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Abundance and distribution of transparent exopolymer particles in the estuarine turbidity maximum of Chesapeake Bay

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ABSTRACT: Transparent exopolymer particle (TEP) concentrations were measured in the estuarine turbidity maximum (ETM) region of Chesapeake Bay during 8 research cruises over 2 yr. TEP concentrations ranged from 37 to 2820 µg xanthan gum equivalent l^{-1} and accounted for an estimated average (±SD) of 32 ± 16% of particulate organic carbon (POC). Spatially averaged TEP and chlorophyll *a* (chl *a*) concentrations were positively correlated over the 2 yr period, although these parameters were rarely correlated on a sample-to-sample basis. Maximum TEP concentrations were often spatially separated from chl *a* maxima, suggesting that TEP in ETM regions is controlled by formation, concentration, and transport processes rather than proximity to precursor source material. Significant correlations between TEP and phaeophytin *a*, POC, dissolved organic carbon (DOC), total suspended solids, and degree of stratification were observed during some sampling periods. Settling tube experiments revealed a positive correlation between TEP concentration and the fraction of settling particulate matter, indicating either enhanced local aggregation and settling or transport and accumulation of aggregates formed elsewhere in the ETM region. These results indicate that TEP constitutes a very large fraction of POC in ETM regions, and suggest that TEP contributes to the formation and maintenance of ETM.

KEY WORDS: Phytoplankton · Bacterioplankton · Seasonal variability · Interannual variability · Suspended particulate matter · Particulate organic matter · Stratified system · Sedimentation rates

INTRODUCTION

The estuarine turbidity maximum (ETM) of Chesapeake Bay is a region of high turbidity caused by the entrainment of tidally resuspended sediment. Located near the limit of salt intrusion in the upper Chesapeake Bay, the ETM is created by tidal asymmetries in particle transport brought about by the effect of gravitational circulation on tidal flows (Sanford et al. 2001). The Chesapeake Bay ETM ecosystem serves as nursery habitat for larval stages of white perch *Morone americana* and striped bass *M. saxatilis* (North & Houde 2006), because it hosts abundant mesozooplankton prey (Roman et al. 2001, 2005), and because its turbid waters offer a refuge from visual predators. The suspended particles that cause this high turbidity are aggregates composed of both mineral grains and organic material (Zabawa 1978). Aggregation of particles in ETM is thought to be enhanced by organic matter including material produced during phytoplankton blooms (van der Lee 2000a, Lartiges et al. 2001, Mikes et al. 2004, Verney et al. 2009), but little is known about the composition and concentration of this material.

In aquatic systems, aggregated particles such as marine snow are bound together by transparent exopolymer particles or TEP (Alldredge et al. 1993, Passow & Alldredge 1995a, Grossart et al. 1997). TEP are

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clear, gel particles composed of acidic polysaccharides produced by phytoplankton and bacteria, and they form a major component of the matrix of aggregates (Passow 2002). Both laboratory and field studies have demonstrated the importance of TEP for the aggregation and sinking of diatoms, bacteria, and other microorganisms (Passow & Alldredge 1995b, Passow et al. 2001, Bar-Zeev et al. 2011), most likely by increasing the stickiness of particles (Jackson 1995, Engel 2000). In addition to their ability to increase particle aggregation and sinking, the high carbon content of TEP make them an important part of the global oceanic carbon cycle. The C:N ratio of TEP is well above the Redfield ratio, making sinking TEP a pathway for the flux of excess carbon to the deep ocean (Engel & Passow 2001, Engel 2004).

TEP are produced either by coagulation of dissolved polysaccharides (Chin et al. 1998), or by direct release of TEP by organisms including phytoplankton, bacteria, and filter-feeding mollusks and ascidians (Decho 1990, Hoagland et al. 1993, McKee et al. 2005, Heinonen et al. 2007), all of which are common in estuaries. Dissolved polysaccharides (TEP 'precursors') can be released from growing phytoplankton and bacteria, through 'sloppy feeding' or grazing by zooplankton, and via viral or osmotically-induced cell lysis (Passow 2002, Verdugo et al. 2004). The abiotic coagulation of dissolved precursors into TEP is dependent on physical processes such as stratification and turbulence that control the frequency of collisions between TEP precursors (Precali et al. 2005, Beauvais et al. 2006), and on chemical conditions that influence the stickiness of the precursors. Examples of these chemical conditions include salinity, which has a positive effect on stickiness (Mari et al. 2012), and dissolved metal ions, which have a negative effect on stickiness (Mari & Robert 2008). Also, cations (e.g. Ca^{2+}, Mg^{2+}, H^{+}) appear to stabilize TEP (Passow 2002) and influence TEP formation in estuaries (Wetz et al. 2009),

There are few published studies of TEP in estuaries (Wurl & Holmes 2008, Wetz et al. 2009, Mari et al. 2012) and no studies of TEP in ETM, despite the likely importance of TEP in estuarine environments. Studies in the coastal and open ocean have shown a general increase in TEP concentrations along a gradient from oligotrophic to more eutrophic environments (Passow 2002), a pattern which appears to extend into estuaries (Wurl & Holmes 2008, Wetz et al. 2009). The influence of TEP on particle aggregation and sedimentation may have a profound effect on the fate of particulate organic matter (POM) in highly productive estuaries.

This manuscript presents one of the first studies of TEP in a strongly stratified estuarine environment. We hypothesized that TEP production in ETM enhances particle aggregation and promotes the attachment of labile POM capable of forming the base of a detrital food web. We surveyed TEP concentrations across the ETM region of the Chesapeake Bay during 8 research cruises over 2 yr and compared these measurements to a suite of biological, chemical, and physical measurements. We found very high concentrations of TEP that were spatially and temporally variable. Across the ETM region, TEP was most often spatially correlated with measures of particulate material and degree of water column stratification, and temporally correlated with chlorophyll concentration. We also found a positive correlation with the fraction of settling particles in the water column suggesting that TEP contributes to the process of ETM particle aggregation, sinking, and accumulation.

MATERIALS AND METHODS

Samples were collected during 8 research cruises aboard the RV 'Hugh R. Sharp' in the ETM region of Chesapeake Bay (Fig. 1) in winter (January or February), early and late spring (April and May), and fall (October) of 2007 and 2008 (see Table 1). During each cruise at least two 5-station axial surveys through the ETM region were undertaken, with sampling at 3 depths per station (surface, mid-depth, and ~1 m above bottom). Bottom sampling depth ranged from 5.7 m at the freshwater station to 23.7 m down-estuary of the ETM region. In addition, samples were collected at anchor stations upstream, within, and downstream of the ETM zone. Samples were collected with 10 l plastic Niskin bottles attached to a rosette equipped with a suite of sensors for measuring conductivity, temperature, depth, chlorophyll fluorescence (ECO/AFL fluorometer), and turbidity as optical backscatter (OBS-3, D&A Instrument). Water samples from each depth were collected in 2 Niskin bottles, combined in 20 l plastic buckets equipped with sampling ports, and gently stirred with large stir-bars to keep particles suspended during subsampling.

TEP were measured using the spectrophotometric method of Passow & Alldredge (1995b). Samples were filtered in triplicate onto 0.40 µm pore-size, 47 mm diameter polycarbonate filters (Millipore), stained for ~2 s with 1 ml of a 0.02% (w/w) aqueous solution of Alcian Blue (8GX) and immediately rinsed with distilled water to remove unbound dye. Sample volume was chosen carefully to avoid clogging the filter

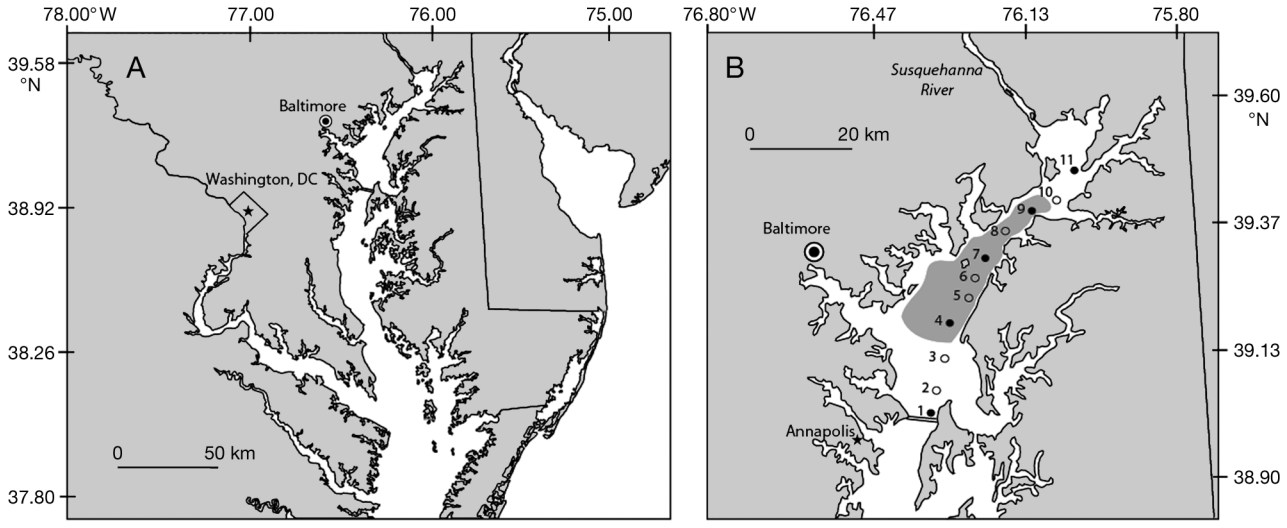

Fig. 1. (A) Chesapeake Bay and (B) the upper Chesapeake Bay region. The typical location of the estuarine turbidity maximum (ETM) is shaded medium grey. Closed circles: axial survey stations for all cruises except early spring 2007, when samples were collected at Stns 1, 3, 6, 8, and 11; open circles: other stations used for CTD casts. Five stations were sampled per axial survey: the southern- and northern-most stations were sampled in every survey, while the middle 3 stations were selected based on the location of the estuarine turbidity maximum (ETM) in each survey

(range 20 to 200 ml). Low vacuum (<15 cm Hg) was used to avoid destroying the delicate TEP. Stained samples were stored at −20°C until processed.

To measure TEP-bound Alcian Blue, the sample filters were soaked in 6 ml of an 80% sulfuric acid solution for 3 h, and vortexed every hour. This solution was then loaded into a 96-well plate, with 300 µl added per well, and the absorbance read at 788 nm with a BioTek Synergy HT microplate reader. TEP was quantified using a standard curve prepared with xanthan gum (XG) particles for each batch of Alcian Blue as described in Passow & Alldredge (1995b). Standard curves were prepared for each batch of dye by filtering 0.25 to 2.0 ml of XG solution through 6 filters for each volume; 3 pre-weighed filters for measuring mass and 3 filters for TEP analysis. Filters of XG for mass were held in a drying oven for at least 24 h (~60°C), allowed to equilibrate at room temperature for 2 h, and weighed on a Sartorius microbalance. Filters of XG for TEP analysis were stained with Alcian Blue and analyzed as described above.

Dissolved organic carbon (DOC) measurements were performed on samples of filtrate from pre-ashed 25 mm glass fiber filters (Whatman GF/F or Sterlitech GF75). DOC samples (20 ml) were stored frozen at −20°C in polypropylene vials and analyzed by Horn Point Laboratory (HPL) analytical services using a Shimadzu TOC-5000 total organic carbon analyzer (Sugimura & Suzuki 1988). DOC analyses were referenced against deep Sargasso Sea water provided by the Hansell Laboratory, University of Miami.

The concentration of total suspended solids (TSS) was determined from water samples filtered through ashed and pre-weighed 25 mm glass fiber filters (Wheaton GF/F or Sterlitech GF75). Duplicate sample filters were dried at 60°C for 48 h before being weighed with an Ohaus Adventurer microbalance.

Particulate organic carbon (POC) was determined from water samples filtered through ashed glass fiber filters (Whatman GF/F or Sterlitech GF75), which were dried, fumed under concentrated (12 N) HCl overnight, and dried for 24 h at 60°C before being crimped into silver capsules. The samples were then analyzed at the University of California Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon).

Chlorophyll *a* (chl *a*) and phaeophytin *a* (pheo *a*) were measured using EPA method 445.0 (Arar & Collins 1992). Briefly, samples were collected by filtering water through 25 mm glass fiber filters (Whatman GF/F) under low light conditions to minimize photodegradation of the pigments and stored at −20°C. The pigments were extracted with 90% acetone, and their concentrations measured fluorometrically.

The degree of physical water column stratification at each sampling depth was quantified by analyzing vertical salinity profiles for each sample using data from the CTD. The profiles were smoothed via a 1.75 m moving average (the height of the CTD rosette). The salinity 1.5 m above the sample depth was

then subtracted from the salinity at the sample depth and the change in salinity was divided by 1.5 m to give an approximation of ds/dz in units of m^{-1}. Since the tops of the Niskin bottles were 1.5 m above the CTD sensor, this is equivalent to the salinity stratification sampled by the bottles. This measure of stratification indicates whether the sample was taken in a strong pycnocline (high stratification) or in a relatively well-mixed part of the water column (low stratification).

Average TEP values for each cruise were calculated from axial surveys of the upper Chesapeake Bay omitting the shallow and often freshwater Stn 11 (i.e. spatial average of 4 stations, 3 depths), and were also calculated for all samples collected at 3 salinity ranges during each research cruise (<1, 1–5, >5). Average antecedent Susquehanna River flow ($m^3 s^{-1}$) was calculated for each cruise from USGS daily flow measurements at Conowingo Dam, just upstream of the conjunction of the Susquehanna River with Chesapeake Bay (http://waterdata.usgs.gov/nwis). These calculations were done in conjunction with estimates of residence time using the fraction of freshwater method (e.g. Asselin & Spaulding 1993). An initial estimate of the fraction of freshwater residence time (t_{res}) was calculated based on the annual mean discharge of the Susquehanna River (1100 $m^3 s^{-1}$), the average salinity and the highest salinity calculated from each axial survey, and the volume of upper Chesapeake Bay down to the southernmost sampling station (Cronin 1971). Susquehanna River flow prior to each cruise was averaged applying a backwards exponential weighting in time, scaled by the initial estimate of t_{res}. A new estimate of t_{res} was derived based on this new estimate of river flow, and the process repeated until the estimates stabilized. Estimates of the average top to bottom salinity difference and the average water temperature were also calculated for each axial survey. These estimates of physical factors were compared to each other and to spatially averaged TEP values.

To compare the settling characteristics of suspended material in the ETM to those of particles in source waters, a modified Owen-style settling tube (Owen 1976) was used to collect water samples at 3 locations during each cruise: near-surface freshwater at the northern-most station, near-bottom water in the ETM, and higher salinity water collected below the pycnocline at the southern-most station. The sampling apparatus consisted of a 20 l Niskin bottle lined with a straight-walled acrylic tube (inner diameter = 7.62 cm, height = 1.04 m) that holds 5 l of water. To sample, the tube was attached to a specialized frame and deployed with an A-frame over the stern of the ship. Stabilizing vanes (i.e. 'fins') attached to the frame oriented the tube in a horizontal position into the water flow, allowing water and suspended particles to flow through the tube. When pneumatically tripped, the end caps closed and the bottle swung into a vertical position within the frame. Once on deck, 1-l water samples were periodically drawn from a valve installed in the bottom end cap (typically 7, 16, 34, 63 min after bottle tipped to vertical, plus a final 1 l sample), the exact volumes of these samples were recorded, and TSS was measured as described above. While on deck, the tube was wrapped in a reflective Mylar blanket to minimize internal convection cells; while it was not possible to completely eliminate internal motions, observed motions were very small and did not appear to be associated with either thermal effects or ship motion.

Settling velocity spectra were calculated from TSS and volume data using a spreadsheet implementation of Owen's (Owen 1976) original graphical method (see Microsoft Excel spreadsheet in the Supplement at www.int-res.com/articles/suppl/m486p023_supp.xlsx). This method estimates the suspended sediment concentration binned by settling velocity. For present purposes, concentrations were calculated for 2 groups of particles that settled either faster or slower than 0.06 mm s^{-1}, which is the slowest settling speed distinguished by the settling tube. At this settling speed, particles settle 1.3 m in 6 h or 5.2 m in one day. The fraction of fast settling particles was defined operationally as the mass settling faster than 0.06 mm s^{-1} divided by the total mass of particles in the tube. For samples in which more than half of the particles settled faster than 0.06 mm s^{-1}, the median settling speed was estimated by linear interpolation to the 50th percentile of the cumulative TSS distribution. For samples in which more than half of the particles settled slower than 0.06 mm s^{-1}, the median settling speed was set to 0.03 mm s^{-1} as a reasonable estimate of an unknown underlying distribution. The precise value of this slow settling velocity is not important, as long as it is a reasonable representation of slowly settling particles.

RESULTS

TEP concentrations ranged from 37 to 2820 µg XG eq. l^{-1}, and were often elevated in the ETM region (Fig. 2). Spatially averaged TEP values ranged from 492 µg XG eq. l^{-1} in fall 2008 to 1326 µg XG eq. l^{-1} in early spring 2007 (Table 1, Fig. 3). In 2007, TEP con-

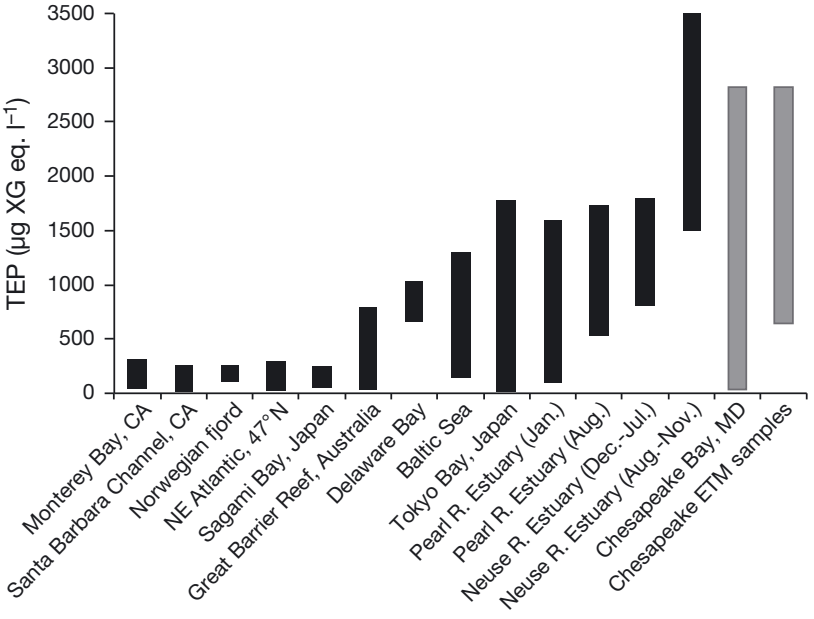

Fig. 2. Range of TEP concentrations (as xanthan gum equivalents, XG eq.) observed in various ecosystems. Gray shaded bars represent this study. ETM samples were defined as bottom and middle depth samples from the ETM region containing elevated concentrations of particles during each cruise. Modified from Passow (2002); additional data from Ramaiah & Furuya (2002; Tokyo Bay), Sun et al. (2012; Pearl R Estuary), and Wetz et al. (2009; Neuse R. Estuary)

centrations were high in winter and early spring and declined through fall (Fig. 3). In early and late spring of that year, higher concentrations were observed in samples with salinity >1, while in the winter and fall TEP concentrations were similar across all salinities. In 2008, average TEP concentrations were more seasonally and spatially consistent, and lower than in 2007 in 3 out of 4 cases.

The concentration of TEP correlated positively with TSS and POC aggregating across all sampling dates (Fig. 4), but on some individual sampling dates these relationships were not significant. Spearman's correlation analysis showed that TEP concentration was more often correlated with environmental measurements in 2007 than in 2008 (Table 2). In 2007, TEP concentrations were positively correlated with TSS during February, April, and May (p-values range from <0.05 to <0.0001). In addition, TEP was positively correlated with salinity, pheo *a*, chl *a*, POC, and DOC concentrations in April and May (p-values range from <0.05 to <0.0001; Table 2), and degree of stratification in May. In 2008, TEP correlated with TSS in January ($p < 0.01$), DOC in April ($p < 0.05$), POC in May ($p < 0.05$), salinity in April ($p < 0.05$), and degree of stratification in April and May ($p < 0.05$; Table 2). TEP concentration did not correlate with any environmental measurements in October of either year.

Susquehanna River flow was the dominant control on the physical environment of upper Chesapeake Bay (Table 1). Average salinity (–), average top to bottom salinity difference (+), and residence time (–) all correlated strongly and significantly with flow ($p \ll 0.05$), where the + or – signifies the sense of the correlation. Temperature varied independently of flow at these time scales, increasing monotonically from the first to the last cruise during each year. Cruise-averaged TEP was not significantly correlated to any of these averaged physical indicators.

TEP concentrations varied across the sampled region, and in some surveys (e.g. February 2007, May 2008) high concentrations of TEP co-occurred with high concentrations of chl *a* (Fig. 5). But TEP concentrations were also relatively high at locations upestuary of peak chl *a* (e.g. April 2007, 2008, January 2008). Because of this, TEP and chl *a* concentrations were correlated only during 2 cruises (Table 2), and

Table 1. Sampling dates, residence time estimates (t_{res}, d), averaged antecedent Susquehanna River flow ($m^3\ s^{-1}$), spatially averaged salinity, spatially averaged top to bottom salinity difference (ΔS), spatially averaged temperature (°C), and spatially averaged TEP (µg XG eq. l^{-1}) for each cruise

Year	Season	Dates	t_{res}	Flow	Ave. salt	ΔS	Ave. temp	Ave. TEP
2007	Winter	Feb 23–26	26	953	7.5	3.1	0.9	1214
	Early spring	Apr 9–15	12	2283	7.3	7	7.6	1326
	Late spring	May 8–14	15	1822	7.7	6.3	14.8	682
	Fall	Oct 2–8	57	205	12.9	3	23.4	497
2008	Winter	Jan 23–26	14	1585	9.2	8	3	513
	Early spring	Apr 17–23	16	1947	6	6.1	11.2	511
	Late spring	May 16–22	18	1550	6.6	5.4	15.7	574
	Fall	Oct 3–9	53	265	12	2	20.2	492

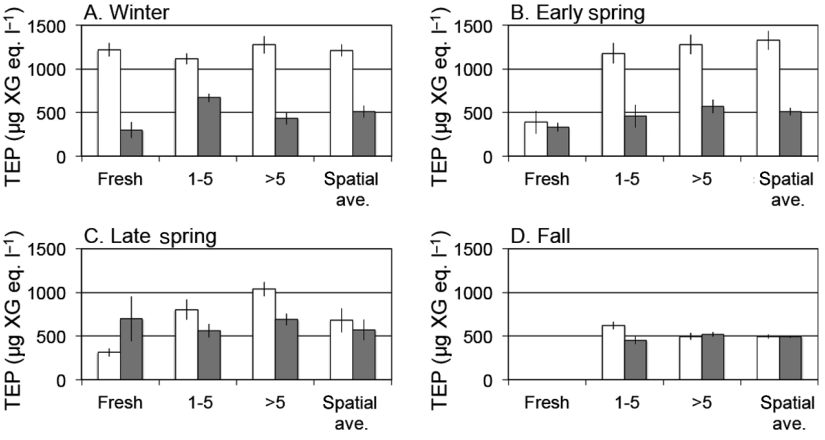

Fig. 3. Spatially averaged TEP concentrations (±SE) observed during cruises in (A) winter, (B) early spring, (C) late spring, and (D) fall. Averages are given for all samples collected in freshwater (salinity < 1), mid-salinity (1 < salinity < 5) and higher salinity (salinity > 5) water, and for samples from complete axial surveys (4 stations, 3 depths) within each cruise (total). Open bars are data from 2007, filled bars from 2008. No data are presented for freshwater in the fall because low river flow at that time of year made freshwater inaccessible

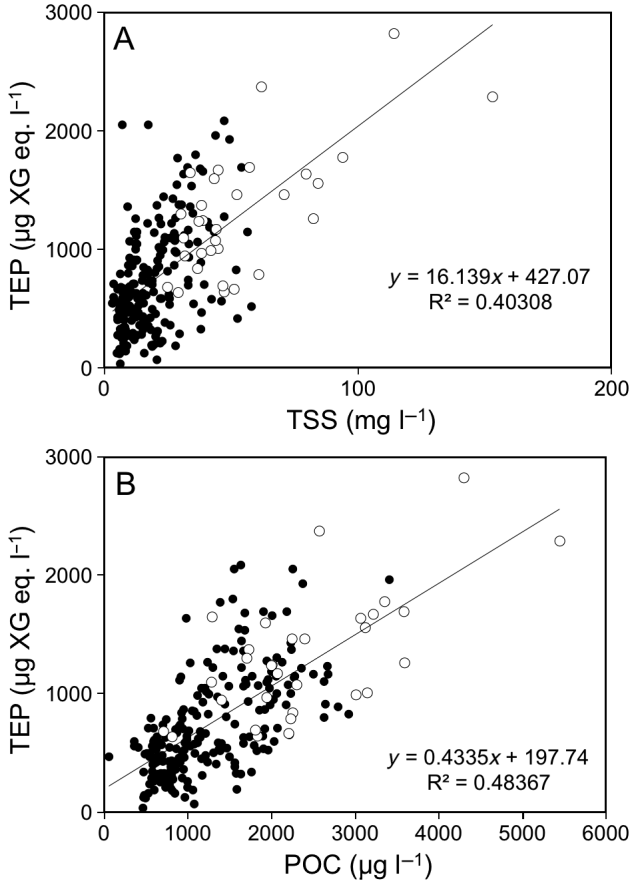

Fig. 4. TEP concentration versus (A) total suspended solids (TSS) and (B) particulate organic carbon (POC) for all samples. Open circles: samples collected from the ETM, identified as regional peaks in turbidity; closed circles: samples collected outside the ETM

showed no overall relationship (Fig. 6). However, a significant correlation was observed between spatially averaged TEP and spatially averaged chl *a* concentrations calculated for each cruise over the 2 yr study period (Fig. 6; Spearman's rho = 0.93, $p < 0.01$).

Median particle settling speed determined with the modified Owen-style settling tube ranged from below our detection limit (0.06 mm s^{-1}) to 2.5 mm s^{-1}, and was faster in ETM samples (mean ±SD 0.47 ± 0.73 mm s^{-1}) than in samples collected up or down estuary (0.19 ± 0.39 mm s^{-1}, and 0.06 ± 0.1 mm s^{-1} respectively). The fraction of particles that settled faster than 0.06 mm s^{-1} was highly variable, and ranged from 0 to 90% of the suspended particle mass. TEP measurements carried out concurrently with settling tube samples show that total TEP concentration correlated positively with the fraction of settling suspended solids (Spearman's rho = 0.68, $p < 0.05$; Fig. 7). ETM samples tended to have both higher TEP concentrations and higher fractions of settling suspended solids than samples collected in freshwater farther up-estuary or in higher salinity water farther down-estuary (Fig. 7).

DISCUSSION

TEP concentrations were persistently high in the ETM region of Chesapeake Bay compared to those observed in coastal and open-ocean environments (Fig. 2; Passow 2002, Ramaiah & Furuya 2002, Engel 2004, Sugimoto et al. 2007), and were similar to concentrations published in other estuaries (Wurl & Holmes 2008, Wetz et al. 2009, Sun et al. 2012). This is consistent with the observed trend of increasing TEP concentrations along productivity gradients (Passow 2002, Engel 2004), and likely reflects the eutrophic state of Chesapeake Bay (Kemp et al. 2005). Maximum TEP concentrations were found at or below the pycnocline in the oligohaline region of the upper Chesapeake Bay (Fig. 5), although concentrations were high in freshwater during fall (October) and winter (January–February) (Fig. 3). Also, TEP concentrations were sometimes elevated in waters down-estuary of the ETM in association with phytoplankton blooms at and above the pycnocline (Fig. 5). These spatial patterns indicate that there are multi-

Table 2. Spearman's rho, significance, and number of samples for correlation analyses between TEP and phaeophytin (pheo *a*), chlorophyll *a* (chl *a*), particulate organic carbon (POC), dissolved organic carbon (DOC), total suspended solids (TSS), and degree of stratification (strat). Bold indicates $p < 0.05$

Cruise		pheo *a*	chl *a*	POC	DOC	TSS	Strat	Salinity
Feb 07	rho	0.041	−0.099	0.112	−0.006	**0.379**	−0.404	−0.050
	p	0.830	0.604	0.557	0.977	**0.039**	0.077	0.795
	n	30	30	30	30	**30**	20	30
Apr 07	rho	**0.585**	**0.361**	**0.598**	**0.442**	**0.509**	0.254	**0.455**
	p	**0.000**	**0.011**	**0.000**	**0.001**	**0.000**	0.160	**0.001**
	n	**49**	**49**	**49**	**49**	**49**	32	**49**
May 07	rho	**0.742**	**0.387**	**0.810**	**0.621**	**0.834**	**0.395**	**0.654**
	p	**0.000**	**0.001**	**0.000**	**0.000**	**0.000**	**0.017**	**0.000**
	n	**66**	**66**	**66**	**66**	**66**	**36**	**66**
Oct 07	rho	0.267	−0.013	−0.107	0.179	−0.326	−0.276	0.091
	p	0.337	0.965	0.703	0.523	0.236	0.440	0.746
	n	15	15	15	15	15	10	15
Jan 08	rho	0.471	0.075	0.639	0.242	**0.631**	−0.238	0.181
	p	0.049	0.766	0.004	0.334	**0.005**	0.570	0.472
	n	18	18	18	18	**18**	8	18
Apr 08	rho	0.335	−0.448	−0.104	**0.539**	0.150	**0.706**	**0.603**
	p	0.223	0.094	0.713	**0.038**	0.593	**0.023**	**0.017**
	n	15	15	15	**15**	15	**10**	**15**
May 08	rho	0.074	−0.009	**0.452**	NA	0.034	**0.581**	0.244
	p	0.750	0.965	**0.023**	NA	0.872	**0.023**	0.241
	n	21	25	**25**	NA	25	**15**	25
Oct 08	rho	0.214	0.174	0.210	0.027	0.110	0.023	−0.074
	p	0.284	0.385	0.302	0.892	0.592	0.934	0.715
	n	27	27	26	27	26	15	27
2007	rho	**0.514**	**0.307**	**0.695**	0.148	**0.732**	**0.264**	**0.323**
	p	**0.000**	**0.000**	**0.000**	0.061	**0.000**	**0.009**	**0.000**
	n	**160**	**160**	**160**	160	**160**	**98**	**160**
2008	rho	0.111	−0.029	**0.264**	0.220	0.129	**0.379**	0.172
	p	0.323	0.794	**0.015**	0.091	0.243	**0.008**	0.115
	n	81	85	**84**	60	84	**48**	85

ple sources of TEP to the Chesapeake Bay ETM, and that TEP is retained and concentrated in the ETM.

Inter-annual variability

Seasonal patterns in TEP concentrations differed dramatically between years. TEP concentrations were similar in October of both years, but were much higher in 2007 than in 2008 during winter and spring (Fig. 3). In winter 2007, TEP concentrations were very high in freshwater samples collected in the upper portion of the ETM region, averaging 2 to 4 times higher than all subsequent sampling dates (Fig. 3). This cruise coincided with the breakup of a large ice cover in northern Chesapeake Bay. Water samples in the freshwater region featured large amounts of filamentous algae colonies, which grew on the bottom and margins of the floating ice. We hypothesize that the melting and breakup of the ice cover caused these normally sessile colonies to enter the water column, where stress due to differing light regimes and osmotic pressure caused them to leak potential TEP precursors into the water column. The formation of TEP from senescent algae and algal detritus has been demonstrated in both field and laboratory studies (Liu & Buskey 2000, Ramaiah et al. 2001). It is also possible that algae growing in freshwater ice (Frenette et al. 2008) produce exopolymeric substances similar to those produced by sea ice algae (Krembs et al. 2002, Underwood et al. 2010), and that this material contributed to water column TEP during ice breakup.

Seasonally varying spatial averages of salinity, degree of overall stratification, and freshwater residence time were all significantly related to antecedent Susquehanna River Flow, as expected (e.g. Sanford et al. 2001). However, neither these factors nor water temperature were significantly related to spatially averaged TEP, when compared across all cruises. Within several cruises, and across all cruises, TEP was strongly related to TSS, which was higher in the ETM than upstream or downstream. These correlations clearly show associations between TEP and suspended sediment, but they may also indirectly support an association between TEP and turbulence (Beauvais et al. 2006). This is because most of the high TSS samples were collected near the bottom during maximum tidal resuspension. Sanford et al. (2005) show a clear correlation between tidal sediment resuspension and near bottom turbulence levels in the Chesapeake ETM, implying a potential connection between high turbulence, high TSS, and high TEP. However, observed correlations between TEP and stratification in the pycnocline (Table 2) may indicate a connection between the very low turbulence levels there and TEP formation. Further investigation is warranted.

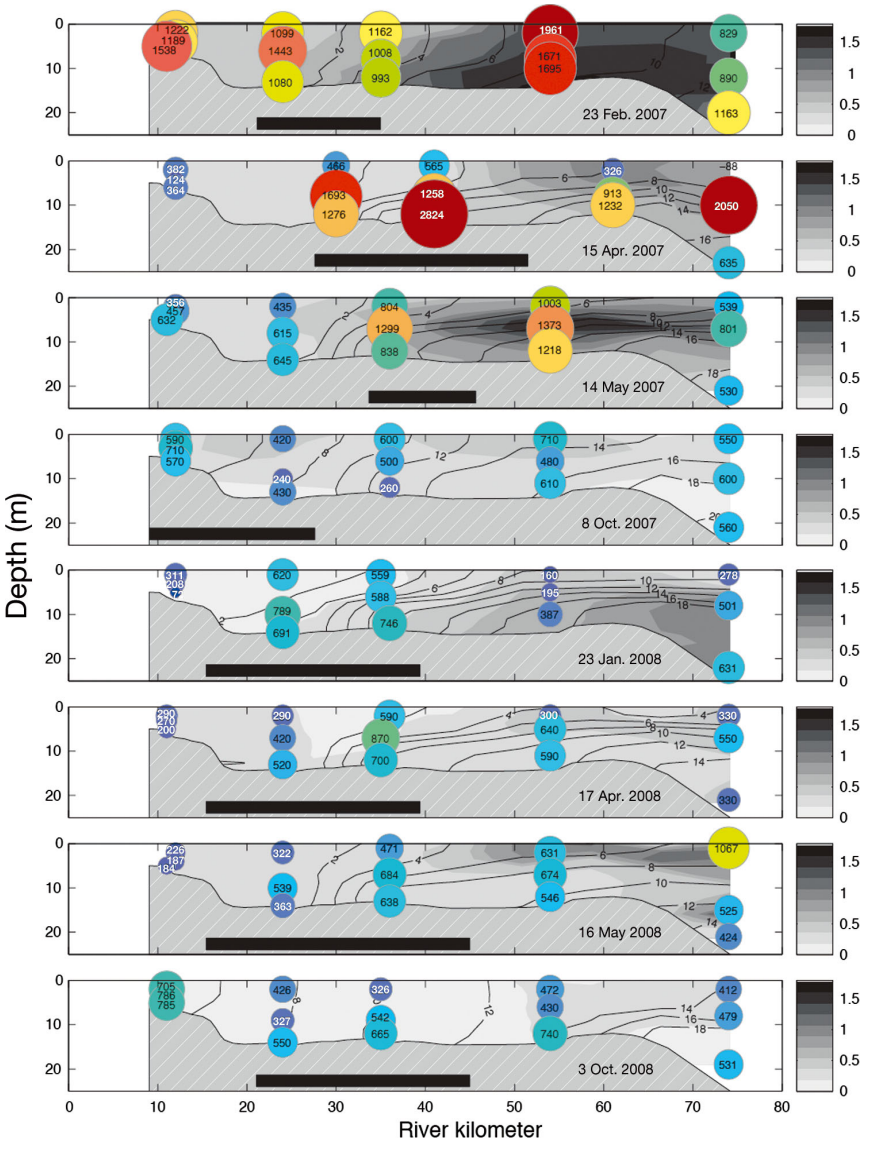

Fig. 5. Distribution of TEP during selected axial surveys through ETM region for one axial survey per research cruise. Circles are scaled to TEP concentration (in µg XG eq. l^{-1}), with warmer colors (yellow to red) indicating higher concentrations. Contours indicate salinity. Shading indicates chl *a* fluorescence (in voltage units). Regions of peak bottom-water turbidity are indicated with black bars

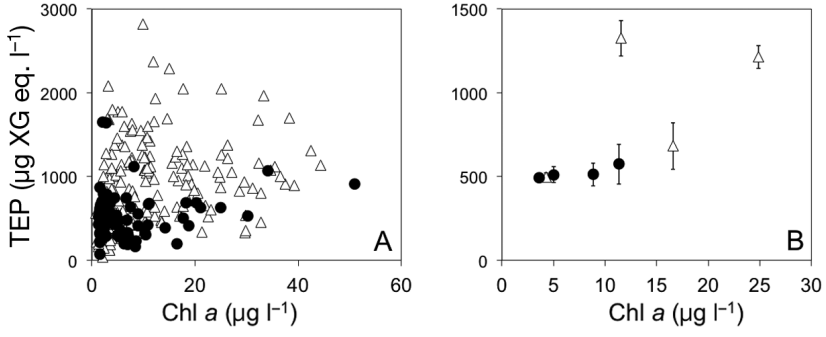

Fig. 6. (A) TEP concentration versus chl *a* concentration for all samples, and (B) spatially averaged TEP concentration (±SE) for each cruise versus average chl *a* concentration. Triangles denote 2007 cruises, circles denote 2008 cruises

TEP organic carbon

TEP often made up a large fraction of the POC in the water column. The ratio of TEP to POC was highly variable, ranging from 0.07 to 1.68 µg XG eq. (µg POC)$^{-1}$, with a mean (±SD) ratio of 0.61 ± 0.30 across all samples (Fig. 4). To determine if carbon in TEP represents a significant fraction of POC in the upper Chesapeake Bay, we converted TEP concentration to carbon concentration using a conversion factor. Engel & Passow (2001) measured the carbon content of TEP produced from a variety of pure diatom cultures as well as a natural assemblage of diatoms, and found that the carbon content of TEP ranged from 0.53 to 0.88 µg C (µg XG eq.)$^{-1}$, with an average value of 0.75 µg C (µg XG eq.)$^{-1}$. These conversion factors were determined for organisms grown in media with much higher salinity than our estuarine samples; thus, we applied the lowest value reported by Engel & Passow (2001) as a conversion factor (0.53 µg C [µg XG eq.]$^{-1}$) to conservatively estimate the concentration of TEP-derived carbon (TEP-C) in the ETM region of the Chesapeake Bay. We calculated that TEP-C constitutes on average (±SD) 32 ± 16% of the total measured POC in the upper Chesapeake Bay, and ranges as high as 89%. If we apply the improved carbon conversion factor calculated by Engel (2004) (0.63 µg C [µg XG eq.]$^{-1}$), then these values are higher. It should be noted that the difference in pore size of the filters used to measure TEP and POC (0.4 µm polycarbonate and 0.7 µm glass fiber, respectively) could cause these calculations to overestimate the portion of TEP-C (Passow & Alldredge 1995b, Engel & Passow 2001). Nevertheless, it is clear that TEP make up a significant portion of the POC in the upper Chesapeake Bay (Wetz et al. 2009).

TEP are consumed directly by zooplankton (Passow & Alldredge 1999, Ling & Alldredge 2003), and the tendency for TEP to aggregate with bacteria-sized particles may shorten trophic

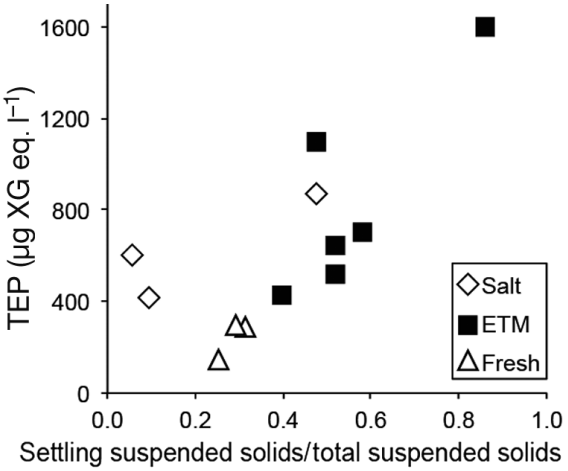

Fig. 7. TEP concentration versus concurrently measured fraction of settling suspended solids for freshwater samples collected near the surface at Stn 1, ETM samples collected at near-bottom depth, and higher-salinity samples collected below the pycnocline down-estuary of the ETM

linkages allowing larger zooplankton and juvenile fish to graze on much smaller food items (Grossart et al. 1998, Mari & Rassoulzadegan 2004). Our results show that TEP is an abundant potential food source for zooplankton (and possibly fish) in the Chesapeake ETM during the winter-spring transition when juvenile striped bass *Morone saxatilis* and the white perch *M. americana* rely on abundant zooplankton prey (North & Houde 2003). During this period in May 1998, abundance of *Eurytemora affinis* copepodites and adults averaged 40 988 (±11 159 SE) m^{-2} and peaked at >175 000 m^{-2}. TEP particles and associated microorganisms may support the development of these large populations of zooplankton during early spring (Roman et al. 2005) that become prey for juvenile fish.

Aggregation and sinking

Particle sedimentation is essential for the formation of ETM (Festa & Hansen 1978, Geyer 1993, Sanford et al. 2001), and particle settling speeds are generally increased by the process of aggregation into larger particles (Van der Lee 2000b, Xia et al. 2004, Sanford et al. 2005, Graham & Smith 2010, Smith & Friedrichs 2011). Our results show that the fraction of rapidly settling particles (with settling speeds greater than 0.06 mm s^{-1}) is positively correlated with TEP concentration (Fig. 7). There are 2 potential reasons for this association. Higher concentrations of suspended particles promote aggregation (Mehta et al. 1989, Verney et al. 2009). Both total particle concentration and TEP concentration are higher in ETM samples than in freshwater and saltwater end-member samples. Thus, conditions are optimal for aggregation and the formation of rapidly settling particles in the ETM. Alternatively, if TEP increases the rate of formation of large, rapidly settling particles anywhere in the upper estuary, these particles will tend to be accumulated preferentially in the ETM and maintained in the water column by resuspension (Geyer 1993, Sanford et al. 2005). In this case, TEP is accumulated in the ETM because of its association with large, rapidly settling particles that are transported there from elsewhere.

Our ETM samples contained higher fractions of settling particles than the end-member samples partly because they were collected close to the sediment during resuspension events, while the end-member samples were collected higher in the water column. However, this sampling bias is still consistent with either the enhanced local aggregation mechanism or the remote aggregation and subsequent transport mechanism. It is likely that both factors are important, such that TEP promote aggregation and settling of suspended material throughout this estuarine system, as they do in other marine and freshwater environments (Leppard 1995, Logan et al. 1995, Passow & Alldredge 1995a, Engel 2004), and thereby contribute to ETM particle trapping, which in turn further concentrates TEP in the ETM.

The settling speed of aggregated particles is also influenced by excess particle density, which tends to decrease as aggregate size increases (Van der Lee 2000b, Xia et al. 2004, Smith & Friedrichs 2011). Ballast-free, 'pure' TEP are less dense than water, with an estimated density between 0.70 to 0.84 g cm^{-3} (Azetsu-Scott & Passow 2004). In laboratory experiments, TEP have been shown to decrease the settling velocity of diatom aggregates by decreasing the excess bulk density of aggregates (Engel & Schartau 1999). Relatively high concentrations of TEP can even induce an upward flux of particles (Azetsu-Scott & Passow 2004). However, ballast-free TEP are unlikely to exist in the ETM due to high concentrations of suspended inorganic particulate matter. Using an Owen-type settling tube sampler similar to that used in this study and a video settling tube, Sanford et al. (2005) showed that large aggregates in the Chesapeake Bay ETM sank much faster (0.25 to 8 mm s^{-1}) than their component silt and clay particles (0.0005 to 0.2 mm s^{-1}), regardless of the lesser density of the larger particles. In addition, TEP concentrations were positively correlated with aggregate size in the bottom water of

the Mecklenburg Bight, where, similar to the Chesapeake Bay ETM, much of the suspended particulate material is resuspended sediment (Jahmlich et al. 1999). This suggests that increases in size for TEP-associated aggregates dominated over any decreases in excess density, resulting in the observed correlation between the fraction of rapidly settling suspended solids and high TEP concentrations in the Chesapeake Bay ETM.

Mechanisms of TEP formation

Since the most likely source for TEP and TEP precursors are growing and senescing phytoplankton (Passow et al. 2001, Passow 2002), we expected positive correlations between TEP concentration and measurements of chl *a* and pheo *a*. While we observed these correlations in April and May 2007, and for the year 2007 as a whole, the lack of a clear relationship during the other cruises and 2008 was puzzling (Table 2). By averaging the TEP and chl *a* measurements for each cruise (Fig. 6), we found a positive correlation between spatially averaged TEP and chl *a* concentrations. Spatially averaged TEP also correlated with spatially averaged chl *a* plus pheo *a* (Spearman's rho = 0.83, p = 0.01). These correlations suggests that primary production is a first-order predictor of spatially averaged TEP concentrations on seasonal and interannual timescales over broad spatial scales, but that instantaneous spatial patterns of chl *a* and pheo *a* alone are not sufficient to explain the spatial variability of TEP observed across the upper Chesapeake Bay.

TEP is often directly correlated with chl *a* concentrations (Passow & Alldredge 1995b, Ramaiah & Furuya 2002, Wurl & Holmes 2008, Ortega-Retuerta et al. 2009), but several studies have shown temporal or spatial disconnects between TEP and chl *a* (Schuster & Herndl 1995, Garcia et al. 2002, Corzo et al. 2005). For example, Corzo et al. (2005) found an inverse relationship between TEP and chl *a* concentrations in certain areas of the Bransfield Strait, Antarctica, likely due to a time lag between maximum biomass and maximum TEP production within a phytoplankton bloom. Garcia et al. (2002) reported similar findings in the Gulf of Cadiz, where TEP and chl *a* maxima were spatially distinct. TEP production by phytoplankton is highly variable, and is influenced by a variety of factors including species composition, growth phase, nutrient levels, and turbulence (Passow 2002, Ramaiah & Furuya 2002, Beauvais et al. 2006) that could lead to maximum TEP production becoming decoupled from maximum chl *a* concentrations. In the present case, we postulate that the rapid physical variability characteristic of the ETM region of Chesapeake Bay (e.g. North et al. 2005) and the transport lag of settling particles relative to water circulation (e.g. Sanford et al. 2001) combine with temporal lags between chl *a* biomass and TEP production to decouple their spatial distributions.

In some shallow estuarine waters, primary production by phytobenthos and submerged grasses is significant (e.g. Bergamasco et al. 2003, Lawson et al. 2007), and might contribute to TEP production. However, benthic primary productivity is not usually important in the Chesapeake ETM region. Even though the average water depth of this region is only 4 m, turbidity levels are high enough to completely block light penetration to the bottom (attenuation coefficient, K_d; ~2 m^{-1}; Xu et al. 2005). Indeed, even the plankton community of the ETM region is net heterotrophic due to limited light availability (Boynton et al. 1997). In mesocosm experiments examining interactions between resuspension and ecosystem processes, Porter et al. (2010) found that tidal resuspension similar to that in the Chesapeake ETM was sufficient to shift their systems from benthic dominance to pelagic dominance. Extensive grass beds can flourish seasonally in the freshwater shallows upstream of the ETM, but we generally found lower TEP levels in these same waters. Thus, it is unlikely that benthic primary productivity was an important contributor to TEP production in our study.

Bacterial processes also influence TEP concentrations, by producing TEP or TEP precursors themselves (Passow 2002, Sugimoto et al. 2007), by stimulating TEP production by phytoplankton, or by degrading TEP or consuming TEP precursors (Grossart & Simon 2007). The interplay of these mechanisms by which bacteria regulate TEP concentrations are complex, often species-specific (Grossart et al. 2006), and difficult to predict *in situ*. We observed highly variable levels of bacterial production over the course of the study (data not shown) in both the particle-attached and free-living communities, but no relationships were found between bacterial production and TEP concentration.

TEP concentration was significantly correlated with degree of stratification in April and May 2007, May 2008, and 2007 as a whole (Table 2). Several mechanisms exist by which stratification could influence TEP concentrations in the Chesapeake Bay ETM region. Sinking TEP-rich particles could accumulate on the pycnocline when they reach a water density at which they become neutrally buoyant.

This same mechanism is responsible for the formation of mucilaginous 'false bottoms' in the Adriatic Sea (Alldredge & Crocker 1995, Precali et al. 2005). In the ETM region, vertical stratification was frequently high, at times greater than 2 $\Delta S\ m^{-1}$, which is the same stratification level associated with 'false bottom' formation in the Adriatic (Precali et al. 2005). Alternately, stratification could enhance the formation of TEP. Since the Mg^{2+} and Ca^{2+} cations necessary for the coagulation of TEP from dissolved or colloidal precursors are 2 orders of magnitude greater in seawater than in freshwater discharged from the Susquehanna River (USGS site number 01578310, http://nwis.waterdata.usgs.gov/usa/nwis/qwdata) (Bianchi 2007), the concentrations of these cations should be correlated with salinity. A positive correlation observed between TEP concentration and salinity in the Neuse River Estuary was attributed to Mg^{2+} and Ca^{2+} availability (Wetz et al. 2009). Thus, the interface between low and higher salinity waters could be a hotspot of TEP formation, provided that TEP formation is limited in low-salinity waters by low concentrations of Mg^{2+} and Ca^{2+} cations.

Based on the observed relationships between TEP concentration and chl *a*, degree of stratification, and TSS, we propose a conceptual model to explain the distribution of TEP in the upper Chesapeake Bay. The observed relationship between spatially averaged TEP and chl *a* concentrations suggests that photoautotrophic production is the main source for TEP and TEP precursors, but physical factors that enhance the coagulation of TEP precursors, aggregation of TEP with other ETM particles, and rapid transport of TEP-containing water causes TEP to be concentrated in the ETM and, thus, spatially decouples TEP and chl *a* concentrations across the ETM region. The abiotic coagulation of TEP from dissolved organic matter is dependent on chemical conditions (Mg^{2+} and Ca^{2+} concentration, pH) that change across salinity gradients, making the pycnocline a likely hotspot of abiotic TEP production. Furthermore, changes in water density associated with the pycnocline could allow TEP and TEP-containing aggregates to accumulate (even if just temporarily) in zones where they become neutrally buoyant, and then aggregate with resuspended ETM particles into larger, rapidly settling, TEP-rich aggregates. These processes, coupled with the particle-trapping behavior of the ETM result in elevated TEP concentrations in ETM.

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LITERATURE CITED

Alldredge AL, Crocker KM (1995) Why do sinking mucilage aggregates accumulate in the water column? Sci Total Environ 165:15–22

Alldredge AL, Passow U, Logan BE (1993) The abundance and significance of a class of large, transparent organic particles in the ocean. Deep-Sea Res I 40:1131–1140

Arar EJ, Collins GB (1992) *In vitro* determination of chlorophyll *a* and pheophytin *a* in marine and freshwater phytoplankton by fluorescence. USEPA Method 445, Office of Research and Development, US Environmental Protection Agency, Cincinnati, OH

Asselin S, Spaulding ML (1993) Flushing times for the Providence River based on tracer experiments. Estuaries 16: 830–839

Azetsu-Scott K, Passow U (2004) Ascending marine particles: significance of transparent exopolymer particles (TEP) in the upper ocean. Limnol Oceanogr 49:741–748

Bar-Zeev E, Berman T, Rahav E, Dishon G, Herut B, Kress N, Berman-Frank I (2011) Transparent exopolymer particle (TEP) dynamics in the eastern Mediterranean Sea. Mar Ecol Prog Ser 431:107–118

Beauvais S, Pedrotti ML, Egge J, Iversen K, Marrasé C (2006) Effects of turbulence on TEP dynamics under contrasting nutrient conditions: implications for aggregation and sedimentation processes. Mar Ecol Prog Ser 323:47–57

Bergamasco A, De Nat L, Flindt MR, Amos CL (2003) Interactions and feedbacks among phytobenthos, hydrodynamics, nutrient cycling and sediment transport in estuarine ecosystems. Cont Shelf Res 23:1715–1741

Bianchi TS (2007) Biogeochemistry of estuaries. Oxford University Press, USA, New York, NY

Boynton WR, Boicourt W, Brandt S, Hagy J and others (1997) Interactions between physics and biology in the estuarine turbidity maximum (ETM) of Chesapeake Bay, USA. ICES Annual Meeting, CM 1997/S:11

Chin WC, Orellana MV, Verdugo P (1998) Spontaneous assembly of marine dissolved organic matter into polymer gels. Nature 391:568–572

Corzo A, Rodriguez-Galvez S, Lubian L, Sangra P, Martinez A, Morillo JA (2005) Spatial distribution of transparent exopolymer particles in the Bransfield Strait, Antarctica. J Plankton Res 27:635–646

Cronin WB (1971) Volumetric, areal, and tidal statistics of the Chesapeake Bay estuary and its tributaries. The Chesapeake Bay Institute of the Johns Hopkins University, Baltimore, MD

Decho AW (1990) Microbial exopolymer secretions in ocean environments—their role(s) in food webs and marine processes. Oceanogr Mar Biol Annu Rev 28:73–153

Engel A (2000) The role of transparent exopolymer particles (TEP) in the increase in apparent particle stickiness (alpha) during the decline of a diatom bloom. J Plankton Res 22:485–497

Engel A (2004) Distribution of transparent exopolymer particles (TEP) in the northeast Atlantic Ocean and their potential significance for aggregation processes. Deep-Sea Res I 51:83–92

Engel A, Passow U (2001) Carbon and nitrogen content of transparent exopolymer particles (TEP) in relation to their Alcian Blue adsorption. Mar Ecol Prog Ser 219:1–10

Engel A, Schartau M (1999) Influence of transparent exopolymer particles (TEP) on sinking velocity of *Nitzschia closterium* aggregates. Mar Ecol Prog Ser 182:69–76

Festa JF, Hansen DV (1978) Turbidity maxima in partially mixed estuaries: a 2-dimensional numerical model. Estuar Coast Mar Sci 7:347–359

Frenette JJ, Thibeault P, Lapierre JF, Hamilton PB (2008) Presence of algae in freshwater ice cover of fluvial LAC Saint-Pierre (St. Lawrence river, Canada). J Phycol 44: 284–291

Garcia CM, Prieto L, Vargas M, Echevarria F, Garcia-Lafuente J, Ruiz J, Rubin JP (2002) Hydrodynamics and the spatial distribution of plankton and TEP in the Gulf of Cadiz (SW Iberian Peninsula). J Plankton Res 24:817–833

Geyer WR (1993) The importance of suppression of turbulence by stratification on the estuarine turbidity maximum. Estuaries 16:113–125

Graham GW, Smith W (2010) The application of holography to the analysis of size and settling velocity of suspended cohesive sediments. Limnol Oceanogr Methods 8:1–15

Grossart HP, Simon M (2007) Interactions of planktonic algae and bacteria: effects on algal growth and organic matter dynamics. Aquat Microb Ecol 47:163–176

Grossart HP, Simon M, Logan BE (1997) Formation of macroscopic organic aggregates (lake snow) in a large lake: the significance of transparent exopolymer particles, phytoplankton, and zooplankton. Limnol Oceanogr 42:1651–1659

Grossart HP, Berman T, Simon M, Pohlmann K (1998) Occurrence and microbial dynamics of macroscopic organic aggregates (lake snow) in Lake Kinneret, Israel, in fall. Aquat Microb Ecol 14:59–67

Grossart HP, Czub G, Simon M (2006) Algae-bacteria interactions and their effects on aggregation and organic matter flux in the sea. Environ Microbiol 8:1074–1084

Heinonen KB, Ward JE, Holohan BA (2007) Production of transparent exopolymer particles (TEP) by benthic suspension feeders in coastal systems. J Exp Mar Biol Ecol 341:184–195

Hoagland KD, Rosowski JR, Gretz MR, Roemer SC (1993) Diatom extracellular polymeric substances—function, fine-structure, chemistry, and physiology. J Phycol 29: 537–566

Jackson GA (1995) TEP and coagulation during a mesocosm experiment. Deep-Sea Res II 42:215–222

Jahmlich S, Thomsen L, Graf G (1999) Factors controlling aggregate formation in the benthic boundary layer of the Mecklenburg Bight (western Baltic Sea). J Sea Res 41: 245–254

Kemp WM, Boynton WR, Adolf JE, Boesch DF and others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Mar Ecol Prog Ser 303:1–29

Krembs C, Eicken H, Junge K, Deming JW (2002) High concentrations of exopolymeric substances in Arctic winter sea ice: implications for the polar ocean carbon cycle and cryoprotection of diatoms. Deep-Sea Res I 49:2163–2181

Lartiges BS, Deneux-Mustin S, Villemin G, Mustin C and others (2001) Composition, structure and size distribution of suspended particulates from the Rhine River. Water Res 35:808–816

Lawson SE, Wiberg PL, McGlathery KJ, Fugate DC (2007) Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. Estuar Coast 30: 102–112

Leppard GG (1995) The characterization of algal and microbial mucilages and their aggregates in aquatic ecosystems. Sci Total Environ 165:103–131

Ling SC, Alldredge AL (2003) Does the marine copepod *Calanus pacificus* consume transparent exopolymer particles (TEP)? J Plankton Res 25:507–515

Liu HB, Buskey EJ (2000) Hypersalinity enhances the production of extracellular polymeric substance (EPS) in the Texas brown tide alga, *Aureoumbra lagunensis* (Pelagophyceae). J Phycol 36:71–77

Logan BE, Passow U, Alldredge AL, Grossart HP, Simon M (1995) Rapid formation and sedimentation of large aggregates is predictable from coagulation rates (half-lives) of transparent exopolymer particles (TEP). Deep-Sea Res II 42:203–214

Mari X, Rassoulzadegan F (2004) Role of TEP in the microbial food web structure. I. Grazing behavior of a bacterivorous pelagic ciliate. Mar Ecol Prog Ser 279:13–22

Mari X, Robert M (2008) Metal induced variations of TEP sticking properties in the southwestern lagoon of New Caledonia. Mar Chem 110:98–108

Mari X, Torreton JP, Claire BTT, Bouvier T, Thuoc CV, Lefebvre JP, Ouillon S (2012) Aggregation dynamics along a salinity gradient in the Bach Dang estuary, North Vietnam. Estuar Coast Shelf Sci 96:151–158

McKee MP, Ward JE, MacDonald BA, Holohan BA (2005) Production of transparent exopolymer particles (TEP) by the eastern oyster *Crassostrea virginica*. Mar Ecol Prog Ser 288:141–149

Mehta AJ, Hayter EJ, Parker WR, Krone RB, Teeter AM (1989) Cohesive sediment transport. I: process description. J Hydraul Eng 115:1076–1093

Mikes D, Verney R, Lafite R, Belorgey M (2004) Controlling factors in estuarine flocculation processes: experimental results with material from the Seine Estuary, northwestern France. J Coast Res 41(Spec Issue):82–89

North EW, Houde ED (2003) Linking ETM physics, zooplankton prey, and fish early-life histories to striped bass *Morone saxatilis* and white perch *M. americana* recruitment. Mar Ecol Prog Ser 260:219–236

North EW, Houde ED (2006) Retention mechanisms of white perch (*Morone americana*) and striped bass (*Morone saxatilis*) early-life stages in an estuarine turbidity maximum: an integrative fixed-location and mapping approach. Fish Oceanogr 15:429–450

North EW, Hood RR, Chao SY, Sanford LP (2005) The influence of episodic events on transport of striped bass eggs to the estuarine turbidity maximum nursery area. Estuaries 28:108–123

Ortega-Retuerta E, Reche I, Pulido-Villena E, Agusti S, Duarte CM (2009) Uncoupled distributions of transparent exopolymer particles (TEP) and dissolved carbohydrates in the Southern Ocean. Mar Chem 115:59–65

Owen MW (1976) Determination of the settling velocities of cohesive muds. Report No. IT 161, Hydraulics Research Station, Wallingford

Passow U (2002) Transparent exopolymer particles (TEP) in aquatic environments. Prog Oceanogr 55:287–333

Passow U, Alldredge AL (1995a) Aggregation of a diatom bloom in a mesocosm—the role of transparent exopolymer particles (TEP). Deep-Sea Res II 42:99–109

Passow U, Alldredge AL (1995b) A dye-binding assay for the spectrophotometric measurement of transparent exopolymer particles (TEP). Limnol Oceanogr 40: 1326–1335

Passow U, Alldredge AL (1999) Do transparent exopolymer particles (TEP) inhibit grazing by the euphausiid *Euphausia pacifica*? J Plankton Res 21:2203–2217

Passow U, Shipe RF, Murray A, Pak DK, Brzezinski MA, Alldredge AL (2001) The origin of transparent exopolymer particles (TEP) and their role in the sedimentation of particulate matter. Cont Shelf Res 21:327–346

Porter ET, Mason RP, Sanford LP (2010) Effect of tidal resuspension on benthic–pelagic coupling in an experimental ecosystem study. Mar Ecol Prog Ser 413:33–53

Precali R, Giani M, Marini M, Grilli F, Ferrari CR, Pecar O, Paschini E (2005) Mucilaginous aggregates in the northern Adriatic in the period 1999–2002: typology and distribution. Sci Total Environ 353:10–23

Ramaiah N, Furuya K (2002) Seasonal variations in phytoplankton composition and transparent exopolymer particles in a eutrophicated coastal environment. Aquat Microb Ecol 30:69–82

Ramaiah N, Yoshikawa T, Furuya K (2001) Temporal variations in transparent exopolymer particles (TEP) associated with a diatom spring bloom in a subarctic ria in Japan. Mar Ecol Prog Ser 212:79–88

Roman MR, Holliday DV, Sanford LP (2001) Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. Mar Ecol Prog Ser 213:215–227

Roman M, Zhang X, McGilliard C, Boicourt W (2005) Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. Limnol Oceanogr 50:480–492

Sanford LP, Suttles SE, Halka JP (2001) Reconsidering the physics of the Chesapeake Bay estuarine turbidity maximum. Estuaries 24:655–669

Sanford LP, Dickhudt L, Rubiano-Gomez M, Yates S and others (2005) Variability of suspended particle concentrations, sizes and settling velocities in the Chesapeake Bay turbidity maximum. In: Droppo IG, Leppard GG, Liss P, Milligan T (eds) Flocculation in natural and engineered environmental systems. CRC Press, Boca Raton, FL, p 211–236

Schuster S, Herndl GJ (1995) Formation and significance of transparent exoploymeric particles in the northern Adriatic Sea. Mar Ecol Prog Ser 124:227–236

Smith SJ, Friedrichs CT (2011) Size and settling velocities of cohesive flocs and suspended sediment aggregates in a trailing suction hopper dredge plume. Cont Shelf Res 31: S50–S63

Sugimoto K, Fukuda H, Baki MA, Koike I (2007) Bacterial contributions to formation of transparent exopolymer particles (TEP) and seasonal trends in coastal waters of Sagami Bay, Japan. Aquat Microb Ecol 46:31–41

Sugimura Y, Suzuki Y (1988) A high-temperature catalytic oxidation method for the determination of non-volatile dissolved organic carbon in seawater by direct injection of a liquid sample. Mar Chem 24:105–131

Sun CC, Wang YS, Li QP, Yue WZ, Wang YT, Sun FL, Peng YL (2012) Distribution characteristics of transparent exopolymer particles in the Pearl River estuary, China. J Geophys Res 117:G4, doi:10.1029/2012JG 001951

Underwood GJC, Fietz S, Papadimitriou S, Thomas DN, Dieckmann GS (2010) Distribution and composition of dissolved extracellular polymeric substances (EPS) in Antarctic sea ice. Mar Ecol Prog Ser 404:1–19

van der Lee WTB (2000a) Parameters affecting mud floc size on a seasonal time scale: the impact of a phytoplankton bloom in the Dollard estuary, The Netherlands. In: McAnally WH, Mehta AJ (eds) Coastal and estuarine fine sediment processes, Proceedings in marine science, Vol 3. Elsevier, Amsterdam, p 403–421

Van der Lee WTB (2000b) Temporal variation of floc size and settling velocity in the Dollard estuary. Cont Shelf Res 20:1495–1511

Verdugo P, Alldredge AL, Azam F, Kirchman DL, Passow U, Santschi PH (2004) The oceanic gel phase: a bridge in the DOM-POM continuum. Mar Chem 92:67–85

Verney R, Lafite R, Brun-Cottan JC (2009) Flocculation potential of estuarine particles: the importance of environmental factors and of the spatial and seasonal variability of suspended particulate matter. Estuar Coast 32: 678–693

Wetz MS, Robbins MC, Paerl HW (2009) Transparent exopolymer particles (TEP) in a river-dominated estuary: spatial-temporal distributions and an assessment of controls upon TEP formation. Estuar Coast 32: 447–455

Wurl O, Holmes M (2008) The gelatinous nature of the sea-surface microlayer. Mar Chem 110:89–97

Xia XM, Li Y, Yang H, Wu CY, Sing TH, Pong HK (2004) Observations on the size and settling velocity distributions of suspended sediment in the Pearl River Estuary, China. Cont Shelf Res 24:1809–1826

Xu JT, Hood RR, Chao SY (2005) A simple empirical optical model for simulating light attenuation variability in a partially mixed estuary. Estuaries 28:572–580

Zabawa CF (1978) Microstructure of agglomerated suspended sediments in northern Chesapeake Bay Estuary. Science 202:49–51

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