison of slopes between our study and those available in the literature. The non–parametric Wilcoxon–Mann–Whitney
206 test was carried out to compare variables, like TEP and POC, among regions. Two main regions were analysed separately
207 due to remarkable differences in nutrient, Chl *a* and TEP concentration: the open Atlantic Ocean (OAO, n = 30), with
208 exclusion of the single sample from the edge of the Canary Coastal Upwelling (CU), which had a much higher TEP
209 concentration; and the SWAS (n = 10).

210

211 **3 Results**

212 **3.1 TEP distribution across the surface Atlantic Ocean**

213 TEP concentrations ranged from 18.3 to 446.8 µg XG eq L^{-1} along the entire Atlantic Ocean transect. Across OAO, CU
214 included, nitrate and phosphate concentrations were low and relatively homogeneous (nitrate: 0.47 ± 0.51 µmol L^{-1};
215 phosphate: 0.11 ± 0.06 µmol L^{-1}). Silicate ranged between 0.20 and 1.42 µmol L^{-1}, and presented the minimum
216 concentrations in the CU station and surroundings, and the maximum concentration at station 14. The temperatures ranged
217 from 20.7 to 29.6 ºC (25.6 ± 23.8 ºC), with maximum values in the Equatorial Counter Current (~0–20° N, 29.1–29.6 ºC),
218 and minimum values around the CU and in the southernmost stations of the OAO (22.6–23.6 ºC). The salinity ranged
219 between 34.8 and 37.4, with the minimum values in the Equatorial Counter Current, and the maximum values around 10–30º
220 S. The Chl *a* concentration was low and quite homogeneous (0.36 ± 0.22 mg m^{-3}), even at the CU (0.25 mg m^{-3}).

221 In the Northeastern Subtropical Gyre and the Canary Current Coastal (stations 1 to 7, Fig. 1) Chl *a* concentration ranged
222 from 0.24 to 0.37 mg m^{-3}. The phytoplankton biomass was generally dominated by *Prochlorococcus*, with an average of
223 $1.68 \times 10^5 \pm 0.81 \times 10^5$ cells mL^{-1}, which corresponded to a biomass of 8.58 ± 4.16 µg C L^{-1}. TEP concentration in this
224 region ranged from 54.2 to 131.7 µg XG eq L^{-1} (average 73.9 ± 27.3 µg XG eq L^{-1}). In the station 8 we sampled the edge of

225 the CU. The decrease in silicate (0.26 μmol L^{-1}) was accompanied by a relative increase of diatoms (9.4–fold increase) and
226 dinoflagellates (1.3–fold increase) with respect to surrounding stations (Fig. 2b,e). *Prochlorococcus* abundance decreased to
227 9×10^3 cell mL^{-1} and a biomass of 0.46 μg C L^{-1}. In this station, TEP concentrations were the highest found along the whole
228 transect (446.7 μg XG eq L^{-1}) but the Chl *a* concentration (0.25 mg m^{-3}) was lower than in the neighbour region.
229 Consequently the TEP:Chl *a* ratio was the highest of the whole transect (1760.4). Moving south, the North Tropical Gyre
230 (stations 9 to 13) showed an increase of silicate concentration, from 0.20 to 0.79 μmol L^{-1}. The Chl *a* concentration ranged
231 from 0.41 to 0.57 mg m^{-3} (Fig. 2c). In the northernmost part of this region (stations 9 to 11), phytoplankton biomass was
232 dominated by *Synechococcus*, with an average of $7.7 \times 10^4 \pm 0.8 \times 10^4$ cells mL^{-1}, which corresponded to a biomass of 13.5 ±
233 1.4 μg C L^{-1}. By contrast, the southernmost stations (12 and 13) were dominated by *Prochlorococcus*, with an average of 2.6
234 $\times 10^5 \pm 0.5 \times 10^5$ cells mL^{-1}, that corresponded to a biomass of 13.2 ± 2.7 μg C L^{-1} (Fig. 2e). TEP concentrations were
235 similar to those in the Northeastern Subtropical Gyre and the Canary Current Coastal, ranging between 78.1 and 123.9 μg
236 XG eq L^{-1}. Station 14, with a relatively high temperature (29.0 ºC) and low salinity (35.2) was probably the most influenced
237 by the Equatorial Counter Current. In this station, the silicate concentration (1.41 μmol L^{-1}) was the maximum observed in
238 the whole transect, and there was an increase of dinoflagellates and “other microalgae”, and a decrease of *Prochlorococcus*.
239 The Chl *a* concentration (0.48 mg m^{-3}) was similar to the surrounding stations and TEP were 49.4 μg XG eq L^{-1}. Moving
240 further south, in the Western Tropical and the South Tropical Gyre (stations 15 to 31) Chl *a* ranged from 0.20 to 0.41 mg m^{-3}
241 and the silicate concentration decreased (0.42–1.39 μmol L^{-1}). TEP presented the lowest average values of the whole
242 transect, ranging from 25.5 to 80.4 μg XG eq L^{-1}. Overall in the OAO (excluding CU), TEP ranged from 18.3 to 131.7 μg
243 XG eq L^{-1} (average 59.9 ± 27.4 μg XG eq L^{-1}) and the TEP:Chl *a* ratio ranged between 81 and 360 (average 183 ± 56; Table
244 1).

245 The southernmost part of the cruise transect corresponded to the SWAS (stations 32 to 41). In this region, temperature (7.6–
246 13.9 ºC) and salinity (32.6–33.6) were lower on average than those found in the OAO (Table 1). The SWAS could be further
247 divided into two regions according to different inorganic nutrient (nitrate and phosphate) concentrations ($p < 0.05$) and
248 phytoplankton composition. The northern SWAS (stations 32 to 36) presented lower nitrate (0.16 to 4.15 μmol L^{-1}) and
249 phosphate (0.31 to 0.62 μmol L^{-1}) concentrations than the southern SWAS (stations 37 to 41; nitrate: 2.16 to 8.92 μmol L^{-1},
250 phosphate: 0.51 to 0.89 μmol L^{-1}). Silicate was more homogeneous throughout (0.31 to 1.27 μmol L^{-1}). Chl *a* concentration
251 across the entire SWAS (1.07–3.75 mg m^{-3}) was significantly higher than in the OAO, with no major differences between the
252 northern and the southern parts. In most of the northern SWAS, phytoplankton biomass was dominated by “other
253 microalgae”, with an average of $10.2 \times 10^5 \pm 6.1\ 10^5$ cells L^{-1}, which corresponded to a biomass of 43.7 ± 25.8 μg C L^{-1}. In
254 station 35, an increase of diatoms (58121 cells L^{-1} and a biomass of 145.2 μg C L^{-1}) and dinoflagellates (44896 cells $L^{-}1$ and
255 a biomass of 3.3 μg C L^{-1}) was observed, coinciding with a decrease in silicate (0.32 μmol L^{-1}). Here in northern SWAS,
256 TEP ranged from 98.6 to 427.2 μg XG eq L^{-1}, with the maxima in stations 34 and 35 (Fig. 2f). In the southern SWAS

257 (stations 37 to 41), phytoplankton biomass was dominated by picoeukaryotes, with an average of $6.34 \times 10^4 \pm 1.93 \times 10^4$

258 cells mL^{-1}, which corresponded to a biomass of 83.6 ± 25.5 µg C L^{-1}. TEP concentration ranged 168.6–395.7 µg XG eq L^{-1}.

259 Overall in the SWAS, TEP ranged from 98.6 to 427.2 µg XG eq L^{-1} (average 255.7 ± 130.4 µg XG eq L^{-1}) and the TEP:Chl

260 *a* ratio ranged from 31 to 165 (average 97 ± 42) (Table 1).

261 **3.2 TEP contribution to POC**

262 TEP and POC covaried significantly and positively across the entire TransPEGASO transect (Spearman rs analysis, r = 0.91,

263 $p< 0.01$, n = 17). The contribution of TEP–C to the POC pool (TEP–C%POC) ranged between 34 and 103 % in the OAO

264 (average 66 ± 19 %), and between 28 and 110 % in the SWAS (average 73 ± 36 %). POC was not analysed in the CU (Fig.

265 3). To better explore the importance of TEP–C with respect to other major quantifiable POC pools, we estimated

266 phytoplankton biomass (phyto–C) and HP biomass (HP–C) throughout the whole cruise (Fig. 2). It is worth mentioning that

267 POC also includes other fractions of non–living non–TEP organic carbon (e.g., cell fragments and Coomassie stainable

268 particles), but phytoplankton and heterotrophic prokaryotes are generally considered the most abundant in open sea water

269 (Ortega-Retuerta et al., 2009b; Yamada et al., 2015). TEP–C contributed the most to the POC pool in the OAO, where it

270 represented twice the share of phyto–C and HP–C. In the SWAS, conversely, TEP–C was not significantly different than

271 phyto–C, and three times higher than HP–C (Fig. 3).

272 **3.3 Relationship to other variables**

273 TEP were significantly and positively related to Chl *a* along the entire transect ($R^2 = 0.61$, $p< 0.001$, n = 39, table 3). The

274 regression equation for log converted TEP vs Chl *a* was log TEP = 2.09 (± 0.04) + 0.66 (± 0.08) × log Chl *a*. Considering

275 the two study regions separately, only in the OAO the relationship was significant, with a higher slope than in the entire

276 transect (log TEP = 2.31 (± 0.10) + 1.13 (± 0.20) × log Chl *a;* $R^2 = 0.56$, $p< 0.001$, n = 29).

277 Across the whole transect, TEP presented a significant ($p< 0.05$) positive relationship with total phytoplankton biomass

278 (Table 3) and with some phytoplankton biomass groups: *Synechococcus* ($R^2 = 0.30$), picoeukaryotes ($R^2 = 0.49$), diatoms (R^2

279 = 0.19) and "other microalgae" ($R^2 = 0.27$), and with HPA ($R^2 = 0.60$). TEP were negatively related to silicate ($R^2 = 0.19$)

280 and coccolithophores ($R^2 = 0.15$). Some differences arose from examining the two regions separately. Within the OAO, TEP

281 presented a significant ($p< 0.001$) positive relationship with Chl *a* ($R^2 = 0.56$), total phytoplankton biomass ($R^2 = 0.47$) and

282 some phytoplankton groups (*Synechococcus*, picoeukaryotes, diatoms, dinoflagellates and "other microalgae", Table 3), but

283 not with HPA. TEP showed a significant ($p< 0.001$) negative relationship with the previous 24 hours–averaged solar

284 irradiance ($R^2 = 0.43$, Fig. 4). Multiple regression analyses showed the combined positive effect of Chl *a* and HPA on TEP

285 distribution in the OAO (Table 4). By contrast, within the SWAS, TEP only presented a significant ($p < 0.05$) positive
286 relationship with total phytoplankton biomass ($R^2 = 0.62$) and HNA ($R^2 = 0.46$, Table 3).

287

288 **4 Discussion**

289 **4.1 TEP across the surface Atlantic Ocean**

290 We present the first distribution of surface (4 m) TEP concentration along a latitudinal gradient in the Atlantic Ocean,
291 covering both open sea and shelf waters. It is worth mentioning that vertical variability within the top surface meters (< 4 m)
292 has sometimes been observed (Wurl et al., 2009), but 4 m is usually considered "surface ocean" in studies where samples are
293 collected with either an oceanographic rosette or an underway pumping system. The existing information about TEP
294 distribution in surface waters of the open oceans is compiled in Table 2. TEP concentrations we measured across the OAO
295 (CU included) fall generally within the range reported in other studies from the open ocean (Table 2). However our levels
296 are higher than those observed in the Mediterranean Sea (Ortega-Retuerta et al., 2010; Ortega-Retuerta et al., 2017), Pacific
297 Ocean (Ramaiah et al., 2005; Kodama et al., 2014; Iuculano et al., 2017b) and one study in the Northwestern Atlantic Ocean
298 (Cisternas-Novoa et al., 2015), and lower than that reported in the Eastern Mediterranean Sea (Bar-Zeev et al., 2011). We
299 believe that one of the reasons for the higher values found in our study compared with these previous studies is the depth.
300 Mean TEP values in some of them (Ortega-Retuerta et al., 2010; Kodama et al., 2014; Cisternas-Novoa et al., 2015; Ortega-
301 Retuerta et al., 2017) correspond to the above mixed layer depth or from 0 to 100 or 200 m. As TEP tend to accumulate in
302 the surface and our values correspond only to the surface (4 m), this could explain the higher values obtained in our dataset.
303 Another reason seems to be the different Chl *a* concentrations, as the main TEP producer is phytoplankton. Chl *a*
304 concentration in the OAO (0.4 ± 0.2 mg m^{-3} (0.2–0.6 mg m^{-3})) was generally higher than in the other studies referred in the
305 Table 2. For example, in Iuculano et al. (2017b) Chl *a* ranged 0.05–0.31 mg m^{-3}, and in Kodama et al. (2014) it averaged
306 0.05 ± 0.01 mg m^{-3}. We can't discard either that differences in TEP chemical composition could cause differences in staining
307 capacity.

308 We found maximum TEP concentrations in the regions with high nutrient supply, namely in the station located in the CU
309 and within the SWAS. Ours are the first TEP concentrations ever measured in the SWAS (Table 1), and only three more
310 studies have reported TEP concentrations in coastal or shelf waters of the Atlantic Ocean (Harlay et al., 2009; Harlay et al.,
311 2010; Jennings et al., 2017). The SWAS is a high nutrient region due to the arrival of cold rich–nutrient Subantarctic water
312 with the Malvinas Current. This current collides near 40 °S with the southward flowing Brazil Current (Gordon, 1989; Piola

313 and Gordon, 1989; Peterson and Stramma, 1991; Palma et al., 2008). The nutrient–rich water in the region is responsible for
314 the proliferation of phytoplankton and HP, which could partly explain the high TEP concentrations in this region. It is also
315 known that large freshwater discharges occur in the shelf (Piola, 2005). These discharges could bring allochtonous HP
316 directly to the shelf or bring DOM loads, which would stimulate autochtonous microbes. Besides, DOM inputs associated to
317 freshwater discharges could also contain TEP and their precursors. Although no previous information on TEP distribution
318 exists for this area, previous studies in similarly productive areas or during phytoplankton blooms already observed high
319 TEP concentrations (Long and Azam, 1996; Harlay et al., 2009; Klein et al., 2011). The TEP levels we measured at the
320 SWAS are generally within the range of those reported for coastal areas (Passow and Alldredge, 1995; Passow et al., 1995;
321 Riebesell et al., 1995; Kiorboe et al., 1996; Hong et al., 1997; Jähmlich et al., 1998; Wild, 2000; Ramaiah et al., 2001; Engel
322 et al., 2002b; García et al., 2002; Radic et al., 2005; Scoullos et al., 2006; Sugimoto et al., 2007; Harlay et al., 2009; Wurl et
323 al., 2009; Harlay et al., 2010; Fukao et al., 2011; Klein et al., 2011; Sun et al., 2012; Van Oostende et al., 2012;
324 Dreshchinskii and Engel, 2017; Jennings et al., 2017). Only two studies, in the western Baltic Sea and the Dona Paula Bay
325 (Arabian Sea), reported TEP levels higher than ours (Engel, 2000; Bhaskar and Bhosle, 2006).

326 **4.2 TEP as an important contributor to ocean surface POC**

327 The significant positive correlation between TEP and POC observed in our study highlighted the importance of TEP
328 determining POC horizontal variations in the surface Atlantic Ocean, suggesting a high contribution of TEP to this pool. A
329 few values of TEP–C%POC were unrealistically higher than 100 %, a feature that has also been observed in other studies
330 (Engel and Passow, 2001; Bar-Zeev et al., 2011; Yamada et al., 2015). This suggests the inaccuracy of the use of standard
331 TEP–to–carbon conversion factors (CF, 0.51 µg TEP–C L^{-1} per µg Xeq. L^{-1} in our case). Therefore there is a need for
332 defining specific CF for diverse regions or environmental conditions. Nonetheless, an alternative explanation for the
333 apparent oversizing of the relative TEP–C pool may be strictly methodological: TEP are determined on filters of 0.4 µm of
334 pore size, whereas POC is measured on glass fibre filters with nominal pore size 0.7 µm. It is plausible, thus, that part of the
335 smaller TEP particles are not taken into account in the POC measurement.

336 All in all, our results clearly show that TEP–C constituted an important portion of the POC pool in the Atlantic Ocean (from
337 28 to 110 %). This contribution is comparable to that reported in the Eastern Mediterranean Sea (Bar-Zeev et al., 2011;
338 Parinos et al., 2017), lower than in the western Arctic (Yamada et al., 2015), but higher than in the Northeast Atlantic Ocean
339 (Harlay et al., 2009; Harlay et al., 2010). Both in the OAO and SWAS, TEP comprised the largest share of the POC pool,
340 with phyto–C being equal or the second most important contributor to POC (Fig. 3). Only in one station in the SWAS phyto–
341 C surpassed TEP–C. The contribution of phyto–C and HP–C to the POC pool should be taken with caution, as the glass fibre
342 filters (nominal pore size 0.7 µm) used to analyse POC could have not retained all the small phytoplankton organisms and

343 prokaryotes (Gasol and Morán, 1999), causing underestimation of the actual POC pool. Furthermore, conversion factors
344 carry quite an uncertainty, as pointed out in the Methods section.

345 A previous study in a eutrophic system reported TEP–C as the dominant POC contributor (Yamada et al., 2015), whereas
346 others found that phyto–C represented the largest share to POC compared to TEP–C and HP–C (Bhaskar and Bhosle, 2006;
347 Ortega-Retuerta et al., 2009b; de Vicente et al., 2010). With our results taken all together, we hypothesize that in
348 oligotrophic conditions TEP–C is the predominant POC fraction, because nutrient limitation favours TEP production by
349 phytoplankton and limits TEP consumption by bacteria. Conversely, in eutrophic conditions, the predominant POC fraction
350 depends on many variables like the community composition, the bloom stage, and sources of TEP different from
351 phytoplankton.

352 **4.3 Main drivers of TEP distribution in the surface ocean**

353 In order to better understand and even predict the occurrence of TEP in the surface ocean, it is important to describe their
354 distribution together with those of their main putative sources (phytoplankton and heterotrophic prokaryotes), sinks and
355 environmental modulators, across large–scale gradients. However, most of the previous studies of TEP in the Atlantic Ocean
356 were restricted to local areas, and, to our knowledge, only one included a complete description of these variables together in
357 a long transect (Mazuecos, 2015).

358 Our dataset suggests that phytoplankton is the main driver of TEP distribution in the surface Atlantic Ocean at the horizontal
359 scale, since significant positive relationships were observed between TEP and both Chl *a* and phytoplankton biomass (Table
360 3). It is worth noting that Chl *a* was a good estimator of phytoplankton biomass when the entire cruise was considered, as
361 these variables were tightly related ($R^2 = 0.79$, p–value < 0.001, $n = 36$). The slope of the log converted TEP–Chl *a*
362 relationship for the whole study ($\beta = 0.66 \pm 0.08$, Table 3) was within the upper range amongst published data (Fig. 5), and
363 the slope in the OAO ($\beta = 1.13 \pm 0.20$) was the highest reported so far (Table 3, Fig. 5). In the SWAS, the TEP–Chl *a*
364 relationship was not significant (p–value > 0.05), yet it was for TEP–phytoplankton biomass (see below).

365 TEP:Chl *a* ratios were significantly ($p < 0.001$) higher in the OAO (both including or excluding the CU) than in the SWAS
366 (Table 1), with the maximum value in the station located in the CU. TEP:Chl *a* values in the OAO (CU included) were
367 comparable to those observed in other oligotrophic areas (Riebesell et al., 1995; García et al., 2002; Prieto et al., 2006;
368 Harlay et al., 2009; Ortega-Retuerta et al., 2010; Kodama et al., 2014; Iuculano et al., 2017b; Parinos et al., 2017) (Table 2),
369 while the values in the SWAS were comparable to those reported in eutrophic waters (Hong et al., 1997; Ramaiah et al.,
370 2001; Engel et al., 2002b; Corzo et al., 2005; Ortega-Retuerta et al., 2009b). The higher TEP:Chl *a* ratios in oligotrophic

371 waters (Prieto et al., 2006) are related to nutrient scarcity, which is suggested to enhance TEP production by phytoplankton
372 and prokaryotes (Myklestad, 1977; Guerrini et al., 1998; Mari et al., 2005; Beauvais et al., 2006). The highest TEP:Chl *a*
373 ratio of the entire transect observed in the station located in the CU was probably associated with the high relative abundance
374 of diatoms and dinoflagellates. These groups are known to be strong TEP producers (Passow and Alldredge, 1994), and
375 besides, previous studies have shown that TEP production rates reach maxima at late stages of the growth cycle, once
376 nutrients have been exhausted (Corzo et al., 2000; Pedrotti et al., 2010; Borchard and Engel, 2015). In the CU, the relatively
377 low Chl *a* level along with low silicate concentrations suggests that the upwelling–triggered bloom maximum had already
378 passed, which resulted in a high TEP:Chl *a* ratio. Although POC was not measured in the CU, high TEP:Chl *a* suggests a
379 high proportion of TEP with respect to other organic particles. In the SWAS, the lower TEP:Chl *a* ratios could be related
380 with a lower rate of TEP production under relatively replete nutrient conditions. Extending our comparison to the literature,
381 TEP:Chl *a* ratio is generally higher in oligotrophic regions (Prieto et al., 2006; Ortega-Retuerta et al., 2010; Kodama et al.,
382 2014; Iuculano et al., 2017b) than in eutrophic regions (Hong et al., 1997; Engel et al., 2002b; Corzo et al., 2005; Ortega-
383 Retuerta et al., 2009b; Klein et al., 2011; Engel et al., 2017).

384 In the OAO, the phytoplankton groups that showed a significant ($p < 0.05$) positive relationship to TEP and hence were
385 candidates to be considered as the main producers of TEP or their precursors were *Synechococcus,* picoeukaryotes, diatoms,
386 dinoflagellates and "other microalgae" (Table 3). All the groups above mentioned have been reported to produce TEP (see
387 references in the introduction). Conversely, coccolithophores and *Prochlorococcus* did not present a significant relationship
388 with TEP. It has been shown in cultures that coccolithophores do not produce high amounts of TEP (Passow, 2002b), and a
389 previous study showed temporal disconnections between coccolithophores and TEP maxima (Ortega-Retuerta et al., 2018).
390 However, in a previous study in the Atlantic Ocean, Leblanc et al. (2009) found an association of TEP with
391 coccolithophores.

392 The oligotrophic ocean covers a big portion of the global ocean and it is mostly dominated by picophytoplankton (Agawin et
393 al., 2000), chiefly *Prochlorococcus* and *Synechococcus* (Partensky et al., 1999). Iuculano et al. (2017b) reported relatively
394 high rates of TEP production by *Prochlorococcus* in culture, and Mazuecos (2015) found a significant and positive
395 relationship of TEP with *Prochlorococcus* abundance in the low latitude oceans. The absence of significant covariation
396 between TEP and the largely abundant *Prochlorococcus* in our study suggests that these picophytoplankters are not the main
397 TEP producers, or their production is strongly modulated by environmental conditions. It is remarkable that, amongst the
398 phytoplankton groups of the present study, *Synechococcus* biomass presented the highest relationship ($R^2 = 0.72$) with TEP
399 concentration in the OAO. Deng et al. (2016) demonstrated TEP production by marine *Synechococcus* in a laboratory study,
400 but only Mazuecos (2015) had previously found a significant and positive relationship ($R^2 = 0.26–0.36$) between these two
401 variables in the ocean, particularly in the Atlantic, North Pacific and Indian oceans. This author actually found that

402 *Synechococcus* was the phytoplankton group with the highest relationship with TEP concentration. Our study supports the
403 importance of *Synechococcus* as a TEP source in the oligotrophic ocean.

404 In the SWAS, unlike in the OAO, the significant relationship between TEP and the total phytoplankton biomass ($R^2 = 0.62$)
405 was not accompanied by any relationship to any phytoplankton group (Table 3). This could be due to the high variability of
406 the phytoplankton composition in the SWAS stations. Since many phytoplankton taxa are capable of TEP production, it is
407 difficult to discern one group playing the main role. Moreover, as mentioned before, in these shelf waters TEP formation
408 could have been further modulated by aggregation of colloids carried by freshwater discharges.

409 Regarding the influence of abiotic factors in TEP distribution, we found a negative relationship ($R^2 = 0.43$) between TEP
410 concentration and the 24 hours–averaged solar irradiance in the OAO (Fig. 4). The OAO stations were exposed to high solar
411 radiation due to water transparency and their location in tropical and subtropical regions. Ultraviolet (UV) radiation causes
412 TEP loss by photolysis (Ortega-Retuerta et al., 2009a) and inhibits TEP formation from precursors (Orellana and Verdugo,
413 2003) . However, it has also been proved that solar radiation harms picophytoplanktonic cells through photobiological stress,
414 inducing TEP production (Agustí and Llabrés, 2007; Iuculano et al., 2017b). Our results suggest that the roles of UV
415 radiation in breaking up TEP and/or limiting their formation from precursors overcome UV stress–induced TEP production.

416 The role of HP as potential drivers of TEP distribution is not straightforward, since their net effect on TEP accumulation
417 depends on local conditions. Across the entire transect, TEP concentration was significantly ($p < 0.001$) and positively
418 related to HPA (Table 3). However, the relationship was not significant considering the regions separately, and only in the
419 SWAS TEP were significantly ($p< 0.05$) and positively related to HNA, considered to be a proxy of the more active cells
420 (Servais et al., 1999; Lebaron et al., 2001). This relationship in the SWAS could indicate that HP used TEP as a significant
421 carbon source or that both HP and TEP were controlled by the same drivers, such as the presence of dissolved
422 polysaccharides, which are substrates for HP as well as TEP precursors (Mari and Kiorboe, 1996). In the OAO, despite the
423 lack of a paired relationship between TEP and HPA, multiple regression analyses showed that both phytoplankton and HP
424 contributed significantly to explain TEP concentration variance (Table 4).

425 In summary, our study describes for the first time the horizontal distribution of TEP across a North–South transect in the
426 Atlantic Ocean. TEP constituted a large portion of the POC pool, larger than phytoplankton at most stations and always
427 larger than heterotrophic prokaryotic biomass. This supports the important role of TEP in the carbon cycle. The drivers of
428 TEP distribution were primarily phytoplankton and, to a lesser extent, heterotrophic prokaryotes among sources, with
429 *Synechococcus* playing an outstanding role in the oligotrophic ocean. Also in the oligotrophic ocean, solar irradiance was a
430 major identifiable sink. We call for the need to carry out more extensive studies in the ocean, across both space and time, in

order to better predict the occurrence of TEP and incorporate diagnostic relationships in model projections. These diagnostic studies must be combined with further process studies if we are to relate TEP concentrations to important biogeochemical processes such as microbial colonization of particles, organic matter export to the deep ocean, gas exchange at the air–water interface and organic aerosol formation.

Author Contribution

M.Z. conducted the field work, analysed samples, processed and analysed the data. E.O–R. and R.S. designed the study and analysed data. S.N., P.R–R., M.E. and M.S. analysed samples and provided data. M.D. helped with data contextualization. M.Z., E.O–R. and R.S. wrote the manuscript with the help of all co–authors.

Competing interests

The authors declare that they have no conflict of interest

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799 **Table 1. Mean, standard deviation and range of temperature (ºC), salinity, 24 hours–averaged solar irradiance (W m^{-2}), nitrate
800 (µmol L^{-1}), silicate (µmol L^{-1}), phosphate (µmol L^{-1}), Chl *a* (mg m^{-3}), POC (µmol L^{-1}), HPA (× 10^5 cells mL^{-1}), TEP (µg XG eq L^{-1})
801 and TEP:Chl *a* in the OAO, the edge of the Canary Coastal Upwelling (CU) and the SW Atlantic Shelf.**

	OAO		**CU**	**SW Atlantic Shelf**	
	Mean ± SD (ranges)	n	Value (n = 1)	Mean ± SD (ranges)	n
Temperature (ºC)	26.0 ± 2.1 (22.6–29.6)	30	23.6	10.7 ± 2.2 (7.6–13.9)	9
Salinity	36.4 ± 0.6 (34.8–37.4)	30	36.1	33.2 ± 0.3 (32.6–33.6)	9
Solar irradiance 24 h (W m^{-2})	265 ± 73 (144–362)	26	–	369 ± 52 (264–425)	10
Nitrate (µmol L^{-1})	0.49 ± 0.53 (0.09–0.77)	30	0.13	4.08 ± 3.08 (0.16–8.9)	10
Silicate (µmol L^{-1})	0.74 ± 0.27 (0.20–1.41)	30	0.26	0.63 ± 0.35 (0.31–1.27)	10
Phosphate (µmol L^{-1})	0.11 ± 0.06 (0.05–0.18)	30	0.16	0.57 ± 0.21 (0.31–0.89)	10
Chl *a* (mg m^{-3})	0.32 ± 0.10 (0.20–0.57)	29	0.25	2.73 ± 0.87 (1.07–3.75)	10
POC (µmol L^{-1})	4.2 ± 1.9 (1.7–7.1)	12	–	16.6 ± 15.8 (6.8–44.3)	5
HPA (× 10^5 cells mL^{-1})	7.83 ± 2.16 (4.34–14.90)	30	14.56	29.04 ± 5.39 (13.00–70.20)	10
TEP (µg XG eq L^{-1})	59.8 ± 27.4 (18.3–131.7)	30	446.8	255.7 ± 130.4 (98.6–427.2)	10
TEP:Chl *a*	183.1 ± 55.8 (81.2–359.7)	29	1760.4	97.2 ± 42.1 (30.8–164.9)	10

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Table 2. Review of open–ocean surface TEP concentrations (mean and ranges; µg XG eq L^{-1}), Chl *a* (mean and ranges; mg m^{-3}) and TEP:Chl *a* ratio (mean ± SE and/or range) available in the literature. bdl: below detection limit.

Geographic area	Conditions	Sampling date	Depth (m)	TEP mean (range) (µg XG eq. L^{-1})	Chl *a* mean (range) (mg m^{-3})	TEP:Chl *a* mean (range)	Reference
Fram Strait (Arctic Ocean)	Bloom and non bloom	Summer 2009–2012 and 2014 (time series) and summer 2014 (transect)	5–150	75 ± 78 (5–517)	0–4.2	45 ± 3–107 ± 10	Engel et al. (2017)
Arctic Ocean	Sea ice covered	Autumn and Spring 2009–2010	Above Mixed Layer Depth	125–1750[a]	0.1–7.8[b]	–	Wurl et al. (2011a)
Eastern tropical and Eastern subarctic, North Pacific Ocean	Eutrophic and oligotrophic	Summer 2009	Above Mixed Layer Depth	78–970[a]	0.3–1.7[b]	–	Wurl et al. (2011)
Western subarctic and North Pacific Ocean	Non bloom	Summer 2001	5	40–60	0.2–1.9	–	Ramaiah et al. (2005)
Northeast Atlantic Ocean	Different bloom stages	Summer 1996	0–70	10[c]–124	0.1–1.1[c,d]	49–104	Engel (2004)
		Autumn 1996	0–50	28.5 ± 10.2	0.07–0.6	61	
Northeast Atlantic Ocean	Late stages bloom	Spring 2005	0–10	20–420[c]	0.1–3[c,e]	–	Leblanc et al. (2009)
Western tropical North Pacific Ocean	Non bloom Oligotrophic	Spring 2013	Surface mixed layer (36 ± 12)	43 ± 7 (18–67[c])	0.05 ± 0.01	832 ± 314	Kodama et al. (2014)
Western North Atlantic Ocean	Oligotrophic	Spring 2014	1	161–460	0.1–1[c]	–	Jennings, et al. (2017)
Western North	Eutrophic and	Spring 2014	2–5	100–200[c]	0.1–2.2	–	Aller (2017)

Atlantic Ocean and Sargasso Sea	oligotrophic						
Sargasso Sea	Oligotrophic	Spring, summer, autumn 2012 and spring 2013	0–100	21 ± 2– 57 ± 3	0.05–1 [c]	–	Cisternas–Novoa et al. (2015)
Mediterranean Sea	Non bloom	Spring 2007	Upper mixed layer	29 (19–53)	bdl–1.8[f]	484 (178–1293)	Ortega–Retuerta et al. (2010)
Western Mediterranean Sea	Oligotrophic	Spring 2012	0–200	16–25[c,g,h]	0.1–0.7[c,h]	–	Ortega–Retuerta et al. (2017)
Eastern Mediterranean Sea	Oligotrophic	Winter–Autumn 2008 Summer 2009	5	345 ±143.2 (116–420)	0.04 ± 0.01 (0.04–0.07)	–	Bar–Zeev et al. (2011)
Gulf of Aqaba (Eilat, Israel)	Oligotrophic	Spring 2008	5	110–228[c]	0.3–1.3[i]	–	Bar-Zeev et al. (2009)
Tropical Atlantic Ocean Pacific Ocean	Oligotrophic Oligotrophic	Spring–Summer 2011 Spring–Summer 2011	3 3	8.18 ± 4.56 24.45 ± 2.3	0.05–0.31	78.6 ± 9.3 357 ± 127	Iuculano et al. (2017b) Iuculano et al. (2017b)
Global Subtropical Atlantic, Indian and Pacific Oceans	Non bloom	Winter 2010–Summer 2011	0–200	14.0 (0.4–173.6)	0–3[c]	–	Mazuecos (2015)
North Indian Ocean -Arabian Sea -Bay of Bengal	Eutrophic	 -August 1996 -September 1996	0–1000	 -60 [j,k] (< 5–102[j]) -7–13[c,j]	–	–	Kumar et al. (1998), Ramaiah et al. (2000)
OAO OAO (CU excluded)	Oligotrophic	Autumn 2014	4	72 ± 74 (18–446) 60 ± 27(18–132)	0.4 ± 0.2 (0.2–0.6) 0.3 ± 0.1 (0.2–0.8)	236 ± 42 (81–1760) 183 ± 56 (81–360)	This study

CU				446	0.25	1760	
Ross Sea	Bloom	Spring 1994	Surface	308 (0–2800)	3.6 (0.3–8.8)	85	Hong et al. (1997)

a: TEP concentrations were given in µmol C L^{-1}. For transformation into XG units, the Engel and Passow (2001) conversion factor of 0.51 µg TEP-C L^{-1} per µg XG eq L^{-1} was applied.

b: 1–8 m

c: extracted from graphs

5 d: 5 m

e: TChl *a*

f: 0–200 m

g: Depth–averaged TEP

h: stations 6–9

10 i: DCM (30–40 m)

j: TEP concentrations were given in milligram equivalent of alginic acid L^{-1} and absorbance was measured at 745 nm instead of 787 nm

k: 0–50 m

15

20

Table 3. Regression equations and statistics describing the relationship between TEP and different variables throughout the TransPEGASO cruise (note all variables were $\log_{10}$–transformed). B= biomass.

		Open Atlantic Ocean (CU excluded)					SW Atlantic Shelf					All			
Dep. Var.	Ind. Var.	R^2	*p*	intercept	slope	n	R^2	*p*	intercept	slope	n	R^2	*p*	intercept	slope
TEP	SST	0.07	0.16			29	0.06	0.51			9	**0.48**	**< 0.001**	**3.80**	**-1.43**
	Salinity	**0.26**	**< 0.05**	**21.78**	**-12.84**	**29**	0.002	0.90			9	**0.57**	**< 0.001**	**25.13**	**-14.97**
	Solar irradiance 24 h	**0.43**	**< 0.001**	**5.67**	**-1.04**	**30**	0.08	0.40			10	0.02	0.33		
	Nitrate	0.06	0.21			30	0.002	0.91			10	**0.13**	**0.02**	**1.97**	**0.23**
	Phosphate	0.04	0.29			30	0.02	0.69			10	**0.37**	**< 0.001**	**2.39**	**0.58**
	Silicate	0.07	0.15			30	0.24	0.15			10	**0.19**	**< 0.005**	**1.75**	**-0.80**
	Chl *a*	**0.56**	**< 0.001**	**2.31**	**1.13**	**29**	0.16	0.24			10	**0.61**	**< 0.001**	**2.09**	**0.66**
	HPA	0.04	0.31			29	0.36	0.06			10	**0.60**	**< 0.001**	**-4.28**	**1.03**
	HNA	0.01	0.57			29	**0.46**	**0.03**	**-0.44**	**0.46**	**10**	**0.51**	**< 0.001**	**-2.31**	**0.75**
	LNA	0.02	0.43			29	0.02	0.71			10	**0.17**	**< 0.05**	**-1.96**	**0.68**
	Prochlorococcus B	0.002	0.80			30	-	-				**-**	**-**		
	Synechococcus B	**0.72**	**< 0.001**	**1.72**	**0.28**	**30**	0.005	0.84			10	**0.30**	**< 0.001**	**1.87**	**0.34**
	Picoeukaryotes B	**0.15**	**< 0.05**	**1.68**	**0.23**	**30**	0.005	0.84			10	**0.49**	**< 0.001**	**1.71**	**0.37**
	Diatoms B	**0.37**	**< 0.001**	**2.11**	**0.28**	**27**	0.42	0.058	2.55	0.16	9	**0.19**	**< 0.05**	**2.23**	**0.25**
	Dinoflagellates B	**0.18**	**< 0.05**	**1.79**	**0.40**	**27**	0.30	0.13			9	0.08	0.08		
	Coccolithophores B	0.01	0.59			27	0.002	0.90			9	**0.15**	**< 0.05**	**1.70**	**-0.23**
	"Other microalgae" B	**0.40**	**< 0.001**	**1.75**	**0.39**	**27**	0.0002	0.97			9	**0.27**	**< 0.001**	**1.86**	**0.28**
	Phytoplankton B	**0.47**	**< 0.001**	**1.04**	**0.61**	26	**0.62**	**< 0.05**	**0.43**	**1.00**	**9**	**0.62**	**< 0.001**	**0.99**	**0.70**

R^2 explained variance, *n* sample size, *p* level of significance

Table 4. Results of multiple regression analyses between TEP and combined variables, all log_{10}–transformed.

		OAO (CU excluded)				**SWAS**				**All**			
Dep. Var.	Ind.Var.	Partial coefficient	Partial *p*	R^2	*p*	Partial coefficient	Partial *p*	R^2	*p*	Partial coefficient	Partial *p*	R^2	*p*
TEP	Phyto B	0.67	< 0.001	0.53	< 0.001	0.82	< 0.05	0.66	< 0.05	**0.47**	**< 0.01**	**0.68**	**< 0.001**
	HPA	0.14	0.58			0.38	0.13			**0.48**	**< 0.05**		
	Phyto B	0.70	< 0.001	0.53	< 0.001	0.76	< 0.05	0.70	< 0.05	**0.54**	**< 0.001**	**0.71**	**< 0.001**
	HNA	0.06	0.70			0.28	0.08			**0.36**	**< 0.01**		
	Chl *a*	**1.26**	**< 0.001**	**0.67**	**< 0.001**	0.48	0.26	0.33	0.10	**0.39**	**< 0.005**	**0.66**	**< 0.001**
	HPA	**0.56**	**< 0.05**			0.59	0.08			**0.54**	**< 0.01**		
	Chl *a*	1.28	< 0.001	0.60	< 0.001	0.30	0.48	0.36	0.08	**0.47**	**< 0.001**	**0.67**	**< 0.001**
	HNA	0.20	0.20			0.42	0.06			**0.37**	**< 0.01**		

R^2 explained variance, *p* level of significance

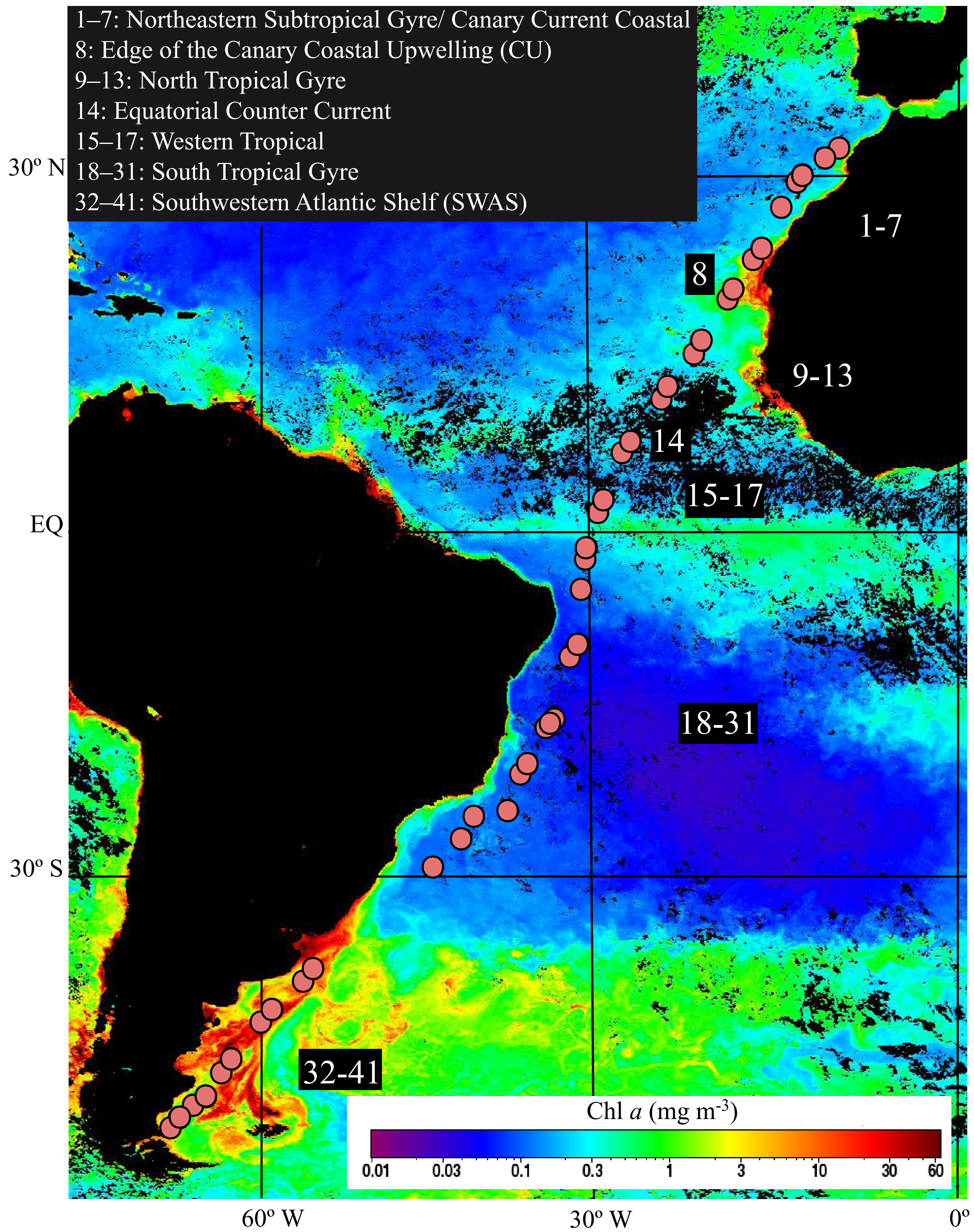
Figure 1: Hydrographic stations (filled circles) of the TransPEGASO cruise, sampled during October–November 2014 in the Atlantic Ocean. Chl *a* concentration (background color; mg m^{-3}) during November 2014 were taken from NASA MODIS AQUA 9–km Products composite.

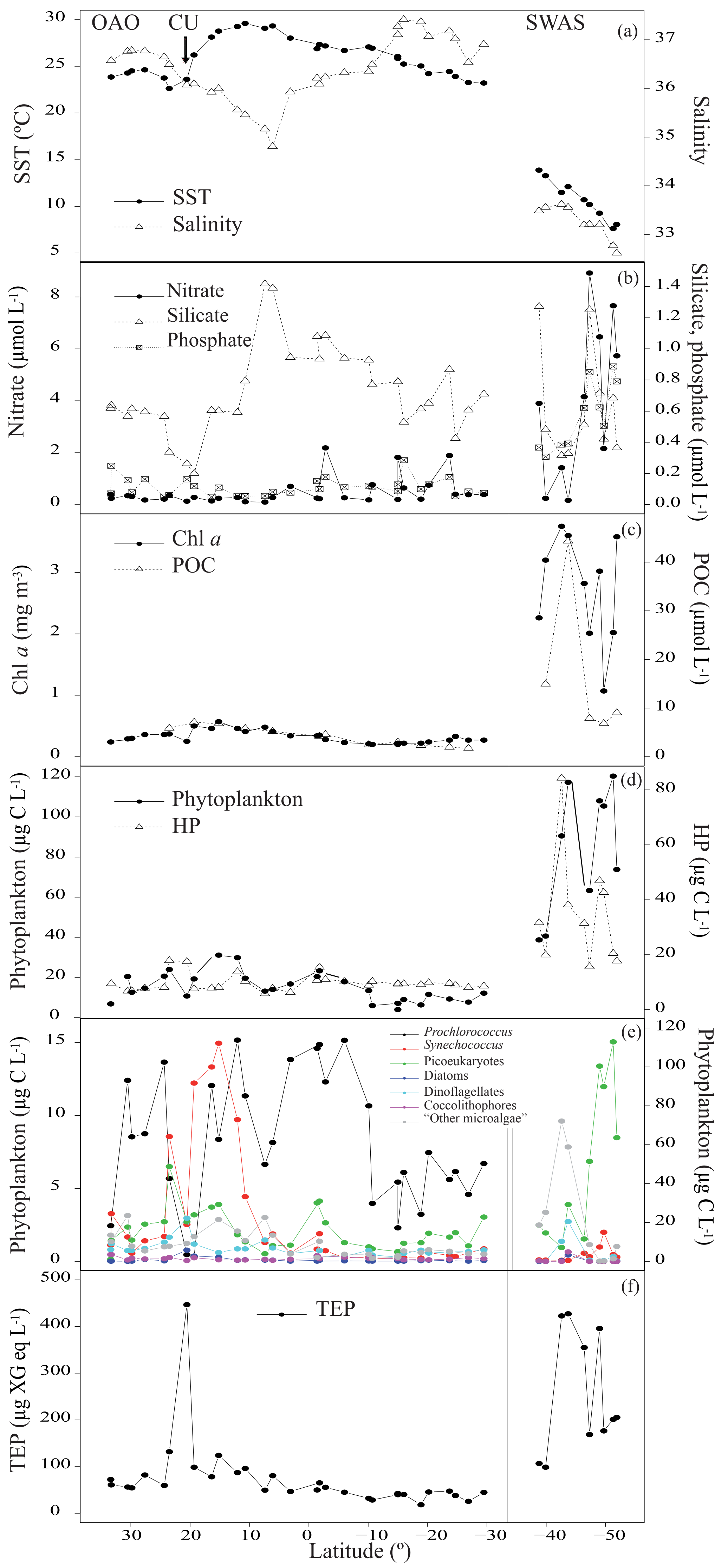
Figure 2: Variations of sea surface temperature (SST, ºC) and salinity (panel (a)), nitrate, silicate and phosphate (µmol L^{-1}) (panel (b)), Chl *a* (mg m^{-3}) and POC (µmol L^{-1}) (panel (c)), biomass of phytoplankton and HP (µg CL^{-1}) (panel (d)), biomass of *Prochlorococcus*, *Synechococcus*, picoeukaryotes, diatoms, dinoflagellates, coccolithophores and "other microalgae" (µg CL^{-1}) (panel (e): For OAO use left axis, for SWAS use right axis) and TEP (µg XG eq L^{-1}) (panel (f)) in the TransPEGASO cruise.

Figure 3: Average and standard deviation of the contribution of TEP, phytoplankton and HP to the POC pool (%) in the OAO and the SWAS.

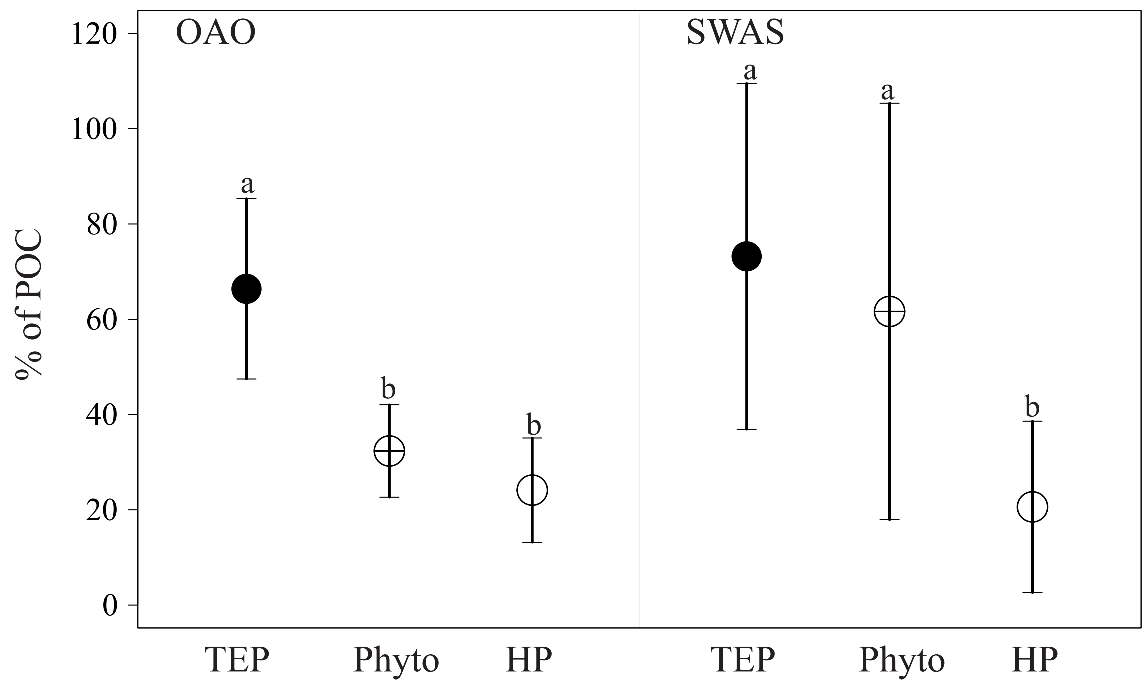
Figure 4: Relationship between the 24 hour–average (previous to sampling) solar irradiance (W m^{-2}) and TEP (µg XG eq. L^{-1}) in the OAO (CU sample excluded). The linear regression line is plotted and the equation indicated.

Figure 5: Relationship between TEP and Chl *a* concentration from the TransPEGASO cruise, with the linear regression line (regression equation in the text). Two regions are distinguished: open Atlantic Ocean (OAO, CU included, filled circles) and SW Atlantic Shelf (SWAS, empty circles). Regression lines from the literature are also shown for comparison. α and β indicate the y intercept and slope, respectively; log TEP (µg XGeq. L^{-1}) = α + β × log Chl *a* (mg m^{-3}); [a] α = 2.45 and β = 0.33, (Engel, 1998 in Passow, 2002a); [b] α = 2.25 and β = 0.65, (Hong et al., 1997); [c] α = 2.27 and β = 0.24, (Yamada et al., 2015); [d] α = 2.06 and β = 0.50, (Ramaiah and Furuya, 2002); [e] α = 1.63 and β = 0.39, (Passow and Alldredge, 1995); [f] α = 1.63 and β = 0.32, (Corzo et al., 2005); [g] α = 1.08 and β = 0.38, (Ortega–Retuerta et al., 2009b).

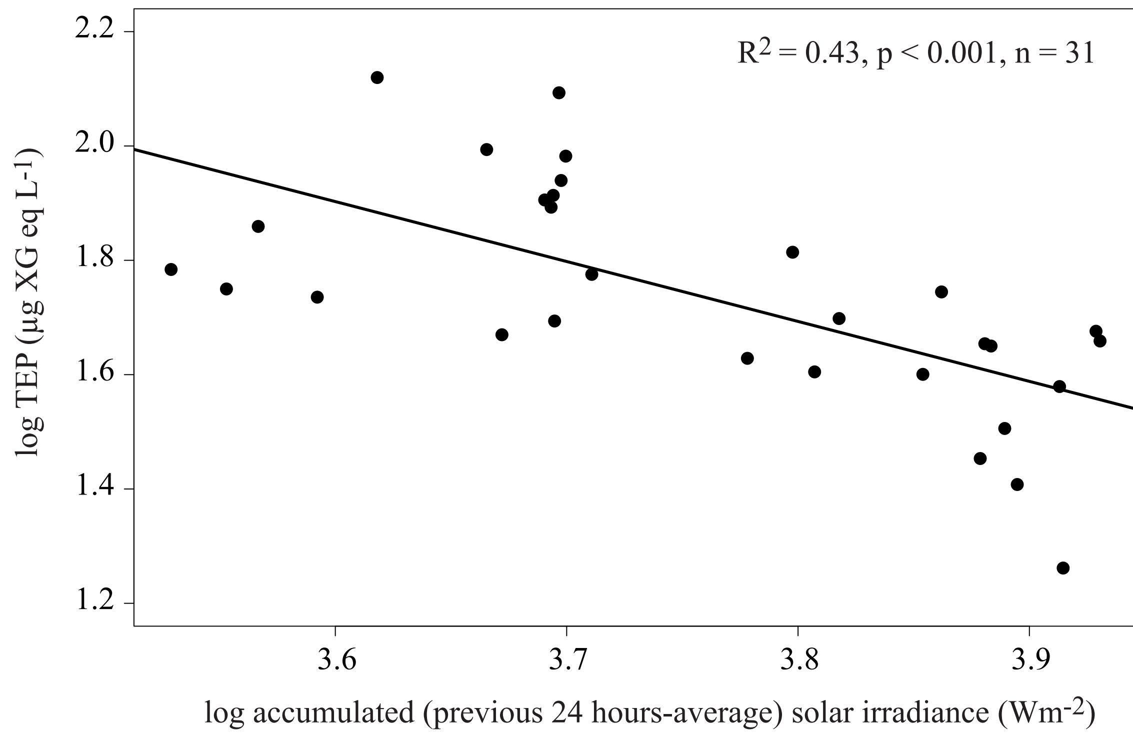

1–7: Northeastern Subtropical Gyre/ Canary Current Coastal
8: Edge of the Canary Coastal Upwelling (CU)
9–13: North Tropical Gyre
14: Equatorial Counter Current
15–17: Western Tropical
18–31: South Tropical Gyre
32–41: Southwestern Atlantic Shelf (SWAS)
30º N
EQ
30º S
60º W
30º W
0º
1-7
8
9-13
14
15-17
18-31
32-41
Chl a (mg m-3)
0.01
0.03
0.1
0.3
1
3
10
30
60

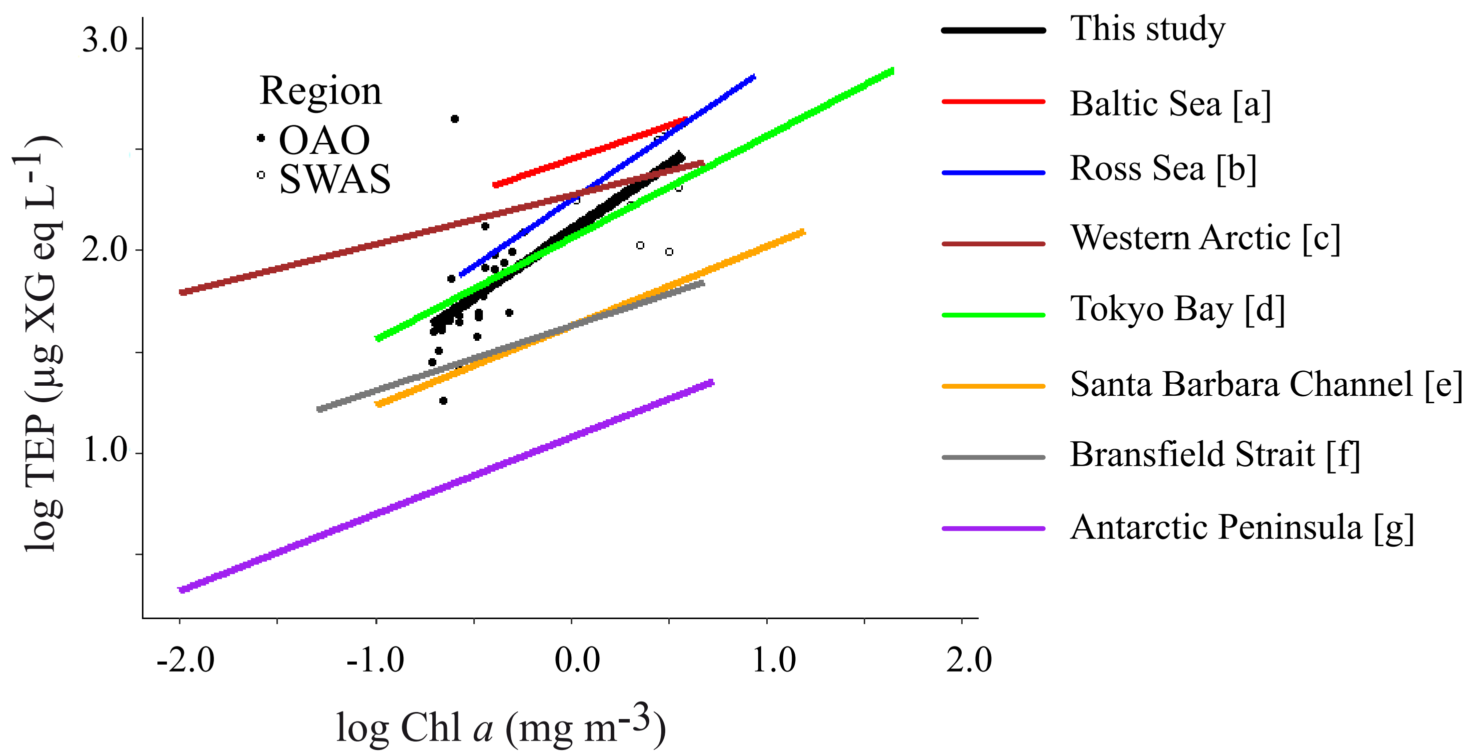


OAO
CU
SWAS
(a)
SST (ºC)
Salinity
SST
Salinity
(b)
Nitrate
Silicate
Phosphate
Nitrate (µmol L-1)
Silicate, phosphate (µmol L-1)
(c)
Chl a
POC
Chl a (mg m-3)
POC (µmol L-1)
(d)
Phytoplankton
HP
Phytoplankton (µg C L-1)
HP (µg C L-1)
(e)
Prochlorococcus
Synechococcus
Picoeukaryotes
Diatoms
Dinoflagellates
Coccolithophores
"Other microalgae"
Phytoplankton (µg C L-1)
Phytoplankton (µg C L-1)
(f)
TEP
TEP (µg XG eq L-1)
Latitude (º)



OAO
SWAS
% of POC
120
100
80
60
40
20
0
a
b
b
a
a
b
TEP
Phyto
HP
TEP
Phyto
HP


R2 = 0.43, p < 0.001, n = 31
log TEP (µg XG eq L-1)
2.2
2.0
1.8
1.6
1.4
1.2
3.6
3.7
3.8
3.9
log accumulated (previous 24 hours-average) solar irradiance (Wm-2)


3.0
2.0
1.0
log TEP (µg XG eq L-1)
Region
OAO
SWAS
-2.0
-1.0
0.0
1.0
2.0
log Chl a (mg m-3)
This study
Baltic Sea [a]
Ross Sea [b]
Western Arctic [c]
Tokyo Bay [d]
Santa Barbara Channel [e]
Bransfield Strait [f]
Antarctic Peninsula [g]