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Contribution of transparent exopolymer particles to carbon sinking flux in an oligotrophic reservoir

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Abstract Transparent exopolymer particles (TEP) compose an important pool of particulate organic matter (POM) in aquatic systems. However, no studies of TEP contribution to C export to sediment exist for freshwaters. We quantify the contribution of TEP to C sinking fluxes in an oligotrophic reservoir (Quéntar, Southern Spain) by monitoring TEP in the water column and TEP, particulate organic carbon (POC) and dry weight in sedimentation traps. TEP sinking fluxes ranged from 0.73 to 183.23 mg C m^{-2} day^{-1} and from 0.51 to 177.04 mg C m^{-2} day^{-1} at the surface and at the bottom layer, respectively. These values represent that, over an annual basis, 5.59 Ton TEP-C (over 61.32 Ton POC) are exported, on an average, from the water column to the sediment of Quentar reservoir. TEP concentrations (average = 48.0 μg XG eq l^{-1}) were lower than the scarce data reported for freshwaters. No significant relationships between TEP and Chl *a* concentrations or BA were observed. Average value for daily sedimentation flux (6.63 g Dry Weight m^{-2} day^{-1}) in the study reservoir was higher than that documented for low productive natural aquatic ecosystems as a consequence of the high amount of allochthonous material input characterizing reservoirs. TEP contributed to C export to sediment with a value that range from 0.02 to 31%. Our results show that even in man-made systems, which are predominantly controlled by allochthonous inputs, TEP may be relevant for explaining POM settling fluxes.

Keywords Carbon · Reservoirs · Sedimentation · Transparent exopolymer particles (TEP)

Abbreviations

BA	Bacteria abundance
Chl *a*	Chlorophyll *a*
DOC	Dissolved organic carbon
DW	Dry weight
POC	Particulate organic carbon
POM	Particulate organic matter
PIM	Particulate inorganic matter
TEP	Transparent exopolymer particles

Introduction

Inland waters (lakes, rivers and reservoirs) have been largely ignored in the carbon cycle at global or regional scales. However, recently it has been quantified that the transfer of terrestrial carbon (C) to inland waters is considerably larger than delivery

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to the sea (Cole et al. 2007). Thus, these ecosystems should to be active components of the C cycle by losing CO_2 to the atmosphere and/or storing organic C in their sediments (12% of the terrestrially-derived carbon). In particular, it has been calculated that man-made impoundments store 0.16–0.2 Pg C $year^{-1}$ in their sediments (Cole et al. 2007).

Several components contribute to the sedimentary organic C: (1) direct sinking of aquatic organisms, (2) sedimentation of terrestrial matter and (3) processes that involve the conversion of dissolved organic matter (DOM) to particulate organic matter (POM) in the overlying water. In this sense, the self-assembly of dissolved precursor material to form transparent exopolymer particles (TEP), represent an unexplored pathway in freshwaters. TEP, composed by acidic polysaccharide mainly released by phytoplankton and bacteria (Grossart et al. 1997; Passow 2002a, b), act as the interstitial matrix to form macroscopic aggregates (lake snow) that can export organic carbon from the surface to the sediments. Several evidences support the idea that the formation of TEP (which is driven by biological factors, water chemistry and physical forcing), has an outstanding effect on settling processes. However, the ultimate fate of TEP (sinking versus floating) can be determined by environmental variables as pH (Azetsu-Scott and Passow 2004; Wurl and Holmes 2008). On the other hand, TEP as highly sticky particles are likely increasing the sedimentation of inorganic particles by aggregation (De La Rocha et al. 2008).

Although TEP compose an important pool of POM in freshwater systems (Grossart et al. 1998), no studies of TEP settling fluxes and its contribution to C settling fluxes do exist. However, a previous study carried out in marine systems confirms that elevated TEP fluxes were frequently associated with peaks in POM flux (Passow et al. 2001) suggesting their promoter role. In addition, sedimentation is a key process for nutrient dynamics in freshwater ecosystems (see among others, de Vicente et al. 2005) transferring particulate material from the source (euphotic or coastal zone) to the bottom of the system. Settling matter is exposed to a variety of complex physical, chemical and biological processes while it settles along the water column, which ultimately can cause a release or uptake of nutrients from the particulate matter. Additionally, in reservoirs, which are increasing worldwide, i.e., the water volume in impoundments has increased by an order of magnitude between the 1950s and the present (Shiklomanov and Rodda 2003; Downing et al. 2006), sedimentation represents a key problem as it reduces their water storage capacity and hence, directly affects to water resources management (Nagle et al. 1999). Although sedimentation of POM is very well-known in reservoirs, as yet no studies deal with the contribution of TEP as major drivers to the C sinking flux.

In this study, we first quantify the contribution of TEP to C sinking fluxes in an oligotrophic reservoir (Quéntar, Southern Spain). We performed a simultaneous monitoring of variables in the water column (TEP, DOC, Chlorophyll *a* and Bacterial Abundance) and in sedimentation traps (DW, POM and TEP) to asses that contribution.

Methods

Study site

Quentar reservoir is located on the headwaters of the Genil river, a tributary of the Guadalquivir river, the largest river in southern Spain. Catchment characteristics, morphometry, age and anthropogenic influence are summarized in Table 1. Its oligotrophic status is mainly a consequence of its location on a mountain area, across closed-valley areas that render a low surface: depth ratio. It can be considered as a warm monomictic reservoir exhibiting a broad metalimnetic layer, as a result of deep extractions along the summer, with temperature gradients of 0.35°C m^{-1} extending from 5 to 30 m (de Vicente et al. 2008).

Monitoring of the water column

Hydrological records (volume) were provided by the Water Management Board: "Confederación Hidrográfica del Guadalquivir". Water samples were collected on a weekly basis in the epilimnion (merged water from three depths over the thermocline) and in the hypolimnion (30 m), using a Van Dorn bottle, at the deepest site of Quentar reservoir from February 2004 to March 2006. All chemical and biological analysis were performed by duplicates (coefficient of variation, CV = 8%).

Table 1 Main characteristics of the study reservoirs (modified from de Vicente et al. 2008)

	Quentar
Year of improudment	1973
Altitude a.s.l. (m)	1,030
Total volume (V; 10^6 m^3)	13.6
Reservoir area (A_R; ha)	42
Catchment area (A_C; ha)	1,000
A_C:A_R	23.8
T_W (years)	3.85

T_w is the water residence time

TEP concentration was determined colorimetrically following Passow and Alldredge (1995). 100–300 ml-samples were fixed with formaldehyde (1% final concentration) and stored in the dark until analysis. Then, samples were filtered onto 0.4 μm polycarbonate filters (Isopore), stained with Alcian Blue solution, soaked in 80% sulphuric acid (5 ml) for 3 h and measured spectrophotometrically at 787 nm, using empty, stained filters as blanks. Alcian Blue absorption was calibrated using a solution of the polysaccharide Xanthan Gum. TEP concentration was expressed in microgram of Xanthan Gum (XG) equivalents per litre (μg XG eq l^{-1}) and in carbon units using the conversion factor of 0.75 μg C μg XG l^{-1} proposed by Engel and Passow (2001).

Chlorophyll *a* concentration (Chl *a*) was measured using the trichromatic method proposed by Jeffrey and Humphrey (1975). Phytoplankton carbon content was estimated from Chl *a* concentration using conversion factors of 40 μg C μg Chl a^{-1} proposed by Banse (1977) and 50 μg C μg Chl a^{-1} proposed by Cho and Azam (1990) to establish a probable range of values.

Bacterial abundance (BA) was measured by epifluorescence microscopy (Porter and Feig 1980). Water subsamples of 3–5 ml were filtered onto 0.2-μm polycarbonate filters and stained with DAPI (4,6-diamidino-2 phenylindole) to a final concentration of 1 μg ml^{-1}. At least 350 cells in 15 random fields were counted for each sample. Bacterial abundance was converted into carbon unit using the conversion factors of 10 and 20 fgC $cell^{-1}$ proposed by Christian and Karl (1994) and Lee and Fuhrman (1987), respectively, to establish a probable range of values.

Samples for dissolved organic carbon (DOC) analyses were collected after filtration through pre-combusted Whatman GF/F filters into pre-combusted 30 ml glass ampoules, acidified with hydrochloric acid (final pH < 2), sealed and stored at 4°C until analysis. DOC was analyzed by High-Temperature Catalytic Oxidation on a Shimadzu TOC-V CSH.

Sinking matter

Traps for collecting settled material were deployed at different depths (5, 15 and 30 m) at the deepest site of the reservoir. The traps consisted of twin-plexiglass cylinders, with an aspect ratio (Height: Diameter = 50 cm × 6.4) higher than 6 (Bloesch and Burns 1980). Settling matter was collected, with no preservative addition, from October 2004 to December 2005 usually every 2 weeks (Table 2). Longer periods than 15 days corresponded exclusively to autumn and winter (periods 1, 2 and 3) except for the periods 5, 6 and 7 (spring and early summer). The time interval was extended during these seasons to warranty the collection of enough particulate material

Table 2 Time periods for sampling the settled matter in the sedimentation traps

Period	Month/day/year (number of days)
1	10/26/04–11/23/04 (28)
2	11/23/04–12/21/04 (28)
3	12/21/04–01/13/05 (23)
4	04/11/05–04/19/05 (8)
5	04/19/05–05/24/05 (35)
6	05/24/05–06/14/05 (21)
7	06/14/05–07/05/05 (21)
8	07/05/05–07/19/05 (14)
9	07/19/05–08/02/05 (14)
10	08/02/05–08/16/05 (14)
11	08/16/05–08/30/05 (14)
12	08/30/05–09/13/05 (14)
13	09/13/05–09/27/05(14)
14	09/27/05–10/11/05 (14)
15	10/11/05–10/25/05 (14)
16	10/25/05–11/08/05 (14)
17	11/08/05–11/22/05 (14)
18	11/22/05–12/07/05(15)
19	12/07/05–12/20/05 (13)

to get accurate estimates. As bacterial degradation of organic matter depends on temperature (e.g., Arnosti et al. 1998), we assumed minor mineralization losses due to the low temperatures. In particular, average values of temperature at 5, 15 and 30 m were 8, 14.7 and 13.8°C during periods 1 and 2, while during period 3 average temperatures at all depths were lower than 10°C. In addition, during periods 5, 6 and 7, average temperatures were 13.4°C (5 m), 8.3°C (15 m) and 5.8°C (30 m). Once in the laboratory, the suspension was filtered through precombusted and preweighed Whatman GF/C filters and dry weight (DW, 104°C, 24 h) was measured in order to determine the settling flux (g DW m^{-2} day^{-1}). The sinking flux of particulate material (S, g DW m^{-2} day^{-1}) was calculated according to:

$$S = M \cdot V_T \cdot V_F^{-1} \cdot A^{-1} \cdot T^{-1} \quad (1)$$

where M is the mass of particulate material quantified as the difference in dry weight of filters before and after filtering a known volume (V_F) of the settling homogenized suspension; V_T is the trap volume, 1.6 l; A is the collection area, 32.17 cm^2 and T is the time between consecutive sampling, when settling matter was collected (range from 11–35 days).

Settled matter was analysed for organic matter concentration by combustion (450°C, 5 h) being particulate inorganic matter (PIM) the weight after combustion and particulate organic matter (POM) the difference between pre- and after combustion. From the content of organic matter in the settling seston (POM) and using a conversion of 2.4 (Margalef 1983), we estimated particulate organic carbon (POC) content in the settled matter.

TEP concentration in sediment trap material was analysed as proposed by Passow et al. (2001), performing dilutions from 5:20 to 15:20 ml to avoid underestimating TEP flux. From TEP concentration in suspended matter (μg XG eq l^{-1}), we estimated TEP settling fluxes (μg XG eq m^{-2} day^{-1}), by considering volume of suspended material (l), surface area of trap (m^2), and time of trap exposition (day).

Statistical analysis

Statistical analyses were performed using Statistica 6.0 Software (StatSoft Inc 1997) and Excel. For Student t tests, unless otherwise stated, the significance level was set at $p < 0.05$.

Results

Spatiotemporal distribution of TEP, DOC, Chl *a* and bacteria abundance in the water column

TEP concentration ranged from 2.1 to 162.9 (average 47.7) μg XG eq l^{-1} in the epilimnion and from 1.9 to 335.2 (average 48.3) μg XG eq l^{-1} in the hypolimnion (Table 3; Fig. 1). Seasonal variability was very pronounced at both depths showing the maximum variability at the bottom layers (CV = 89%). The higher values of TEP concentrations were measured during summer 2005 except for the bottom layer

Table 3 Mean, minimum and maximum values of TEP (μg XG eq l^{-1}), Chl-*a* (μg l^{-1}) and BA ($\times 10^5$ cell ml^{-1}) in the water column and of settling rates of DW (g DW m^{-2} day^{-1}), POM (g DW m^{-2} day^{-1}) and TEP (mg C m^{-2} day^{-1}) during the whole study period (from February 2004 to March 2006)

	5 m		30 m		All data	
	Mean	Range	Mean	Range	Mean	Range
Concentrations						
TEP (μg XG eq l^{-1})	47.7	2.1–162.9	48.3	1.9–335.2	48.0	1.9–335.2
Chl *a* (μg l^{-1})	2.02	0.58–6.92	1.99	0.86–3.96	2.00	0.58–6.92
BA ($\times 10^5$ cell ml^{-1})	18.2	4.6–60.6	12.7	5.0–27.7	16.1	4.6–60.6
DOC (mg l^{-1})	1.55	0.33–4.14	1.34	0.06–3.39	1.46	0.06–4.14
Sinking rates						
DW (g DW m^{-2} day^{-1})	5.69	1.23–15.54	7.69	2.44–22.69	6.63	1.23–22.69
POM (g DW m^{-2} day^{-1})	0.93	0.17–3.67	1.04	0.26–2.08	0.98	0.17–3.67
TEP (mg C m^{-2} day^{-1})	39.95	0.73–183.23	43.87	0.51–177.04	41.65	0.51–183.23

where the maximum concentration was detected at the end of March 2005 (Fig. 1).

Chl *a* concentration ranged from 0.58 to 6.92 μg l^{-1} in the epilimnion and from 0.86 to 3.96 μg l^{-1} in the hypolimnion (Table 3; Fig. 1). Average Chl *a* concentration did not differ significantly from surface (2.02 μg l^{-1}) to deep waters (1.99 μg l^{-1}).

Bacteria abundance (BA) was significantly higher and more time-variable in the surface waters (18.32 × 10^5 ± 12.31 × 10^5 cell ml^{-1}; CV = 67%) than in the deep waters (12.68 × 10^5 ± 4.20 × 10^5 cell ml^{-1}; CV = 33%) (Table 3; Fig. 1). Highest BA (60.58 × 10^5 cell ml^{-1}) was observed on July 2004 (Fig. 1).

During the whole study period, average DOC concentrations ranged from 0.33 to 4.14 mg l^{-1} in the epilimnion and from 0.06 to 3.39 mg l^{-1} in the hypolimnion (Table 3). The highest DOC concentrations were recorded during spring 2005 in the bottom layer but no clear seasonal pattern was observed.

No significant linear correlations were found between TEP concentrations and either Chl *a* or

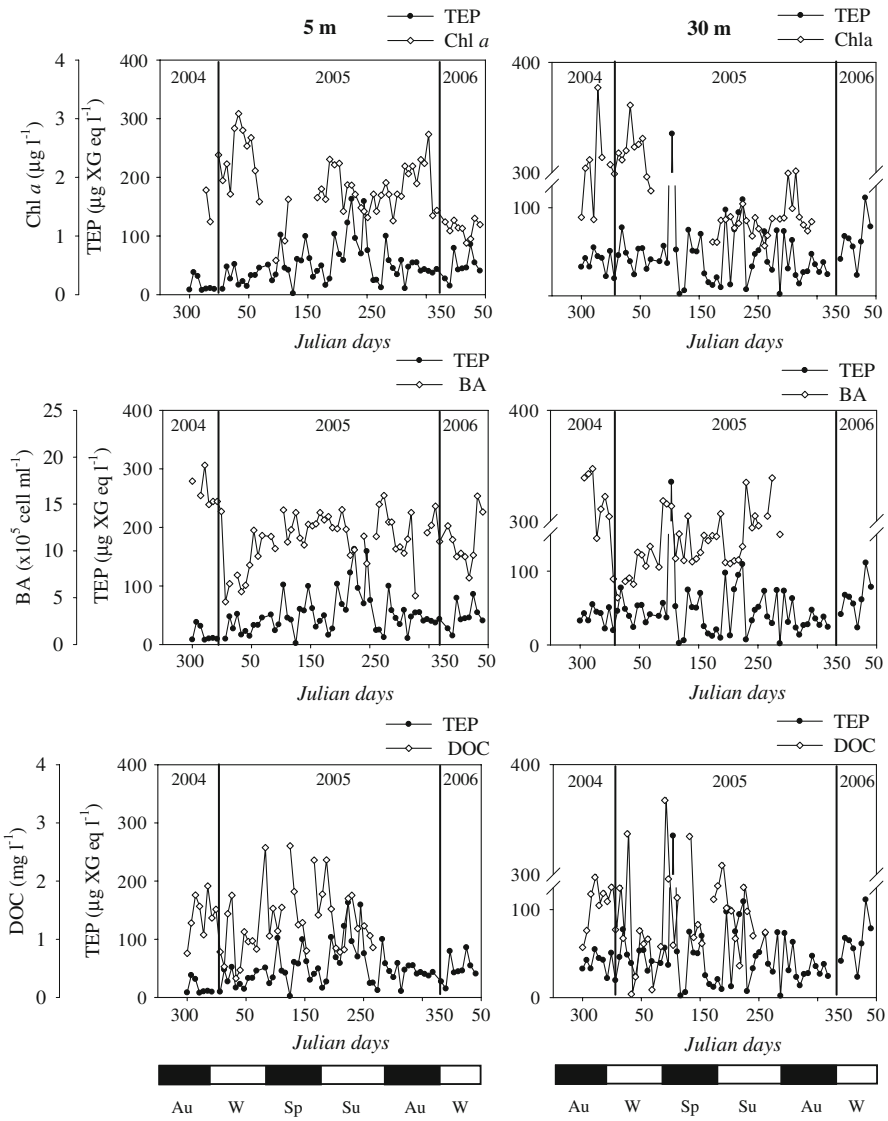

Fig. 1 Seasonal changes of TEP (μg XG eq l^{-1}), Chl *a* (μg l^{-1}), BA (×10^5 cell ml^{-1}), and DOC (mg l^{-1}) the water column. *Left and right panels* correspond to 5 and 30 m, respectively. *Sp*, spring; *Su*, summer; *Au*, autumn; and *W*, winter

bacteria abundance measured at the same date and even with a one-sampling time lag, both in the epilimnion and in the hypolimnion.

Considering carbon units, TEP concentration averaged 35.2 μg TEP-C l^{-1} in the upper layer and 36.2 μg TEP-C l^{-1} in the bottom layer, showing especially high temporal variability in this layer (Fig. 2). Maximum TEP-C concentrations were reported during summer in the upper layer, contributing with almost 40% to the non-detrital OM pool. Phytoplankton C showed, using the C conversion factors of 40–50 μg C μg Chl a^{-1}, of 70.3–87.9 μg l^{-1} average values, in the upper layer and of 73.6–91.4 μg l^{-1} in the bottom layer, representing the most important non-detrital OM fraction (>50%) at both depths in particular during autumn. On an average, bacteria C comprised the lower non-detrital OM fraction (7–19%), showing average concentrations of 24.3 and 11.9–23.7 μg l^{-1} in the upper and in the bottom layer, respectively, when considering C conversion factors of 10–20 fgC $cell^{-1}$.

Sinking flux of DW, POM and TEP

Daily sedimentation flux ranged from 1.23 to 15.54 g DW m^{-2} day^{-1} in the epilimnion (5 m) and from 2.44 to 22.69 g DW m^{-2} day^{-1} in hypolimnion (30 m) (Table 3; Fig. 3b). Values of sinking sestonic fluxes in the epi- and hypolimnion were positive correlated ($r = 0.75$; $p < 0.05$) but a clear increasing tendency of sinking sestonic fluxes with depth was found. Seasonal variations based on coefficient of variation (CV) were especially noteworthy for both depths (>60%). Maximum values for DW settling fluxes were measured during autumn 2004 and early spring 2005, concomitant with maximum water discharge on the reservoir (Qin) and accumulated rainfall (Fig. 3a). In particular, the highest DW settling flux was measured at any of the three sampling depths during autumn 2004 when accumulated rainfall reached values up to 27.4 mm. A significantly positive relationship between DW settling flux and water discharge at 15 ($p < 0.01$) and 30 m ($p < 0.05$) have been found while no significantly but positive relation was observed at 5 m.

POM sinking fluxes ranged from 0.17 to 3.67 g DW m^{-2} day^{-1} in the epilimnion (5 m) and from 0.26 to 2.08 g DW m^{-2} day^{-1} in the hypolimnion (30 m). These values indicate that, on an average value and over an annual basis, 61.32 Ton of POC are exported from the water column to the sediment of Quentar reservoir. POM settling fluxes at 5 and 30 m were positive correlated ($r = 0.72$; $p < 0.05$), although they generally increased with depth (Fig. 3b; Table 3). Seasonal variability was extremely important for the material collected at the upper sedimentation traps (CV = 73%).

In Quentar, most of the settling material is inorganic (85% on an average). The weak and non-significant relation found between TEP and PIM settling fluxes may suggest that in our study reservoir TEP formation do not represent a key process for removing inorganic particles from the water column.

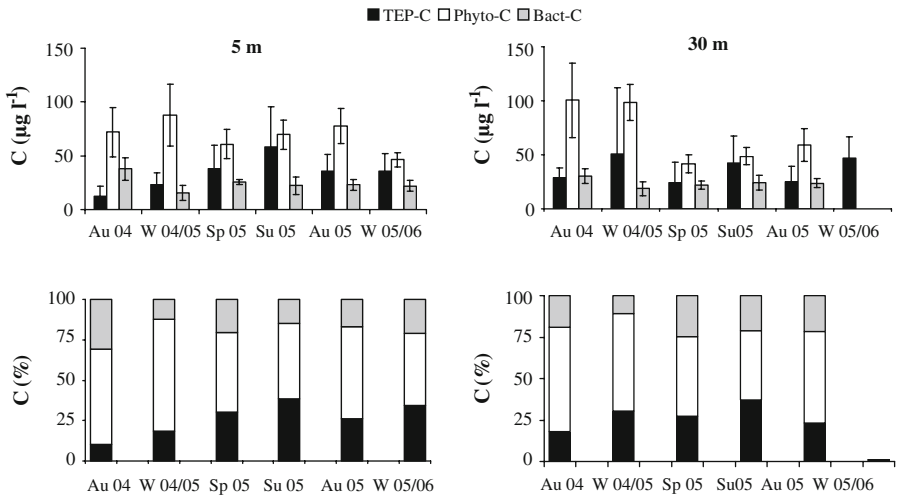

Fig. 2 Seasonal average of C content (μg l^{-1}) and relative contribution (%) to non-detrital organic matter pool of TEP (TEP-C), phytoplankton (Phyto-C) and bacteria (Bact-C) at 5 and 30 m depths using 40 μg C μg Chl a^{-1} and 20 fgC $cell^{-1}$. Note that no data for Phyto-C and Bact-C in winter 2005–2006 are shown

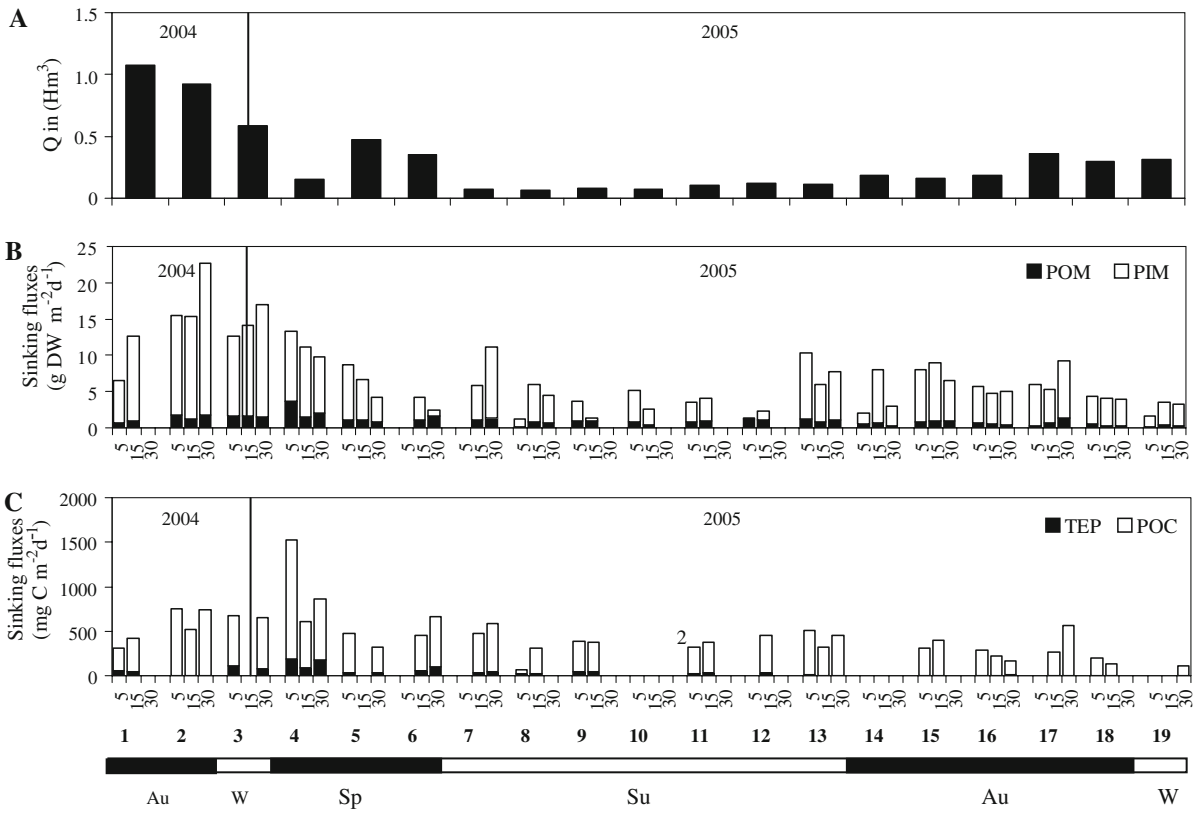

Fig. 3 Seasonal changes in: **a** water discharge, **b** sinking fluxes of particulate organic matter (POM) and particulate inorganic matter (PIM) (g DW m^{-2} day^{-1}) and **c** sinking fluxes of particulate organic carbon (POC) and TEP (mg C m^{-2} day^{-1}) at 5, 15 and 30 m depths. Note that for avoid any confusion, data for C were removed for those samplings with no data for TEP

TEP sinking fluxes ranged from 0.73 to 183.23 mg C m^{-2} day^{-1} in the epilimnion (5 m) and from 0.51 to 177.04 mg C m^{-2} day^{-1} in the hypolimnion (30 m) showing an extremely important temporal variability (CV > 130%) (Fig. 3c; Table 3). Average values were 39.95 and 43.87 mg C m^{-2} day^{-1} in the epilimnion and in the hypolimnion, respectively. On an annual basis, 5.59 Ton of C-TEP are exported from the water column to the sediment. A noteworthy positive correlation ($r = 0.94$; $p < 0.05$) between TEP settling fluxes measured at both depths was found, hence revealing a similar temporal trend of TEP sedimentation along the vertical profile.

TEP sinking fluxes contributed to C export to the sediment with an average value of 7% (Fig. 3c). According to the results of the paired t test performed, no significant vertical differences between fluxes (5 m = 9%; 15 m = 6% and 30 m = 7%) were observed, but these fluxes showed great temporal variations (min = 0.02% and max = 31.03%). The highest contribution of TEP-C to C sinking fluxes was recorded at the surface layer (5 m) during summer 2005, while low values (<1%) were registered during autumn 2005.

TEP sinking fluxes showed inverse trends against TEP concentrations in the water column in the epilimnion ($n = 13$, $r = 0.31$, $p > 0.05$) and hypolimnion ($n = 10$, $r = 0.39$, $p > 0.05$) (Fig. 4a). These inverse trends with TEP sinking fluxes were observed both analyzing water column TEP data for the same day and the sum of TEP concentrations at the beginning and at the end of the same period. TEP settling velocity, estimated as the ratio between TEP settling fluxes and TEP concentrations in the water column, was positive and significantly correlated between surface and deep waters ($r = 0.59$; $p < 0.05$) with average values ranging from 1.12 to 1.31 m day^{-1}, at the bottom and surface waters, respectively. However, TEP sinking fluxes were significant and positively related to C sinking fluxes

at both epilimnion ($n = 14$, $r = 0.76$, $p < 0.05$) and hypolimnion ($n = 10$, $r = 0.66$, $p < 0.05$) (Fig. 4b).

Discussion

Sinking fluxes of TEP, POM and DW

TEP themselves contribute directly to the flux of C (Passow 2002a, b) and they are also promoters of marine and lake snow (Passow 2000; Grossart et al. 1997, 1998). Hence, the knowledge of the relationships between TEP and POM sinking rates are of special relevance when studying the role of inland waters as "sinks" of organic carbon. In this study, we have found that TEP contributed from 0.02 to 31% to the C export to sediments. These contributions to POM sedimentation are conservative, since no preservatives were added to the traps, and a fraction of the polysaccharides from TEP could have been degraded by bacteria. Despite this technical limitation, TEP sinking fluxes appear to promote POC sedimentation (Fig. 4b). No previous published data of TEP settling fluxes and of TEP contribution to POC settling fluxes in freshwaters exist, but the results obtained in the present study are in the range of those reported by Passow et al. (2001) for marine ecosystems. Additionally, TEP are highly sticky particles and accordingly, they could also increase the sedimentation of inorganic particles by aggregation (De La Rocha et al. 2008), but this process was not apparent in Quentar reservoir.

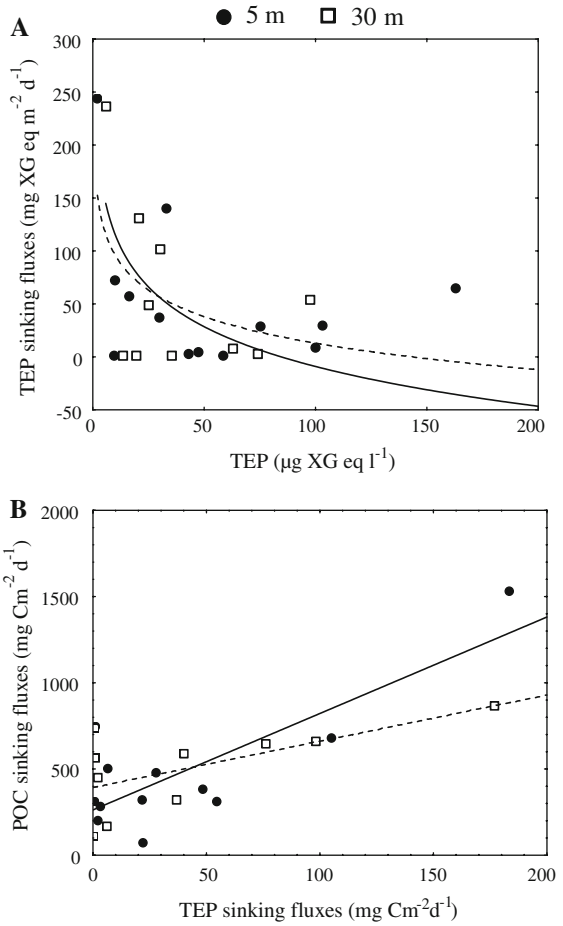

Fig. 4 Relationships between TEP sinking rates and **a** TEP concentrations into the water column at the same sampling time and **b** particulate organic carbon (POC) sinking rates

The average values for daily sedimentation flux measured in the oligotrophic Quentar reservoir are higher than those documented by Tartari and Biasci (1997) for low productive natural ecosystems. High amounts of allochthonous material input characterizing man-made systems could be the reason for such differences between natural and non-natural water bodies. Then, our results show that even in reservoirs, which are predominantly controlled by allochthonous inputs, TEP formation dynamics and its driving factors, are relevant for explaining POC settling fluxes. Additionally, the significantly positive relationship between DW settling flux and water discharge at 15 and 30 m may confirm the relevance of external inputs on sedimentation of particulate matter in Quentar reservoir. The more positive relationship between DW settling fluxes and water discharge at 30 m than at 5 m is likely to support the idea that riverine water is being injected at bottom layers and hence, contribute to an increase of DW settling fluxes at those depths. The injection of riverine water in the hypolimnion is ultimately a consequence of the more similar water temperature between the river and the hypolimnion (e.g., Rueda et al. 2007).

Distribution of TEP, DOC, Chl *a* and bacteria abundance

TEP concentrations in Quentar reservoir were lower than the scarce data reported for freshwaters (Table 4), which seems plausible given the more oligotrophic condition of the study reservoir. Accordingly, Worm and Søndergaard (1998) pointed out that

the high TEP concentration in Frederiksborg Slotssø was presumably related to its eutrophic status. One of the reasons behind such affirmation is that concentrations of dissolved and particulate organic matter usually increase with system productivity (Søndergaard and Middelboe 1995). However, there are a complexity of factors involved in the relationship between TEP and Chl *a*, such as composition of the phytoplankton community and its physiological state. In fact, we did not find a significant relationship between chlorophyll *a* and TEP concentration in this seasonal study (Fig. 1).

Due to the scarcity of data compiled in the literature for freshwaters, it is hard to compare TEP concentrations in both freshwater and marine systems (Table 4). However, there are potential factors for enhancing TEP generation in marine waters compared to freshwaters: (1) the low salinity of freshwaters increases electrostatic repulsion between particles of equal charge (Fletcher 1991); (2) the stickiness of freshwater particles is lower (Kepkay 1994) and (3) marine environments are enriched in cations which are likely to stabilize TEP formation (Passow 2002a, b). In our case, Quentar reservoir has lower Ca^{+2} concentration, which ranged from 16.19 to 37.1 mg l^{-1} (Romera unpublished) than marine waters, which show typical values of 400 mg l^{-1} and hence, this relatively low content of Ca^{+2} in Quentar could explain to some extent the generally lower TEP concentration in Quentar reservoir compared to marine systems with similar Chl *a* concentration.

Although it is apparent that phytoplankton is a major source of TEP (Kiørboe and Hansen 1993; Passow and Alldredge 1994; Passow 2002a, b), we did not find similar seasonal patterns between TEP and Chl *a* concentration in this study. One of the reasons for the lack of this relationship may be that TEP formation is a function of growth rate rather than standing stock (Waite et al. 1995). Actually, a mesocosm study has reported an inverse relationship at the end of the growth phase when TEP production increases as a result of either lysis of cells or sloppy feeding and Chl *a* concentrations decline (Engel et al. 2002).

The scarce data reported for TEP and Chl *a* in freshwater ecosystems makes also difficult to compare the ratio of C-TEP to C-Chl *a* in marine and fresh waters. However, it is likely that similar values for that ratio are measured in both ecosystems (Table 4), except for the case of the Mediterranean Sea, where the highest C-TEP/C-Chl *a* has been measured (Ortega-Retuerta, personal communication).

Bacteria also appear to generate TEP directly (Heissenberger et al. 1996) as it has been reported for deep (below mixed layer) antarctic waters (Ortega-Retuerta et al. 2009). However, we did not find a significant relationship between bacterial abundance and TEP.

This study provides a first quantitative estimate of the contribution of TEP to C settling fluxes in freshwater systems. However, we put forward the need for future research focused on the contribution

Table 4 Compilation of TEP concentrations (μg XG eq l^{-1}) in marine and freshwater systems

System	TEP (μg XG eq l^{-1})	C-TEP/C-Chl *a*	Reference
Marine waters			
Southern Ocean	14.2 (0.0–48.9)	0.71 (0.01–27.97)	Ortega-Retuerta et al. (2009)
Mediterranean Sea	21.39 (4.5–94.3)	9.49 (0.24–232.24)	E. Ortega-Retuerta, personal communication
Antartic	206.9 (10.0–407.0)	2.31 (0.22–13.24)	U. Passow, personal communication
Friday Harbor	82.7 (15.2–159.1)	0.52 (0.09–1.47)	U. Passow, personal communication
Moor	51.6 (0.25–508.7)	1.91 (0.09–53.4)	U. Passow, personal communication
Inland waters			
Lake Kinneret	219 (48–1,160)	0.24 (0–0.68)	Y. Z. Yacobi, personal communication; Berman and Viner-Mozzini (2001)
Quentar reservoir	48.1 (1.9–335.2)	0.59 (0.09–2.10)	This study

Chl *a* in terms of C units was obtained using 40 μg C μg Chl a^{-1}

Average for the whole water column (minimum–maximum). Data from Lake Kinneret were provided by Y. Z. Yacobi. Data from marine waters were provided by U. Passow (Friday Harbour, Antartik and Moor), E. Ortega-Retuerta (Mediterranean Sea) and Ortega-Retuerta et al. (2009) (Southern Ocean)

of TEP to C settling fluxes along gradients of both natural and non-natural inland waters and on the effect of physical (e.g. thermal stability), chemical (e.g. ionic strength) and biological (phytoplankton and bacterial growth rates) conditions on the formation and breakdown of TEP.

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