## Reply to Referee#1

*We thank the reviewer for his valuable comments on our manuscript. We answer below to each comment and question.*

**This is a good manuscript that provides excellent summary of TEP information. A good synthesis of data at hand despite the limitations of coverage in space (data collected only at 4m and at times the discussion is based on 1 sample to represent a hydrographic domain, say CU).**

*We thank the reviewer for his supportive comments. We were not trying to represent a hydrographic domain with a single sample, but we just treated the CU as an independent sample (i.e. removing it when calculating TEP averages and regression analyses between TEP and other environmental and biological parameters) due to its particularity, as indicated in the objectives section (end of the introduction). We are aware that some sentences could have given that impression and we did our best to fix this in the revised version of the MS. For example we have changed the following sentences:*

*Line 46: "with the maximum concentrations in the SWAS and in a station located at the edge of the Canary Coastal Upwelling (CU)"*

*Line 216: "and presented the minimum concentrations in the CU station and surroundings"*

*Lines 308-309: "namely in the station located in the CU and within the SWAS"*

*Line 366: "with the maximum value in the station located in the CU"*

*Lines 372-373: "The highest TEP:Chl a ratio of the entire transect observed in the station located in the CU was probably associated with the high relative abundance of diatoms and dinoflagellates."*

**The authors made the point that TEP contributes majorly to POC than phytos and HP based on the quantification of TEP, phytos and HP carbon pools estimated from available conversion factors. That the authors are well aware of limitations/approximations of these conversion factors, semi-quantitative nature estimations of TEP, phytos and HP pools (the last two are based on cell numbers) one would have expected the authors to critically evaluate their % contributions keeping the associated overall errors (methodology+conversion). This may not alter their conclusions but convinces the readers with appropriate comparisons having taken errors into account. I recommend minor revision of this manuscript before it is accepted for publication.**

*We added information in the manuscript regarding the errors associated with the methodology and conversion factors. More specifics are given in the responses below.*

**1. Lines 65-66: 'Enhancing particle sinking' – The authors may want to see open ocean TEP information from North Indian Ocean (Kumar et al., 1998)**

*We added the suggested reference in the revised version of the MS.*

**2. Line 67: 'can also ascent' gives a meaning that TEP float by themselves but these are mainly transported to surface microlayer by rising bubbles through scavenging**

*We changed the sentence to (lines 70-72): "On their way to aggregation, and due to their low density, TEP and TEP–rich microaggregates formed near the surface may ascend and accumulate in the sea surface microlayer (SML) (Engel and Galgani, 2016), a process that is largely enhanced by bubble-associated scavenging (Azetsu-Scott and Passow, 2004; Wurl et al., 2009; Wurl et al., 2011b)."*

**3. Lines 109-110: "in situ studies of TEP distributions in the ocean are scarce, particularly in the open ocean (Table 2)". But Table 2 specifies TEP in surface layers. Kumar et al. (1998) and Ramaiah et al. (2000) provided the first TEP open ocean data from the Indian Ocean (see below for references).**

*We thank the reviewer for drawing our attention to these references. We have specified in the text and figure legend that we are referring to surface measurements. Note that, for the sake of direct comparison with our study, Table 2 only listed TEP measurements conducted with the spectrophotometric method and Xanthan Gum calibration. However, in order to be more inclusive, we have added the indicated references, as follows.*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 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) |
| North Indian Ocean<br>-Arabian Sea<br>-Bay of Bengal | -Eutrophic | -August 1996<br>-September 1996 | 0–1000 | -60[j,k] (<5–102[j])<br>-7–13[c,j] | | | Kumar et al., (1998), Ramaiah et al., (2000) |

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

**4. Line 115: 'entire POC' will also include non-living non-TEP organic carbon fraction. This was not addressed in the manuscript.**

*We are aware that POC also includes other organic particle fractions such as non-living non-TEP organic carbon (for instance, cell fragments and proteinaceous - Coomassie stainable particles). In the present work we decided to compare our target variable, TEP, with the two pools of POC that are considered most abundant in sea water, namely phytoplankton and heterotrophic prokaryotes. We have added the following sentence in the results to clarify it (lines 265-271):*

*"To better explore the importance of TEP–C with respect to other major quantifiable POC pools, we estimated phytoplankton biomass (phyto–C) and HP biomass (HP–C) throughout the whole cruise (Fig. 2). It is worth mentioning that POC also includes other fractions of non-living non-TEP organic carbon (e.g., cell fragments and Coomassie stainable particles), but phytoplankton and heterotrophic prokaryotes are generally considered the most abundant in open sea water (Ortega-Retuerta et al., 2009b; Yamada et al., 2015). TEP–C contributed the most to the POC pool in the OAO, where it represented twice the share of phyto-C and HP-C. In the SWAS, conversely, TEP-C was not significantly different than phyto-C, and three times higher than HP-C (Fig. 3)."*

**5. Lines 147-148: Given the 18.7% difference in concentrations between TEP duplicates specify the errors in TEP-C estimation to compare with other org C-reservoirs.**

*Errors in TEP-C estimations averaged 8.4 µg C $L^{-1}$ (0.2- 70.3 µg C $L^{-1}$). However, rather than including these numbers, we have propagated the errors in the orf C reservoir calculations (error bars in Fig. 3).*

**6. Lines 175 to 202 and Lines 283-287: How accurate is the cell abundances counting of the respective biological groups? Please specify uncertainties involved. This is particularly important because each of subgroups will carry uncertainties in carbon per cell and that will be additive. Total uncertainties involved assume significance since a comparison is being made with TEP-C, where TEP estimation itself is semi-quantitative! For example, line 232-233 show phytoplankton biomass estimation carries nearly 50% of uncertainties in cell counts and cell C estimations! Authors discussion (Lines 343-353) on uncertainties in TEP-C contribution to POC arising from cell-C conversion and analytical artifacts is well appreciated. But the authors should help the readers by providing a comparative evaluation including errors in estimated carbon pools in a Table.**

*Replicates for the prokaryotic abundance measurement with flow cytometry were not done because the standard errors obtained are usually very low (i.e around 1.5 % in Pernice et al. (2015)).*

*Lines 190-191: "Only one replicate was analysed since standard errors of duplicates are usually very low (around 1.5 % in Pernice et al., 2015)."*

*Microscopic observations must be interpreted with caution due to the following (Kozlowski et al., 2011; Cassar et al., 2015):*

- *They are biased towards relatively large forms (> 5 µm) of phytoplankton groups with identifiable morphological characteristics*
- *Problems associated with biovolume estimates*
- *Problems with the microscopic identification of naked and small-celled groups*

*Lines 168-170: "Uncertainty sources for micro-phytoplankton biomass estimates are the conversion factors, biovolume estimates, and proper identification based on morphological characteristics, harder for naked cells*

*and those at the lower size edge (5-10 µm) (Kozlowski et al., 2011; Cassar et al., 2015)."*

*Regarding the phytoplankton biovolume-to-carbon conversion factors, we show the 95 % confidence intervals obtained by Menden-Deuer and Lessard (2000) for phytoplankton biomass estimation: log pg C cell$^{-1}$=log a (95 % C.I.) + b (95 % C.I.) x log V (µm$^3$), where log a is the y-intercept, b is the slope and 95% C.I. is the 95 % confidence intervals:*

*Protist plankton: log pg C cell$^{-1}$=log -0.665 (0.132) + 0.939 (0.041) x log V (µm$^3$)*
*Diatoms: log pg C cell$^{-1}$=log -0.541 (0.099) + 0.811 (0.028) x log V (µm$^3$)*

*Lines 164-167: "Cell C content was calculated using conversion equations of Menden-Deuer and Lessard (2000), log pg C cell-1 = log a (95 % confidence intervals) + b (95 % confidence intervals) × log volume (V; µm3): one for diatoms (log pg C cell-1 = log -0.541 (0.099) + 0.811 (0.028) × log V) and one for the other algae groups (log pg C cell-1 = log -0.665 (0.132) + 0.939 (0.041) × log V)."*

*As for the bacterial cell-to-carbon conversion factor, we added the following explanation:*

*Lines 194-197: "Ducklow (2000) summarized the carbon contents of free-living marine bacteria reported in the literature for a number of oceanic regions, bays and estuaries. The average ± standard deviation for open ocean regions was 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), fgC cell$^{-1}$ = 0.12 (µm$^3$ cell vol)$^{0.72}$, for an average bacterial biovolume of 0.04 µm$^3$."*

*In relation to line 222-223: "The phytoplankton biomass was generally dominated by Prochlorococcus, with an average of 233 1.68 × 10$^5$ ± 0.81 × 10$^5$ cells mL$^{-1}$, which corresponded to a biomass of 8.58 ± 4.16 µg C L$^{-1}$.", the standard deviation of biomass is not the uncertainty of the estimate, but the variability (standard deviation) of biomass along the Northeastern Subtropical Gyre.*

**7. Line 310: 'we present the first inventory of surface TEP concentration' – can the seawater samples collected from 4 m depth be treated as representative of surface layer to make an inventory? Here seems to be an incompatibility that needs to be clarified.**

*We agree with the reviewer that 4 m may at times not be representative of surface waters. Relatively high variability within the top surface meters has sometimes been observed (Wurl et al., 2009). However, 4 meters is usually considered as surface in most oceanographic studies, where sampling is mostly*

*conducted either with the CTD rosette or with an underway pumping system. Nonetheless, the word 'inventory' may induce misunderstanding, and we changed it to 'distribution'. We have modified lines 290-293 of the manuscript as follows:*

*"We present the first distribution of surface (4 m) TEP concentration along a latitudinal gradient in the Atlantic Ocean, covering both open sea and shelf waters. It is worth mentioning that vertical variability within the top surface meters (< 4 m) has sometimes been observed (Wurl et al., 2009), but 4 m is usually considered "surface ocean" in studies where samples are collected with either an oceanographic rosette or an underway pumping system."*

**8. Lines 360-364: Given the large uncertainties involved statements such as 'Only in one station of the SWAS phyto–C dominated the TEP–C (line 360-1)' and 'with the maximum concentrations in the edge of the Canary Coastal Upwelling (CU, n = 1) (lines 45-46)' may be avoided as these oversimplify a complex reality of spatial variability in horizontal and vertical (see line 310 comment above) dimensions.**

*As explained above, we were not trying to represent a hydrographic domain with a single sample, so, we made the appropriate changes in the text to clarify that we are just referring to our dataset without any purpose to generalise. E.g.:*

*Lines 45-46: "with the maximum concentrations in the station located in the edge of the Canary Coastal Upwelling (CU) and the SWAS"*

**10. Line 448: Please show the negative relation in a diagram.**

*We have added this plot as Fig. 4:*

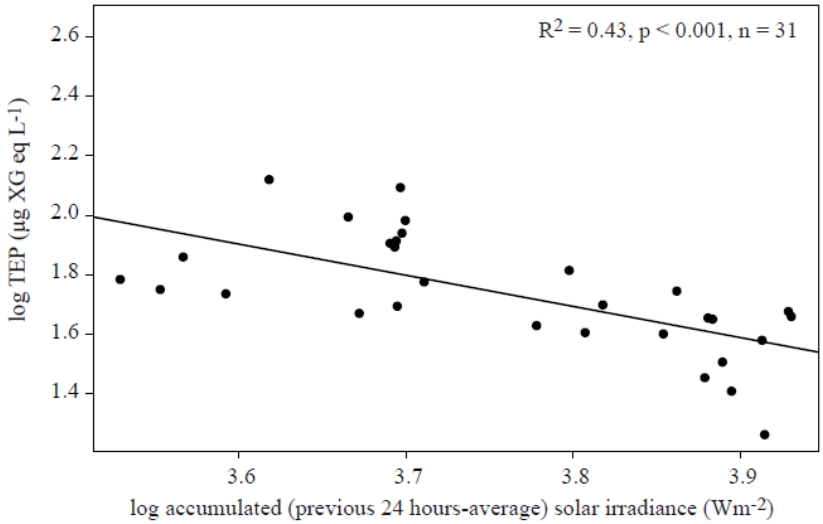


*Figure 4: Relationship between the 24 hour–average (previous to sampling) solar irradiance (W m-2) and TEP (µg XG eq. L-1) in the OAO (CU sample excluded). The linear regression line is plotted and the equation indicated.*

**11. Lines 462-463: Figure 3 suggests that in spite of higher (nearly double) contribution of phytos to %POC in SWAS than in OAO, TEP and HP contributions to %POC are nearly the same. It appears that HP is more important in regulating TEP concentrations in the Atlantic, in general. This is slightly different from what has been said in lines 472-473 (The drivers of TEP distribution were primarily phytoplankton and, to a lesser extent, heterotrophic prokaryotes)**

*The identification of drivers of TEP distribution is based on regression analyses of covariation (Table 3). In OAO, the largest share of TEP variance is explained by Chl a ($R^2$=0.56) and phytoplankton biomass (0.47), particularly Synechococcus biomass (0.72), and in the SWAS it is phytoplankton biomass (0.62) followed by High nucleic acid containing prokaryotic heterotrophs (0.46). The fact that phytoplankton mainly drive TEP variability despite very different contribution to total POC is further exemplified by the large difference in the TEP:Chl a ratio between the two regions. In other words, the two regions are characterized by phytoplankton differently prone to TEP production, but in both phytoplankton are the main TEP drivers.*

## REFERENCES


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## Reply to Referee #2

**General comments**

**This is a good manuscript, well written and very informative about TEP distribution in surface waters of the Atlantic Ocean, taking into account many other studies. The main limitations, in my opinion, rely on the number of data collected and the depth, only at 4 m, which probably underestimates other processes related to TEP presence especially close to the depth of the chlorophyll maximum.**

> *We thank the reviewer for his/her positive general comments. We fully agree that it would be more informative to show vertical TEP profiles within the euphotic layer, but we consider that the study, which was carried out during a transit (i.e. no opportunities for CTD stations), adds valuable information for many processes happening at the ocean surface, as pointed out in the introduction.*

**As pointed out by the other referee, conversions factors may be approximative and a proper critical consideration on any limitation should be included in the manuscript.**

> *We have added information about the uncertainty of phytoplankton and heterotrophic prokaryotes biomass estimate (see responses to Referee#1).*

**Another general recommendation: TEP importance in processes such as air-sea gas exchange, aerosol formation, marine snow and carbon export and cycling should be better addressed in the whole study, as focal points of TEP influence on carbon dynamics, please see my comments in the introduction and discussion. I recommend that the following points are addressed before publication.**

**Abstract:**

**Lines 37-38: The authors should be aware that air-sea gas exchange and aerosol emissions are complex processes, which are not properly explained in the manuscript. I would thus remove this sentence that in the abstract appears a bit vague and would concentrate on the role of TEP in channeling the carbon produced by primary productivity (see Mari et al. 2017).**

> *We appreciate the reviewer's comment. We removed the sentence about aerosol emission. We have mentioned the role of TEP channeling the biological pump.*
>
> *Lines 36-39: "Transparent exopolymer particles (TEP) are a class of gel particles, produced mainly by microorganisms, which play important roles in biogeochemical processes such as carbon cycling and export. TEP (a) are colonized by carbon-consuming microbes; (b) mediate aggregation and sinking of organic matter and organisms, thereby contributing to the biological carbon pump; and (c) accumulate in the surface microlayer (SML) and affect air–sea gas exchange."*

**Lines 50-51: it could also be an inhibited TEP-aggregation by UV, not just breaking. I would rephrase the sentence.**

*We have change this sentence in the revised version of the MS as follows (line 50:*
*"suggesting that sunlight, particularly UV radiation, is more a sink than a source for TEP. "*

*We also mentioned it in the introduction (see comments below), and the discussion:*

*Lines 411-412: "Ultraviolet (UV) radiation causes TEP loss by photolysis (Ortega-Retuerta et al., 2009a) and inhibits TEP formation from precursors (Orellana and Verdugo, 2003)."*

*Lines 414-415: "Our results suggest that the roles of UV radiation in breaking up TEP and/or limitating their formation from precursors overcome UV stress–induced TEP production."*

**Introduction:**

*We thank the reviewer for his/her thorough effort to improve the introduction section of our manuscript.*

***Lines 63-75: The introduction is a bit vague, I would introduce the concept of a marine gel, the composition and cross-links in the molecule that make TEP water insoluble but still subject to fragmentation and further aggregation processes, and the size distribution in the ocean, mentioning the size range we are talking about. 0.4 μm falls into the truly dissolved phase, and a discussion on the continuum of sizes linking DOM and POM should be added.***

*We have added the concept of DOM-POM continuum and evoke the gel polymer theory introducing a sentence like this in the revised version of the MS (lines 59-64): "Transparent exopolymer particles (TEP) are defined as a class of non–living organic particles in aqueous media, mainly consisting of acidic polysaccharides, which are stainable with Alcian Blue (Alldredge et al., 1993). They are formed from dissolved precursors that self–assemble to form TEP (operationally defined as particles > 0.4 μm) (Passow and Alldredge, 1994; Chin et al., 1998; Thuy et al., 2015). TEP are stabilized by covalent links or ionic strength (Cisternas-Novoa et al., 2015) and therefore, the formation and fragmentation of TEP from/to dissolved precursor material spans the dissolved to particulate continuum of organic matter in the sea.". However, one could consider 0.4 μm as a fraction included in the particulate phase if the 0.2 μm cutoff (one most widely used) is taken into account.*

**Several species can directly release TEP or macrogels, but such macromolecules can also form from dissolved abiotic material in the absence of phytoplankton (Chin, W.-C., Orellana, M.V., Verdugo, P., 1998. Spontaneous assembly of marine dissolved organic matter into polymer gels. Nature 391, 568–572.)**

*We already mentioned this process in former line 82 but we have made sure that the spontaneous assembly of DOM into TEP is not hidden (See comment above).*

**Moreover, the importance of TEP and marine snow should be mentioned. The role of TEP in the sea-surface microlayer should be either expanded or left out. The description presented here about air-sea gas exchange and aerosol is a bit vague and not precise. I would suggest spending more words on it, especially because 4 m depths is close to the surface so surface ocean processes and air-sea interaction should be properly mentioned. The role of TEP in the sea-surface microlayer depends on many factors: wind speed, primary productivity, and they are not the only class of gel particles present (e.g., highly productive region, see Engel and Galgani 2016, Biogeosciences, Wurl, O., Miller, L., Röttgers, R., and Vagle, S.: The distribution and fate of surface-active substances in the seasurface microlayer and water column, Mar. Chem., 115, 1–9, 2009. Wurl, O., Miller, L., and Vagle, S.: Production and fate of transparent exopolymer particles in the ocean, J. Geophys. Res., 116, C00H13, doi:10.1029/2011JC007342, 2011).**

*We added a few sentences to better introduce why TEP accumulates in the sea surface, implications and factors affecting this accumulation.*

*Lines 59-78: "Transparent exopolymer particles (TEP) are defined as a class of non–living organic particles in aqueous media, mainly consisting of acidic polysaccharides, which are stainable with Alcian Blue (Alldredge et al., 1993). They are formed from dissolved precursors that self–assemble to form TEP (operationally defined as particles > 0.4 µm) (Passow and Alldredge, 1994; Chin et al., 1998; Thuy et al., 2015). TEP are stabilized by covalent links or ionic strength (Cisternas-Novoa et al., 2015) and therefore, the formation and fragmentation of TEP from/to dissolved precursor material spans the dissolved to particulate continuum of organic matter in the sea. Due to their stickiness, TEP favour the formation of large aggregates of organic matter and organisms (typically named marine snow), enhancing particle ballast and sinking and thereby contributing to the biological carbon pump (Logan et al., 1995; Kumar et al., 1998; Passow et al., 2001; Burd and Jackson, 2009). The presence of TEP also affects the microbial food–web, as they can be used as a food source for zooplankton (Decho and Moriarty, 1990; Dilling et al., 1998; Ling and Alldredge, 2003) and heterotrophic prokaryotes (HP) (Passow, 2002b) through microbial colonization of aggregates (Alldredge et al., 1986; Grossart et al., 2006; Azam and Malfatti, 2007). On their way to aggregation, and due to their low density, TEP and TEP–rich microaggregates formed near the surface may ascend and accumulate in the sea surface microlayer (SML) (Engel and Galgani, 2016), a process that is largely enhanced by bubble–associated scavenging (Azetsu-Scott and Passow, 2004; Wurl et al., 2009; Wurl et al., 2011b). This accumulation in the SML, also contributed by local TEP production (Wurl et al., 2011b), can supress the air–sea exchange of CO2 and other trace gases by acting as a physicochemical barrier or modifying sea surface hydrodynamics at low wind speeds (Calleja et al., 2008; Cunliffe et al., 2013; Wurl et al., 2016). Sea surface TEP can also be released to the atmosphere by bubble bursting (Zhou et al., 1998; Aller et al., 2005; Kuznetsova et al., 2005), contributing to organic aerosol and possibly acting as cloud*

*condensation nuclei and ice nucleating particles (Orellana et al., 2011; Leck et al., 2013; Wilson et al., 2015). All in all, TEP play important roles in microbial diversity, carbon cycling and carbon exports to both the deep ocean and the atmosphere."*

**Line 69: specify what do you mean by "affect air-sea gas exchange".**

*Some studies, revised in Cunliffe et al. (2013), show the influence of surface active components of the SML (including biogenic polysaccharides) on air-sea gas exchange, either acting as a physicochemical barrier or modifying sea surface hydrodynamics, which in turn results in a suppression of air-water gas exchange. For example, Calleja et al. (2008) found that the organic matter content of the surface water supressed $CO_2$ gas exchange between the air and the ocean at low and intermediate wind speeds (> 5 m $s^{-1}$). Wurl et al. (2016) found enrichments of TEP, POC, PON, total prokaryotic cell numbers and picophytoplankton abundances in sea microlayers at multiple stations of different regions, compared to the underlying bulk water, being higher in slick surfaces than non-slick ones, and estimated that slicks could reduce $CO_2$ fluxes by up to 15 %, which highlight the importance of slicks in regulating air-sea interactions. Jenkinson et al. (2018) reviewed recently known and suspected mechanical aspects of how biologically produced organic matter modulates air-sea fluxes of $CO_2$.*

*We have briefly added some of this information in the introduction section. See comment above.*

**Lines 70-71: caution is needed here. Orellana et al. discuss about micro and nanogels, determined with a different method with respect to the one reported here. When gels are present in the sea-surface microlayer, it will depend on their size distribution whether they will be part of the organic aerosol fraction or not. Aerosol particles smaller than 1 µm will be part of the accumulation mode of sea-spray aerosols, but when further aggregating and reaching sizes above 2.5µm they won't actually stay in the atmosphere longer than a few hours – as their size distribution is described as coarse mode aerosols. TEP as macromolecules are between accumulation and coarse mode but not ice-nucleating particles or cloud condensation nuclei. Another consideration is that if high wind speed are present (above 5 m/s), there might be increased aggregation rates of TEP with solid particles which will favour the formation of negatively buoyant aggregates that will sink out of the surface microlayer and surface waters in general.**

*We agree with the reviewer that the microgels measured by Orellana et al. (2011), defined as those stabilized with calcium bridges, may not fully correspond to TEP, defined by their stainability with Alcian Blue (thus on their polysaccharide composition). However, some studies have demonstrated that some TEP (about 30 %) are also stabilized by divalent cations (Passow, 2002; Cisternas-Novoa et al., 2015). In addition, even though TEP were measured in the particulate phase, we believe that TEP precursors could be measurable whenever TEP are present if they are in a dynamic equilibrium with their precursors (Verdugo, 2012). Thus exopolymers in the dissolved and colloidal phases, i.e. those potentially acting as CCN, would covary with TEP*

*concentration (hypothesis yet to test). Furthermore, the exopolymer particles could depolymerise in the atmosphere due to ultraviolet light (Orellana and Verdugo, 2003) or acidification (Chin et al., 1998) and form nano-sized particles (Karl et al., 2013). It is also worth mentioning that Kuznetsova et al. (2005) found the presence of TEP (i.e. Alcian Blue-stained polymers) in natural and simulated marine aerosols, and Russell et al. (2010) showed the high carbohydrate composition of submicron aerosols in remote regions of the North Atlantic and Arctic oceans that contained organic hydroxyl groups from primary emissions of the ocean.*

*Since this is not the subject of the manuscript, we have not included this discussion but have toned down a bit the statement referring to aerosol and clouds:*

*Lines 76-77: "contributing to organic aerosol and possibly acting as cloud condensation nuclei and ice nucleating particles (Orellana et al., 2011; Leck et al., 2013; Wilson et al., 2015)."*

**Line 80: not just photolysis but also UV inhibited aggregation of precursor polymers limits TEP formation.**

*We have added the following information in the revised version of the manuscript:*

*Lines 98-99: "high solar radiation can stimulate TEP production by Prochlorococcus during cell decay (Iuculano et al., 2017), but also can limit TEP formation inhibiting the aggregation of the precursor polymers (Orellana and Verdugo, 2003)."*

**Line 102: What does this sentence mean? Please explain how HP affect TEP production and assembly of precursors.**

*Several experiments have found that the presence of bacteria stimulate or are necessary for TEP production by diatoms. Specifically, Guerrini et al. (1998) observed that the presence of bacteria during phosphate limitation conditions in batch cultures stimulated the production of polysaccharides by the diatom Cylindrotheca fusiformis. Gärdes et al. (2011) demonstrated that specific bacterial strains attached to the diatom Thalassiosira weissflogii was necessary for TEP production and suggested that direct interaction between bacteria and diatoms could be required for TEP formation.*
*Moreover, through different mechanisms, HP seem to facilitate the self–assembly of dissolved precursors into TEP. In a seawater culture experiment, Sugimoto et al. (2007) observed that TEP formation appeared to be related with increases in bacterial abundance. Bacterial TEP production was not enough to explain the overall TEP formation and they suggested the self-assembly of TEP precursors coupled with bacterial growth. Ding et al. (2008) demonstrated that the amphiphilic exopolymers released by the bacterium Sagitula stellata induced DOM self-assembly and formation of marine microgels.*
*We have added some of this previous information to better explain the processes involving prokaryote-TEP relationships.*

*Lines 100-103: "HP have been found to stimulate TEP production by diatoms, suggesting that HP-diatom interaction is required for TEP formation (Guerrini et al., 1998; Gärdes et al., 2011). HP may also facilitate TEP production from DOM self-assembly (Sugimoto et al., 2007), e.g., through the release of amphiphilic exopolymers that induce microgel formation ( Ding et al., 2008)."*

**Line 106: I suggest introducing the concept of biological carbon pump and the importance of TEP in ocean carbon cycle, as this is a central idea of the study. How much estimated primary production carbon is channeled into the TEP pool? (See Mari et al., 2017). This could also help making confrontations with phytoplankton-derived carbon, still estimates but could be interesting.**

*We have introduced the concept of biological carbon pump and the importance of TEP in the ocean carbon cycle. Beginning of the Introduction (lines 64-67):*
*"Due to their stickiness, TEP favour the formation of large aggregates of organic matter and organisms (typically named marine snow), enhancing particle ballast and sinking and thereby contributing to the biological carbon pump (Logan et al., 1995; Kumar et al., 1998; Passow et al., 2001; Burd and Jackson, 2009)."*

*As for how much PP is channelled into TEP, we added the following:*
*Lines 104-109: "The aforementioned importance of TEP in carbon fluxes in the pelagic ocean can be further stressed by considering the following rough numbers: if the percentage of extracellular carbon release during planktonic primary production is generally constrained within 10-20 % (Nagata, 2000) but can reach >50% (López-Sandoval et al., 2011), and half of the extracellular release is in the form of reactive polysaccharides (Biddanda and Benner, 1997), then the production rate of TEP precursors may represent 5-10 %, but reach >25%, of planktonic primary production, without considering production by heterotrophs."*

**Lines 107-108: As mentioned already, TEP span over a wide range - DOC or POC is just an operational definition. From colloids (dissolved) to macrogels (particulate) (see Verdugo 2012 Annual Rev. of marine sciences).**

*We thank the reviewer for her/his comment. We made the following changes to clarify it:*

*Lines 109-110: "This calls for the need to quantify their occurrence across the oceans, elucidate their main distribution drivers, and determine their contribution to the organic carbon reservoir."*

*In the objectives section (end of introduction section), we changed the first sentence (lines 111-112) to "we describe the horizontal distribution of TEP (> 0.4 µm) in surface waters across a North–South transect in the Atlantic Ocean,"*

**Methods:**

**If you have DOC data, I think it would be worth showing them and looking for the missing fraction that drives POC underestimation with respect to TEP, as TEP are connecting both pools of organic matter. Can you provide a standard deviation or error estimation for POC filters?**

*Unfortunately, we don't have DOC data and there was only one replicate per POC measurement. However, we added that the reproducibility of the elemental analyser used to measure POC (based on the coefficient of variation of the calibration slopes) is about 1 % for carbon. Regarding the coefficient of variation of the replicates, which takes into account the reproducibility of the whole process (sampling, filtering and analysis), we have obtained, in previous studies, a value of around 5 %.*

*We added the following:*

*Line 147-148: "No POC replicates were run, but replication in a previous study yielded a coefficient of variation of around 5 %."*

**Do you have wind speed information? This would be useful in estimating whether TEP could accumulate in the surface layer.**

*We have wind speed information but we can't estimate TEP relative accumulation in the surface layer as we only have data at one depth. The regression of TEP vs wind speed gave $R^2$=0.2 in OAO and 0.3 in the SWAS, both with a negative slope. Contrasting results have been found in previous studies: Engel and Galgani (2016) found depletion of TEP in the SML above 5 m $s^{-1}$, while earlier observations found enrichment in the microlayer also at higher wind speed (Wurl et al., 2009; Wurl et al., 2011).*

**Discussion:**

**Lines 317-319: Can you provide any reason why you think your values are higher than those observed in the Mediterranean Sea and Pacific Ocean? Is it related to nutrient concentration/time of year, different analysis method (e.g. spectroscopy vs microscopy for gel particles identification), depth?**

*We believe that one of the reasons is the depth. Mean TEP values in some of them (Ortega-Retuerta et al., 2010; Kodama et al., 2014; Ortega-Retuerta et al., 2017) correspond to the upper mixed layer depth or from 0 to 200 m. As TEP tend to accumulate in the surface and our values correspond only to the surface, this could explain the higher values obtained in our dataset. In fact, if we had provided integrated measurements within the photic layer, we would probably have obtained a lower mean TEP concentration.*
*Another reason seems to be the different Chl a concentrations, as the main TEP producer is phytoplankton. Chl a 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 Table. For example, in Iuculano et al. (2017) Chl a ranged 0.05-0.31 mg $m^{-3}$, and in Kodama et al. (2014) Chl a averaged 0.05 ± 0.01 mg $m^{-3}$. In some cases it*

*is a pity that we don't have the average values, as the range could be a little bit misleading. However, in Ortega-Retuerta et al. (2010), TEP:Chl a ratio was higher than ours, suggesting that Chl a values were also low and gave rise to lower TEP. We can't forget either that differences in TEP chemical composition could cause differences in staining capacity. Regarding analytical methods, all the studies gathered in the table used the spectroscopic method, so this can't be the reason for the contrasting TEP concentrations.*

*We have briefly included these arguments in the discussion:*

*Lines 300-307: "Mean TEP values in some of them (Ortega-Retuerta et al., 2010; Kodama et al., 2014; Cisternas-Novoa et al., 2015; Ortega-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 the surface and our values correspond only to the surface (4 m), this could explain the higher values obtained in our dataset. Another reason seems to be the different Chl a concentrations, as the main TEP producer is phytoplankton. Chl a 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 Table 2. For example, in Iuculano et al. (2017) Chl a ranged 0.05-0.31 mg $m^{-3}$, and in Kodama et al. (2014) it averaged 0.05 ± 0.01 mg $m^{-3}$. We can't discard either that differences in TEP chemical composition could cause differences in staining capacity."*

**Lines 355-356: The authors should mention here any limitation of the conversion factors.**

*We have mentioned it as follows:*

*Line 343-344: "Furthermore, conversion factors carry quite an uncertainty as pointed out in the Methods section".*

**Line 331: is the organic matter that influences HPA concentration and their TEP production or ..? How does the organic matter pool influences TEP formation? If you mean, by abiotic assembly of a pool of dissolved precursors, this concept should be mentioned early in the introduction.**

*We realized this sentence was ambiguous and changed it. In the revised MS we now clarify the concept of abiotic formation. What we meant is that heterotrophic prokaryotes can be discharged directly with freshwater outflow, but also autochtonous microbes can be stimulated due to allochtonous DOM inputs. On the other hand, DOM inputs from freshwaters could also contain TEP and their precursors.*

*We have made the following change:*

*Lines 313-317: "The nutrient–rich water in the region is responsible for the proliferation of phytoplankton and HP, which could partly explain the high TEP*

*concentrations in this region. It is also known that large freshwater discharges occur in the shelf (Piola, 2005). These discharges could bring allochtonous HP directly to the shelf or bring DOM loads, which would stimulate autochtonous microbes. Besides, DOM inputs associated to freshwater discharges could also contain TEP and their precursors."*

**Lines 370-374: Again, the fate of TEP depends on further aggregation processes. Generally less dense than water could accumulate in the surface microlayer but wind speeds, high heterotrophic activity, coagulation with other organic and mineral particles thanks to their stickiness should be mentioned to describe their fate in the area. Which one do you think would predominate?**

*We agree with the reviewer that TEP accumulation in the surface is the result of a complex suite of aggregation/consumption processes. Besides, the reference to the effects of TEP-richness on the fate of POC was a bit misplaced here, where we were discussing the potential reasons why TEP contribution to POC is larger in oligotrophic waters. We have removed the sentence to leave the paragraph:*

*Lines 347-351: "With our results taken all together, we hypothesize that in oligotrophic conditions TEP–C is the predominant POC fraction, because nutrient limitation favours TEP production by phytoplankton and limits TEP consumption by bacteria. Conversely, in eutrophic conditions, the predominant POC fraction depends on many variables like the community composition, the bloom stage, and sources of TEP different from phytoplankton."*

**Lines 409-410: Again on aerosol formation, it's a complex process and without any information on the size distribution of TEP in this study I would recommend caution in making such affirmations. Here, it's a bit a "stand alone" sentence without any further explanation, which does not make much sense. It should be expanded and explained better. Also, please see the paper by Quinn et al. 2014 "Contribution of sea surface carbon pool to organic matter enrichment in sea spray aerosol" Nature Geoscience, which actually breaks up the concept of organic aerosols related to phytoplankton blooms (and in this case, TEP).**

*We agree this sentence was a bit stand alone and too speculative, and have removed it.*

**Line 444: as mentioned, TEP can also be produced by aggregation of colloids in the absence of phytoplankton, that is, in the presence of polymeric precursors in the dissolved phase. Thus, it would be interesting to see the relationship of TEP to DOC or acidic sugars.**

*Unfortunately we don't have DOC or acidic sugars data to check this relationship. However, it is worth mentioning that covariation of TEP with DOC or dissolved carbohydrates are not always observed in the field (see for instance Ortega-Retuerta et al. (2009b) in the Southern Ocean). We have added the following information (lines 407-408):*

*"Moreover, as mentioned before, in these shelf waters TEP formation could have been further modulated by aggregation of colloids carried by freshwater discharges".*

**Line 454: UV also inhibits gel aggregation (Orellana and Verdugo 2003, Ultraviolet radiation blocks the organic carbon exchange between the dissolved phase and the gel phase in the ocean, Limnology and Oceanography). It should be mentioned here.**

*We added this comment:*

*Lines 414-415: "Our results suggest that the roles of UV radiation in breaking up TEP and/or limiting their formation from precursors overcome UV stress–induced TEP production."*

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

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

## 1 Introduction

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

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

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

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

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

## 2 Material and methods

### 2.1 Study site and sampling

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

### 2.2 Chemical and biological analysis

#### 2.2.1 Particulate organic matter (TEP and POC)

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

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

### 2.2.2 Chlorophyll *a* (Chl *a*)

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

### 2.2.3 Inorganic nutrients

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

### 2.2.4 Microscopic phytoplankton identification

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

### 2.2.5 Picoplankton abundance

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

### 2.2.6 Heterotrophic prokaryotic abundance (HPA)

HPA was determined by flow cytometry using the same fixing protocol and instrument as for picoplankton. Before analyses, samples were thawed, stained with SYBRGreen I (Molecular Probes) at a final concentration of 10 µM and left in the dark 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 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 standard. Heterotrophic prokaryotes (HP) were detected by their signature in a plot of side scatter versus FL1 (green fluorescence). HP were enumerated separately as high–nucleic–acid–containing (HNA) and low–nucleic–acid–containing cells (LNA), and the prokaryote counts presented are the sum of these 2 types. Data were gated and counted in the SSC vs FL1 plot using the BD CellQuest™ software. HPA was expressed in cells $mL^{-1}$. Only one replicate was analysed since standard errors of duplicates are usually very low (around 1.5 % at Pernice et al. (2015)). In order to estimate the number of HP, cyanobacteria abundance (*Prochlorococcus* and *Synechococcus*) measured in the same but non–stained samples were subtracted from the total number of prokaryotes counted. HPA was converted into carbon unit (HP–C) using the conversion factor of 12 fg C $cell^{-1}$. Ducklow (2000) summarized the carbon contents of free–living marine bacteria reported in the literature for a number of oceanic regions, bays and estuaries. The average ± standard deviation for open ocean regions was 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 $cell^{-1}$ = 0.12 (µ$m^3$ cell volume)$^{0.72}$, for an average bacterial biovolume of 0.04 µ$m^3$.

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

the CU. The decrease in silicate (0.26 µmol $L^{-1}$) was accompanied by a relative increase of diatoms (9.4–fold increase) and dinoflagellates (1.3–fold increase) with respect to surrounding stations (Fig. 2b,e). *Prochlorococcus* abundance decreased to $9 \times 10^3$ 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 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. Consequently the TEP:Chl *a* ratio was the highest of the whole transect (1760.4). Moving south, the North Tropical Gyre (stations 9 to 13) showed an increase of silicate concentration, from 0.20 to 0.79 µmol $L^{-1}$. The Chl *a* concentration ranged 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 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 ± 1.4 µg C $L^{-1}$. By contrast, the southernmost stations (12 and 13) were dominated by *Prochlorococcus*, with an average of 2.6 $\times 10^5 \pm 0.5 \times 10^5$ cells $mL^{-1}$, that corresponded to a biomass of 13.2 ± 2.7 µg C $L^{-1}$ (Fig. 2e). TEP concentrations were similar to those in the Northeastern Subtropical Gyre and the Canary Current Coastal, ranging between 78.1 and 123.9 µg XG eq $L^{-1}$. Station 14, with a relatively high temperature (29.0 ºC) and low salinity (35.2) was probably the most influenced by the Equatorial Counter Current. In this station, the silicate concentration (1.41 µmol $L^{-1}$) was the maximum observed in the whole transect, and there was an increase of dinoflagellates and "other microalgae", and a decrease of *Prochlorococcus*. 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 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 $m^{-3}$ and the silicate concentration decreased (0.42–1.39 µmol $L^{-1}$). TEP presented the lowest average values of the whole 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 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 1).

The southernmost part of the cruise transect corresponded to the SWAS (stations 32 to 41). In this region, temperature (7.6–13.9 ºC) and salinity (32.6–33.6) were lower on average than those found in the OAO (Table 1). The SWAS could be further divided into two regions according to different inorganic nutrient (nitrate and phosphate) concentrations ($p < 0.05$) and phytoplankton composition. The northern SWAS (stations 32 to 36) presented lower nitrate (0.16 to 4.15 µmol $L^{-1}$) and 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 $L^{-1}$, 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 across the entire SWAS (1.07–3.75 mg $m^{-3}$) was significantly higher than in the OAO, with no major differences between the northern and the southern parts. In most of the northern SWAS, phytoplankton biomass was dominated by "other 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 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 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, 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

(stations 37 to 41), phytoplankton biomass was dominated by picoeukaryotes, with an average of $6.34 \times 10^4 \pm 1.93 \times 10^4$ 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 $L^{-1}$. 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 *a* ratio ranged from 31 to 165 (average 97 ± 42) (Table 1).

### 3.2 TEP contribution to POC

TEP and POC covaried significantly and positively across the entire TransPEGASO transect (Spearman rs analysis, r = 0.91, 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 (average 66 ± 19 %), and between 28 and 110 % in the SWAS (average 73 ± 36 %). POC was not analysed in the CU (Fig. 3). To better explore the importance of TEP–C with respect to other major quantifiable POC pools, we estimated phytoplankton biomass (phyto–C) and HP biomass (HP–C) throughout the whole cruise (Fig. 2). It is worth mentioning that POC also includes other fractions of non–living non–TEP organic carbon (e.g., cell fragments and Coomassie stainable particles), but phytoplankton and heterotrophic prokaryotes are generally considered the most abundant in open sea water (Ortega-Retuerta et al., 2009b; Yamada et al., 2015). TEP–C contributed the most to the POC pool in the OAO, where it represented twice the share of phyto–C and HP–C. In the SWAS, conversely, TEP–C was not significantly different than phyto–C, and three times higher than HP–C (Fig. 3).

### 3.3 Relationship to other variables

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 regression equation for log converted TEP vs Chl *a* was log TEP = 2.09 (± 0.04) + 0.66 (± 0.08) × log Chl *a*. Considering the two study regions separately, only in the OAO the relationship was significant, with a higher slope than in the entire transect (log TEP = 2.31 (± 0.10) + 1.13 (± 0.20) × log Chl *a;* $R^2$ = 0.56, p< 0.001, n = 29).

Across the whole transect, TEP presented a significant (p< 0.05) positive relationship with total phytoplankton biomass (Table 3) and with some phytoplankton biomass groups: *Synechococcus* ($R^2$ = 0.30), picoeukaryotes ($R^2$ = 0.49), diatoms ($R^2$ = 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) and coccolithophores ($R^2$ = 0.15). Some differences arose from examining the two regions separately. Within the OAO, TEP presented a significant (p< 0.001) positive relationship with Chl *a* ($R^2$ = 0.56), total phytoplankton biomass ($R^2$ = 0.47) and some phytoplankton groups (*Synechococcus*, picoeukaryotes, diatoms, dinoflagellates and "other microalgae", Table 3), but not with HPA. TEP showed a significant (p< 0.001) negative relationship with the previous 24 hours–averaged solar irradiance ($R^2$ = 0.43, Fig. 4). Multiple regression analyses showed the combined positive effect of Chl *a* and HPA on TEP

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

## 4 Discussion

### 4.1 TEP across the surface Atlantic Ocean

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

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

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

### 4.2 TEP as an important contributor to ocean surface POC

The significant positive correlation between TEP and POC observed in our study highlighted the importance of TEP determining POC horizontal variations in the surface Atlantic Ocean, suggesting a high contribution of TEP to this pool. A few values of TEP–C%POC were unrealistically higher than 100 %, a feature that has also been observed in other studies (Engel and Passow, 2001; Bar-Zeev et al., 2011; Yamada et al., 2015). This suggests the inaccuracy of the use of standard 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 defining specific CF for diverse regions or environmental conditions. Nonetheless, an alternative explanation for the apparent oversizing of the relative TEP–C pool may be strictly methodological: TEP are determined on filters of 0.4 µm of 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 smaller TEP particles are not taken into account in the POC measurement.

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

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

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

### 4.3 Main drivers of TEP distribution in the surface ocean

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

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

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

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

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

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

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

In summary, our study describes for the first time the horizontal distribution of TEP across a North–South transect in the Atlantic Ocean. TEP constituted a large portion of the POC pool, larger than phytoplankton at most stations and always larger than heterotrophic prokaryotic biomass. This supports the important role of TEP in the carbon cycle. The drivers of TEP distribution were primarily phytoplankton and, to a lesser extent, heterotrophic prokaryotes among sources, with *Synechococcus* playing an outstanding role in the oligotrophic ocean. Also in the oligotrophic ocean, solar irradiance was a 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<br><br>Pacific Ocean | Oligotrophic<br><br>Oligotrophic | Spring–Summer 2011<br><br>Spring–Summer 2011 | 3<br><br>3 | 8.18 ± 4.56<br><br>24.45 ± 2.3 | 0.05–0.31 | 78.6 ± 9.3<br><br>357 ± 127 | Iuculano et al. (2017b)<br><br>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<br>-Arabian Sea<br>-Bay of Bengal | Eutrophic | <br>-August 1996<br>-September 1996 | 0–1000 | <br>-60 [j,k] (< 5–102[j])<br>-7–13[c,j] | – | – | Kumar et al. (1998), Ramaiah et al. (2000) |
| OAO<br>OAO (CU excluded) | Oligotrophic | Autumn 2014 | 4 | 72 ± 74 (18–446)<br>60 ± 27(18–132) | 0.4 ± 0.2 (0.2–0.6)<br>0.3 ± 0.1 (0.2–0.8) | 236 ± 42 (81–1760)<br>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

d: 5 m

e: TChl *a*

f: 0–200 m

g: Depth–averaged TEP

h: stations 6–9

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

**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).**