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Composition of Suspended and Benthic Particulate Matter in the Tidal Freshwater James River

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COMPOSITION OF SUSPENDED AND BENTHIC PARTICULATE MATTER IN THE TIDAL FRESHWATER JAMES RIVER

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

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Abstract

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By C. Anne Schlegel, B.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

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Investigating linkages between the compositions of suspended (seston) and benthic particulate matter is important to the understanding of organic matter (OM) cycling and nutrient retention in aquatic systems. We compared the quantity and quality of the truly suspended (TS) and settleable (SB) fractions of seston as well as benthic particulate matter in the tidal freshwater James River, Virginia. The mass of seston and OM was consistently higher in the TS fraction compared to the SB fraction. OM was preferentially retained in the TS fraction relative to seston. The proportional contribution of OM constituents (chlorophyll a, particulate organic carbon and nitrogen) to the two fractions was consistent across observed concentrations whereas increases in seston concentration resulted in decreased proportions in the TS fraction. Benthic constituent

reservoirs were large relative to the SB fraction but the higher proportion of OM in the SB fraction suggests that the settleable material was more labile.

INTRODUCTION

Sedimentation is the process by which suspended particulate matter (seston) settles from the water column and is eventually delivered to the benthos; a key pathway linking pelagic and benthic food-webs and an important vector for material retention in aquatic systems. Seston is derived from multiple sources and is composed of organic and mineral particles with different physical, chemical, and biotic properties. The resulting heterogeneity of particle density allows for a classification of particles based on their settling velocities; a truly suspended fraction which may never settle and a settleable fraction which may go through cycles of sedimentation and resuspension (Alber 2000). The consequential difference in residence times suggests that particles within these two fractions likely have different 'life histories' (Alber 2000) and therefore disparate means by which they are transported or cycled through a system (Tappin et al. 2010). Understanding the quantity and quality of these two fractions is important to the study of carbon (C) and nitrogen (N) cycling in pelagic and benthic food webs.

The retention of N is an important ecosystem service, particularly in coastal regions. Therefore much interest and study has been conducted to understanding the transport and fate of N. Denitrification is the only mechanism of N removal but biotic assimilation of N and subsequent burial in sediments may result in long-term storage (e.g. Webster et al. 2003). Nitrogen storage in sediments is offset by organic matter break-down and subsequent re-mineralization of N. For example, a nitrate addition into the

Parker River estuary indicated that most N was assimilated by phytoplankton during a summer bloom event and deposited to the benthic sediments and that this deposition was balanced by the flux of N from the benthos to the water column (Holmes et al. 2000). This suggests that freshly deposited material was rapidly mineralized through feeding by detritivores and organic matter decomposition by bacteria. Spatial differences in the retention of N as well as C were noted in the Sandon and Brunswick-Simpsons estuaries which exhibited an increase in N and C content in the upper reaches of the estuaries relative to more seaward sites (Ferguson et al. 2003). These differences were attributed to variations in the lability of carbon implying differences in remineralization. Thus retention is determined by the proportion of suspended material which is deposited to the benthos and the proportion of sedimented material that is remineralized.

In estuaries, phytoplankton are an important component of nutrient assimilation and the sedimentation of phytoplankton along with other constituents of seston affect the quantity and quality of benthic particulate matter. The percentage of phytoplankton production lost to sedimentation is highly variable among aquatic systems (e.g., 10% - 72%; Baines and Pace 1994; Lignell et al. 1993). Variation is attributed to differences in phytoplankton sinking rates among communities, depth of the water column, and the intensity of turbulent mixing. For example, in Chesapeake Bay tributaries, diatoms have historically been a dominant class of phytoplankton (Marshall et al. 2009) and sedimentation has been distinguished as an important fate of diatoms relative to other classes of phytoplankton (Hagy et al. 2005). The C and N contained in sinking phytoplankton and other organic matter is deposited to the surficial sediments where it may be utilized by benthic organisms. This deposition of organic matter to the benthos is an important component of estuarine food webs (Ferguson et al. 2003). Benthic food webs are generally considered to be food limited and freshly deposited organic matter e.g. phytoplankton ("phytodetritus") is considered the most labile fraction of particulate matter. In the Baltic Sea regions of high phytoplankton production support greater biomass of benthic amphipods which also exhibit higher fecundity and lipid content (Elmgren et al. 2001; Quijon et al. 2008; Sundelin et al. 2008). Rates of organic matter utilization however are not solely dependent on rates of sediment deposition. Den Heyer and Kalff (1998) found that organic matter (OM) mineralization in sediments was unrelated to overlying water column algal abundance. However, they did find that there was a significant seasonal difference in mineralization suggesting that accumulation of phytodetritus may be subsequently utilized by microbes and benthic detritivores organisms.

The vertical flux of particles to the benthos has been more widely studied in lakes (e.g. Baines and Pace 1994) than in river systems. While lakes have currents, they do not have the strong tidal and fluvial forces associated with estuaries. As such, sedimentation studies are considered to be more technically challenging in estuaries resulting in relatively few studies. However discriminating between settleable and truly suspended fractions of seston is important to our understanding of the fate of seston and its organic matter constituents. Investigations of these two fractions have varied in temporal and spatial resolution but the general conclusion has been that slowly settling particles have a higher concentration of organic matter than the settleable fraction. For example, in the Ogeechee River estuary Alber (2000) examined seston constituent differences in the two fractions by taking multiple samples during one tidal cycle at the same sampling location.

The organic matter content of the truly suspended fraction was higher than the settleable fraction. A study of organic matter in the Elbe Estuary sampled multiple sites along a 60 km reach on three dates within one year and found C content to be between 1.1 and 3.3 fold higher in the truly suspended fraction (Kerner and Krogmann 1994). Each site was not sampled on every sampling date so it cannot be concluded if these differences were spatial or temporal. Particulate organic carbon (POC) and nitrogen (PON) content in the truly suspended fraction was also higher in the Tamar Estuary where one site was sampled once in the winter and once in the summer (Tappin et al. 2010).

There has been even less focus on the relationship between the quantity and composition of seston and its reflection in benthic particulate matter. The paucity of work thus far has primarily been restricted to the flux of phytoplankton to the benthos. For instance, phytoplankton pigments from the water column were compared to settleable and benthic pigments in the Baltic Sea (Bianchi 2002). Results indicated that settleable and benthic pigments were highest during periods of increased pigments in the water column (i.e. bloom events). Further, although utilization of the phytoplankton deposited to the benthos was not directly measured, pigment analysis suggested that at least half of the phytoplankton bloom was decomposed in the benthic sediments. In the Chesapeake Bay, comparisons between benthic and water column CHLa concentrations were made in the upper, mid, and lower reaches of the bay during a spring phytoplankton bloom (Hagy et al. 2005). The only significant correlation was found in the lower bay where increases in water column CHLa resulted in increases in benthic CHLa. The lack of such a relationship in the upper and mid reaches could not be explained.

Overall, prior studies suggest that the delivery of seston to the sediments is an important component of organic matter cycling and retention of mineral nutrients in aquatic systems. Despite its importance, few studies have investigated linkages between the composition of sedimented and suspended particulate matter. The objective of this study was to compare the quantity and quality of the truly suspended and settleable fractions of seston, as well as benthic particulate matter, within the tidal freshwater James River. Further, we aimed to assess temporal and spatial patterns by sampling at multiple sites from summer through early spring.

MATERIALS AND METHODS

Study sites and sampling

The study sites were within the tidal-freshwater zone (TFZ) of the James River Estuary (Virginia, U.S.A.); a sub-estuary of Chesapeake Bay (**Fig 1**). The James River is 545 km in length and has a basin of 26,164 km^2 which is 71% forested, 7% agricultural, 5% urban, 4% open water, and 3% wetland (Smock et al. 2005). Long term mean daily discharge at the Fall Line (Richmond, VA) ranges from 67 $m^3 s^{-1}$ in August to 374 $m^3 s^{-1}$ in March (USGS 2011). The mean daily discharge on the days leading up to and including our sampling dates in October 2010 and March 2011 were above average (**Fig 2**). The tidal freshwater zone accounts for 70 km of the 180 km total length of the James River estuary (Smock et al. 2005). The upper reach of the TFZ is characterized by a deep (>5 m) and narrow (< 1 km) channel before it takes on a wider, more estuarine morphology that includes broad shallow areas (< 1 m depth) lateral to the main channel. Two sites (Jones Neck (JN) and Presquile (PQ)) were located in the constricted upper reach at a distance of ~150 km from the confluence with Chesapeake Bay. The other three sites (Rice, Tar Bay (TB), and Brandon point (JMS56)) were located in the broad, lower channel (**Fig 1**). These three lower sites were located ~120 km (Rice, TB) and 90 km (JMS56) from Chesapeake Bay and in proximity to the Estuarine Turbidity Maximum (ETM; river km 111 - 71). The daily tidal amplitude in the regions of the upper and lower sites is approximately 1.1 m and 0.8 m respectively (Bukaveckas et al. 2011). We sampled suspended and sedimented (benthic) particulate matter monthly from August through November 2010 and in March and April 2011 to assess spatial and seasonal variation in the quality and quantity of particulate matter and to investigate relationships between suspended and benthic particulate matter. Prior investigations have suggested that suspended particulate matter concentrations may vary with tidal stage (Alber 2000; Blanton et al. 1999). Because the goals of this research included temporal and spatial variation on a larger scale than that of a tidal cycle, we did not consider changes within a tidal cycle but include this data in the Appendix (**Table 1**).

Suspended Particulate Matter

Characterization of suspended particulate matter included determination of its composition and concentration as well as separation into "settleable" and "truly suspended" fractions. Water samples were collected 1 m below the surface with a Van Dorn water sampler and stored in Nalgene bottles until processing within several hours of sampling. Depths in this reach of the James River are between 0 and 3 m and the tidal prism is dominant over the freshwater discharge resulting in a well mixed system without stratification (Bukaveckas et al. 2011). Therefore we assumed that the surface samples were representative of whole water column conditions. Water temperature, specific conductivity, dissolved oxygen (DO) and pH were measured concurrent with water sample collection using a multi-parameter YSI sonde (**Table 1**).

Settling tubes (1 L plastic graduated cylinders) were used to separate the settleable and truly suspended fractions (Bienfang 1981; Alber 2000). In the lab, water was poured into two replicate tubes for each site and a sub-sample retained to determine the initial concentrations of total suspended solids (hereafter, seston), chlorophyll a (CHLa), particulate organic carbon (POC) and particulate organic nitrogen (PON). Although the general approach is well standardized, various settling times have been used to distinguish the two fractions. For settling experiments conducted in August-November 2010, we used settling times of 60 and 240 min corresponding to sedimentation rates of 4 and 1 m d^{-1} (respectively). For settling experiments conducted in March and April we discontinued the use of the 60 min settling tube to allow replication of the 240 min trial. Based on typical depths in the study area, the 240 min settling time provided a closer approximation to the daily loss from the water column. A comparison of results from the 60 and 240 min settling times is provided in the Appendix (**Fig 1**). At the conclusion of the settling period, the top 500 ml was removed from each tube by careful siphoning. Samples obtained from the top and bottom halves of the settling tubes were analyzed separately for seston, POC, PON and CHLa. The mass of material remaining in the upper half of the tube was designated the truly suspended (TS) fraction. The gain in mass in the lower tube was designated the settleable (SB) fraction. The change in mass along with settling time and height were used to estimate the settling rate. Each tube was covered to prevent light penetration during settling thus minimizing algal growth. The sum of materials recovered from the upper and lower half of the tubes was compared against initial concentrations to check that no appreciable growth or loss occurred during the settling period (mean recovery values: seston = 97 $\pm$ 5%; POC = 103 $\pm$ 7%; PON = 99 $\pm$ 14%; CHLa = 99 $\pm$ 9%).

Water samples were filtered onto pre-ashed, pre-weighed glass fiber filters (Gelman A/E) and seston was determined gravimetrically. Inorganic carbon was removed via vapor acidification and samples were analyzed using a Perkin-Elmer CHN analyzer. Suspended CHLa concentrations were determined via filtration onto Gelman A/E glass fiber filters which were placed in 15 ml centrifuge tubes and stored at -4 ^{o}C for up to 21 days. CHLa was extracted with 10 ml of buffered ($MgCO_3$) 90% acetone and measured fluorometrically using a Turner Designs fluorometer. Beginning in November 2010, respiration rates were measured in water obtained from the upper and lower half of the settling tubes to assess the effects of particle settling on metabolism. Samples were incubated in three replicate 60 ml BOD bottles at ambient (river) temperature for 24 h. Dissolved oxygen concentrations were measured using the micro-Winkler method (APHA 1992). Respiration was determined from the decrease in oxygen relative to the initials and expressed as µg/L/d.

Benthic Particulate Matter

Three benthic grabs were obtained from each of the sampling locations concurrent with the collection of water samples. The samples were collected using an Ekman or Ponar grab sampler from an area adjacent to the main channel where depth approximated the mean cross-sectional depth (~2-3 m). Duplicate 0-2 cm and one 0-5 cm sediment cores were obtained from each of the three grab samples. One of the 0-2 cm cores was used for CHLa analyses while the 0-5 cm core and the duplicate 0-2 cm core were used to determine bulk density (sediment wet and dry mass) as well as POC and PON. Comparisons between the 0-2 and 0-5 cm cores indicated that sediments were well mixed to at least the 5 cm depth (**Appendix, Fig 2**). All results presented here are based on the 0-2 cm cores.

Samples for bulk density analyses were placed into 50 ml centrifuge tubes of known weight and dried at 60 ^{o}C to determine dry mass. The samples were then manually ground to a fine consistency using two granite blocks and analyzed for C and N content using a Perkin-Elmer CHN analyzer. Final results were expressed on an areal basis (dry mass/cm^2, g C/cm^2, g N/cm^2) and normalized to sediment mass (g C/g dry mass = C% and g N/g dry mass = N%). Samples from one month (November) were acidified via vapor acidification by placing samples in small Petri dishes in a glass dessicator containing a beaker of HCl for a minimum of 24 hours (Hedges and Stern, 1984). Comparison of these results to paired, non-acidified samples indicate that inorganic carbon accounts for approximately 4% of carbon in surficial sediments. Sediment samples from other months were not acidified and may therefore overestimate organic C by 4%.

Sediment samples for CHLa analyses were placed in 50 ml centrifuge tubes and stored at -4 ^{o}C in the dark till later processing within 21 days. After wet weight was determined, the samples were homogenized and two sub-samples were obtained (approx mass=0.5 g). One of the sub-samples was used for CHLa extraction in 10 ml of buffered ($MgCO_3$) 90% aqueous acetone (4 ^{o}C for 18-24 hours). CHLa was measured using a Turner Designs fluorometer. The replicate sub-sample was used to determine the gravimetric dry:wet ratio of the sediment by placing the sub-sample in an aluminum boat of known weight, obtaining the wet weight, and drying the sample at 60 ^{o}C for 24 hours. This ratio was used to determine the dry mass of the sub-sample. Final results were expressed as µg CHLa/g dry mass of sediment and as µg CHLa/cm^2.

Sediment oxygen demand (SOD) of surficial sediments (0-2 cm) was measured as an indicator of the lability of organic matter (Ferguson et al. 2003). Sediment samples were diluted to 50 ml with local (site-specific) river water and shaken vigorously to ensure homogeneity. From this slurry, triplicate 4 ml subsamples were placed into pre-weighed aluminum boats and then dried at 60 ^{o}C to measure sediment dry weight. Six additional 4 ml subsamples were placed in 60 ml BOD bottles. These bottles as well as six control bottles (no sediment) were filled with local water. Three of the sediment and three of the control bottles were analyzed for oxygen content immediately and three were incubated in the dark at ambient temperature for 24 hours. Dissolved oxygen concentrations were determined using the micro-Winkler method (APHA 1992). SOD was calculated as the decrease in oxygen relative to the controls and normalized to sediment POC (µg O_2 mg C^{-1} d^{-1}). It should be noted that these values are not taken to represent *in situ* sediment oxygen demand (as might be obtained from benthic chambers) but rather, as an indicator of sediment lability.

Statistics

Statistical analyses were performed using SAS v9.1 (SAS Institute, Cary, North Carolina). Two-way ANOVAs were used to assess space (site) and time (month) effects on variation in seston, CHLa, C and N in suspended and sedimented particulate matter. Paired t-tests were used to determine if the truly suspended fraction of particulate constituents was significantly different from the settleable fraction. Linear regressions (α =0.05) were used to analyze the relationship or predictability among variables.

RESULTS

Suspended Particulate Matter

During the period of study, CHLa and PON varied more than 10-fold (CHLa = 5 – 140 µg L^{-1}; PON = 0.05 - 0.80 mg L^{-1}) whereas seston and POC varied 4-fold (seston = 15 - 45 mg L^{-1}; POC = 1.5 - 5.7 mg L^{-1}). A two-way ANOVA using site and month as independent variables revealed that both factors, as well as their interaction term, were significant explanatory variables (**Table 2)**. Larger differences were observed among months than among sites with ranges for minimum to maximum average concentrations being 2-fold higher among months (CHLa = 83 µg L^{-1}; POC=2.8 mg L^{-1}; PON=0.49 mg L^{-1}) than for sites (CHLa=38 µg L^{-1}; POC=1.2 mg L^{-1}; PON= 0.14 mg L^{-1}). Similar patterns of seasonal variation in seston properties were observed at all sites (**Fig 3**). Highest concentrations of CHLa, POC and PON were observed during August to November with lower concentrations in March and April. Seasonal variation was also observed in organic matter content (as % of seston) with higher values in summer/fall (mean=20 $\pm$ 1%) and lower values in spring (mean=14 $\pm$ 1.2%). Algal contributions to organic matter were also highest in summer/fall (mean=76 $\pm$ 2.5%) and lowest in spring (mean=15 $\pm$ 2.1%). Seston concentrations were less variable as March-April values were similar to August-November. The March sampling date occurred following a high discharge event (**Fig 2**) and was associated with highly N-depleted material (C/N > 30). Otherwise, C/N ratios exhibited little variability by month (6.9-9.3 molar) or by site (7.5-

8.3 molar) as POC and PON concentrations were strongly correlated (R^2=.87; **Fig 4**). CHLa was a significant predictor of POC (R^2 = .78; **Fig 4**). The slope of this relationship provided an estimate of the average C/CHLa in this system (28$\pm$1 µg g^{-1}) which was used to estimate the algal fraction of particulate organic matter (**Fig 3**, Banse 1977).

Benthic Particulate Matter

In contrast to suspended particulate matter, the mass and composition of benthic matter exhibited less seasonal variability and greater spatial variation (**Table 3, Fig 5**). A two-way ANOVA using site and month as variables revealed that both factors, as well as their interaction term, were significant explanatory variables (**Table 3)**. However, sediment dry mass had relatively small differences among months (range = 1.10 – 1.24 g cm^{-2}; **Table 3**) compared to the more than 2-fold differences in average values among sites. Presquile exhibited the lowest mean concentration of sediment (0.68 $\pm$ 0.04 g cm^{-2}) while Rice exhibited the highest (1.60 $\pm$ 0.05 g cm^{-2}). CHLa, POC, PON also varied by ~2–fold among sites, whereas their variation among months was only ~30%. For example, when averaged by site, CHLa ranged from a low concentration of 42 µg g^{-1} at Rice to a high of 96 µg g^{-1} at PQ during the summer/fall season, but when averaged by month during this same time period, CHLa ranged 53-72 µg g^{-1}. Likewise PON varied from 1.66 mg g^{-1} at Rice to 3.37 mg g^{-1} at PQ compared to a relatively small range by month (2.32 – 2.66 mg g^{-1}). Despite greater spatial variability, seasonal trends in benthic CHLa were apparent. These followed patterns observed in the water column with higher concentrations observed in August to November and lower values in March and April. Unlike the suspended sediment samples, POC and PON concentrations in the benthic sediments increased to peak levels in November (with the exception of JN) and these levels persisted into early spring. This does not appear to be a sediment mass effect because both C and N% were significantly higher (P=.01 and .02 respectively) in November, March, and April (C% = 2.94 $\pm$ .40 and N% = 0.24 $\pm$ .16%) compared to August through October (C% = 2.47 $\pm$ .30 and N% = 0.19 $\pm$ .01%). Inter-site differences in benthic POC and PON generally tracked those of benthic CHLa but, CHLa was not found to be a significant predictor of POC (**Fig 4**). Consistent with water column samples, POC and PON were highly correlated resulting in low variability in benthic C/N ratios (**Fig 4**). C/N ratios of benthic material (14.7 $\pm$ 0.19 molar) were higher than those of suspended material (11.9 $\pm$ 1.3 molar).

As for other sediment parameters, oxygen demand varied more by site than by month (**Table 3, Fig 6**). During the summer/fall season, SOD ranged from 14 µg O_2 mg C^{-1} d^{-1} at PQ to 102 µg O_2 mg C^{-1} d^{-1} at JN while the range in monthly averages was smaller (37-74 µg O_2 mg C^{-1} d^{-1}). Rice exhibited the greatest variation in SOD during the study period (0-169 µg O_2 mg C^{-1} d^{-1}). Lowest rates were measured in November and March and highest rates occurred in April. Variation in SOD was not found to be significantly correlated with sediment dry mass, POC, PON, CHLa, C/N, or water temperature (**Fig 6**).

Settling of Particulate Matter

Measureable differences in constituent concentrations between the upper and lower halves of the tubes were obtained following the 240 minute settling period (**Fig 7**). Respiration was an exception as there were no consistent differences in rates measured in the upper and lower half of tubes. Subsequent analysis focused on differences in seston, CHLa, POC and PON which were used to calculate the truly suspended (TS) and settleable (SB) fractions (**Fig 8**). For seston, the TS fraction was significantly larger than the SB fraction though the difference was relatively small (means = 18.4 mg L^{-1} and 14.3 mg L^{-1}, respectively; paired t-test, $p<.0001$). On average the TS and SB fractions represented 57% and 43% of the total, though their proportional contributions varied across the range of seston concentrations. For example, at 20 mg L^{-1}, TS accounted for 64% of seston, whereas at 50 mg L^{-1}, TS accounted for 52%. Thus, a greater proportion was comprised of settleable material during periods of high seston concentrations. For other constituents (POC, PON, and CHLa) differences between the TS and SB fractions were larger with the former accounting for a greater proportion of the total. This was most apparent for CHLa where the TS fraction was on average 3-fold larger than SB (means = 55.3 $\pm$ 8.7µg L^{-1} and 16.8 $\pm$ 2.7 µg L^{-1}, respectively) and accounted for 78% of total CHLa. Similar differences were observed for POC and PON with the TS fraction accounting for 77% and 86% of the total. For CHLa, POC and PON, the relative proportions of the TS and SB fractions were consistent across the observed range of concentrations as indicated by the strong correlations (R^2 = 0.76 to 0.99). The settleable fractions of POC and PON were similar such that there was no significant difference in C/N between fractions (TS=15.3 $\pm$ 3.8, SB=12.7 $\pm$ 2.4).

DISCUSSION

Results from this study suggest that temporal factors have a greater influence than spatial factors on seston composition and settling properties in the James River TFZ. The importance of temporal variation likely reflects seasonal changes in autochthonous vs. allochthonous sources of particulate matter. Analysis of seston composition allows us to make inferences about seasonal variation in the relative importance of these sources. Large changes in water column CHLa during the study period resulted in corresponding changes in suspended PON and POC. Thus temporal variation in seston composition was determined in part by phytoplankton abundance, as is also indicated by the relatively high proportion of algal C comprising suspended organic matter in summer/fall (76%). Despite large seasonal variation in autochthonous contributions, seston concentrations were fairly consistent throughout the study period. During spring, increases in inorganic constituents compensated for declines in the algal-organic fraction as was reflected by seasonal changes in seston C/N. Summer and fall ratios were lower (6.9-9.3) than early spring (10 – 37). Ratios of 6.7 (Redfield 1958) are representative of phytoplankton whereas C/N ratios of 20-50 are representative of terrestrial materials (Hedges et al. 1997). C/N ratios observed in summer and fall are much closer to Redfield suggesting that most OM during these seasons are derived from autochthonous sources whereas early spring ratios imply an allochthonous influence.

Temporal variation in sources and composition of particulate matter were also reflected in differences in settling properties. While the bulk of material was retained in the truly suspended fraction, proportional differences between the two fractions differed among constituents. Approximately 75% of organic constituents (CHLa, POC, and PON) were retained in the TS fraction but only 57% of seston was retained. Similar results were reported from the Ogeechee River estuary where 84% of POC was in the TS fraction, though they also observed a higher proportion of seston (77%) that was truly suspended (Alber 2000). The differing results between the two studies may be attributed to the fact that the present study used a longer settling time to distinguish the two fractions thus allowing more time for particles with slower settling velocities to settle to the SB fraction. The present study used a settling time of 240 minutes (settling velocity >.001 cm s^{-1}) whereas the Ogeechee River study used a settling time of 32 minutes (settling velocity >.006 cm s^{-1}). The shorter settling time in the Ogeechee study resulted in a greater proportion of seston being classified as truly suspended. Results for the James River show that the fractionation of seston was less consistent than organic constituents. As the concentration of seston increased, the proportion of seston retained in the TS fraction decreased. This suggests that increases in seston are in part a result of an influx of heavier mineral particulates from the watershed. The proportions of organic constituents that were settleable vs. truly suspended were consistent among sites, months and across the range of concentrations observed during the study. Thus, the TS and SB fractions could be readily predicted from water column concentrations using empirical models. For the organic constituents, the proportion in the TS fraction did not vary as a function of concentration. For example, over a range of PON concentration (e.g. 0.2 –

0.8 mg L^{-1}) the proportion retained in the TS fraction ranged from 71 to 82%. To our knowledge, this is the first comprehensive study of seston settling properties (i.e. with multiple measurements across months and sites) and therefore we are unable to conclude whether the consistency observed at this site is a general feature of estuaries.

The proportion of OM that is truly suspended vs. settleable has implications for the pelagic food web and for the transport of material to receiving coastal waters. Fine particles associated with the TS fraction may be transported through the river system in a fashion similar to that of dissolved constituents (Schuchardt and Shirmer, 1991). Dissolved organic nitrogen preferentially adsorbs to fine particles (Hedges et al. 1994) thereby transforming DON to PON with preferential retention to the TS fraction. Results from the Tamar Estuary indicate that 56% of PON is retained in the TS fraction and exported to coastal regions (Tappin et al. 2010). If we assume a similar fate for PON in the James River, approximately 75% of PON entering the estuary would be exported to receiving coastal waters. However, this is an unlikely fate for the bulk of PON in this system. The strong correlation between PON and CHLa (R^2 = .94) suggests that most PON in this system is algal in nature and previous research has shown that only ~ 1/3 of net phytoplankton production was lost to advection in this system (Bukaveckas et al. 2011). Thus, assuming a similar loss to advection in the current study a large proportion of phytoplankton and the associated POC and PON may be important to secondary production. A small fraction (~5%) of phytoplankton losses can be attributed to zooplankton grazing (Bukaveckas et al. 2011). This would suggest that OM in the TS fraction may be important to heterotrophic bacteria. Support for this argument can be found in studies of the Tamar and Columbia estuaries where the smallest particles were associated with a majority of bacterial activity and this activity was also within the TS fraction (Crump and Baross 2000, Plummer et al. 1987). It is then perhaps not surprising that respiration in the upper half of our settling tubes was not significantly different from the lower half even though constituent mass was greater in the lower half. This suggests that the ratio of heterotrophic activity relative to the weight of suspended particulate matter may be higher in the TS fraction.

The settling of OM may provide a nutritious source of food to benthic consumers. Though the SB fraction included a small proportion of OM relative to seston, it was labile (C/N=9.4) relative to benthic constituents (C/N=14.7) during the summer/fall season when seston OM was dominated by phytoplankton. The impact of phytoplankton deposition to the benthos is poorly understood. Quijon et al. (2008) found a rapid utilization of freshly deposited phytoplankton though the response was temporally variable and often ephemeral. However, a large phytoplankton spring bloom in the Chesapeake Bay did not support a proportional response in benthic metabolism (Hagy et al. 2005). In the present study, we did not find a correlation between settleable CHLa and SOD or between benthic CHLa and SOD. This is similar to findings from Narragansett Bay where benthic SOD and water column primary production did not exhibit similar temporal and spatial patterns (Fulweiler et al. 2010). While the authors speculate that the lack of a relationship may be due in part to the possible presence of microphytobenthos, we do not believe that to be a factor in the present study. Previous work within this reach of the river suggests light levels are insufficient for benthic algal production. We have assumed that benthic CHLa is strictly derived from settleable phytoplankton and this is supported by the positive correlation between settleable and benthic CHLa (R^2=.40). The importance of phytoplankton C delivery to the benthos has been implicated in previous research which suggested that ~50% of phytoplankton C in the tidal freshwater James River was utilized in benthic sediments. The fact that results from the present study suggest that ~25% of phytoplankton may settle to the benthos implies that inter-annual differences may exist in this system or that the fate of all phytoplankton is not yet fully understood. Nonetheless, there is evidence that the SB fraction may be an important source of OM to the benthos but the understanding of its utilization will require further research.

The theoretical turnover time of benthic constituents was estimated by comparing deposition (settleable mass) to standing stocks of benthic materials. In the James, the deposition of dry mass, POC and PON was small relative to the benthic constituents in the upper 2 cm. For example, even during peak seston concentrations (135 mg L^{-1}) during the March storm event, the estimated turnover time of benthic sediments is ~92 days. For organic constituents (POC, PON) turnover times during peak (September) concentrations were 140 and 100 days respectively. CHLa had a much lower turnover time (10 days) during peak concentrations (September) suggesting greater lability of this material relative to POC and PON. Although benthic constituent reservoirs are large relative to the SB fraction, the overall proportion of POC, PON, and CHLa in the benthos (as % of dry mass; 2.9, 0.24, 0.005% respectively) is small relative to their concentration in suspended materials (as % of seston; 9.3, 1.3, 0.22% respectively). These findings show that while the storage of particulate matter is orders of magnitude larger in the benthic realm relative to what is suspended in the water column, the suspended material has a greater nutritional value and may support a disproportionate fraction of secondary production.

Unlike suspended particulate matter, benthic particulate matter did not exhibit substantial temporal variation. The large reservoir of constituents in the benthic sediments may preclude a congruent temporal signature. However, our results provide some evidence that benthic sediments are a site for seasonal preservation of OM. Increased flux (settleable mass) of CHLa in November was associated with an increase of benthic CHLa, POC, and PON. Benthic CHLa returned to previous levels by early spring but POC and PON remained at elevated levels. This was particularly evident at TB which had a larger increase in CHLa in November relative to Rice. These results suggest that OM is preserved in benthic sediments in colder months. This is consistent with organic matter degradation of Westerschelde Estuary (UK) benthic sediments which exhibited strong temperature dependence such that degradation decreased markedly during colder months (Middelburg et al. 1996). It could be argued that the increased POC and PON in early spring is a result of increased flux to the sediments rather than preservation however, the mean flux of OM in spring (0.78 mg L^{-1}) was half that of the summer/fall season (1.7 mg L^{-1}).

Spatial variation of benthic constituents was evident between the two upper (JN and PQ) sites and the three lower sites (Rice, TB, JMS56). CHLa, POC, and PON proportions (as percent of dry mass) were greater in the upper sites compared to lower sites and benthic sediment density (as dry mass per unit area) was highest at a lower site (Rice) and lowest at an upper site (PQ). These site differences may be a result of longitudinal variances in tidal and fluvial forces as well as consequential differences in benthic sediment composition (e.g. particle size distribution). Lower sites are closer to the estuarine turbidity maximum where increased energy may cause greater or prolonged resuspension of benthic material compared to the upper sites. Additionally, the lower sites have been shown to have a higher proportion of clay to sand compared to the upper sites (Nichols et al. 1991) which may influence physical, chemical, and biological reactions. However, because the hydrodynamics of the James River are not sufficiently classified, these arguments are purely speculative.

In summary, this study has illustrated the importance of internal and external sources to the temporal variation of seston composition and the resultant fractionation of constituents into the TS and SB fractions in the tidal freshwater James River. Autochthonous sources of particulate matter dominated OM composition in the summer and fall while allochthonous sources became more important in the early spring. Regardless of season the bulk of OM was consistently retained in the TS fraction. Further, the proportions of OM in the TS and SB fractions were very consistent across observed concentrations signifying that the two fractions could be predicted from water column concentrations. Seston was more variable but its bulk was also retained in the TS fraction. The fractionation of seston and OM into the TS and SB fractions may have important implications for the fate of particulate matter. For example, the preferential retention of OM in the TS fraction may be important to secondary production in the water column and the transport of this material to receiving coastal waters. And although OM proportions in the SB fraction were small relative to the TS fraction, they were large relative to benthic particulate matter suggesting that the SB fraction is a nutritious source of food to the benthos. The fact that we did not observe a correlation between SOD and biological variables (CHLa, POC, PON) or water temperature along with a lack of discernable spatial or temporal patterns of SOD suggests that other factors are more important to the utilization of settled OM. Further work is needed to understand benthic community structure and resuspension dynamics in this system and the role they may play in the utilization or retention of OM.

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Table 1. Water quality conditions in the tidal freshwater James River during the period of study. Values shown are averages for all sampling locations.

Date	Temp C^o	pH	DO (mg/L)	DO %	sp Cond (µs/cm)	Turb (NTU)
8/3/2010	29.3	8.55	9.84	129	424	19.7
9/10/2010	25.9	8.17	7.57	115	542	35.2
10/5/2010	18.6	7.42	7.74	83	324	30.7
11/2/2010	16.0	8.28	9.04	112	288	26.5
3/17/2011	12.3	7.04	9.93	92	139	45.0
4/14/2011	17.0	7.17	8.79	91	202	20.4

Table 2. Average concentrations of suspended constituents by site and month for samples collected from four sites in the tidal freshwater James River during August through November, 2010. Letters indicate significant differences by two-way ANOVA with site and month as variables. P-values for site, month, and interaction are provided.

Analyte	Grand Mean	Average by Site				Average by Month				Statisics			
		TB	Rice	PQ	JN	Aug	Sep	Oct	Nov	Site	Month	S x M	R^2
Seston (mg/L)	34	36[a]	39[b]	29[c]	32[d]	36[a]	41[b]	27[c]	32[d]	<.0001	<.0001	<.0001	0.99
CHLa (μg/L)	97	105[a]	111[b]	98[c]	73[d]	126[a]	116[b]	43[c]	101[d]	<.0001	<.0001	<.0001	0.99
POC (mg/L)	3.5	3.7[a]	4.1[b]	3.3[c]	2.9[d]	4.7[a]	4.5[b]	1.9[c]	2.9[d]	<.0001	<.0001	<.0001	0.99
PON (mg/L)	0.53	0.56[a]	0.59[b]	0.53[a]	0.45[c]	0.73[a]	0.66[b]	0.24[c]	0.50[d]	<.0001	<.0001	<.0001	0.99
C:N (molar)	7.9	7.9[a]	8.3[b]	7.5[c]	8.0[a,b]	7.6[a]	7.9[b]	9.3[c]	6.9[d]	<.0001	<.0001	<.0001	0.96

Table 3. Mass and composition of benthic sediments by site and month for 0-2 cm cores collected from four sites on the tidal freshwater James River during August through November, 2010. SOD values are sediment oxygen demand. Letters indicate significant differences by two-way ANOVA with site and month as variables. P-values for site, month, and interaction are provided.

		Grand	Average by Site				Average by Month				Statistics			
Analyte	Unit	Mean	TB	Rice	PQ	JN	Aug	Sep	Oct	Nov	Site	Month	S x M	R^2
Dry Mass	g/cm^2	1.18	1.15[a]	1.60[b]	0.68[c]	1.20[a]	1.11	1.19	1.10	1.24	<.0001	ns	<.0001	0.87
CHLa	$\mu g/cm^2$	50.9	45.1[a]	49.9[a,b]	63.2[b]	45.5[a]	46.3[a,b]	56.4[a,c]	36.4[b]	64.6[c]	0.02	<.001	0.002	0.69
	µg/g DW	65.1	59.5[a]	41.6[a]	96.0[b]	63.3[a]	59.9	75.3	53.2	71.9	<.0001	ns	<.001	0.75
POC	mg/cm^2	31.7	32.2[a]	34.7[a]	26.2[b]	33.4[a]	33.6	32.1	29.7	31.3	<.0001	ns	0.01	0.66
	mg/g DW	30.0	29.2[a]	21.8[b]	38.5[c]	30.3[a]	32.0[a]	29.3[b]	29.8[a,b]	28.7[b]	<.0001	0.004	<.0001	0.94
PON	mg/cm^2	2.52	2.59	2.64	2.29	2.57	2.76[a]	2.58[a,b]	2.35[b]	2.39[a,b]	ns	0.03	ns	0.47
	mg/g DW	2.45	2.37[a]	1.66[b]	3.37[c]	2.42[a]	2.66[a]	2.41[b]	2.43[b]	2.32[b]	<.0001	0.003	<.0001	0.95
C:N	molar	14.6	14.5[a]	15.4[b]	13.3[c]	15.2[a,b]	14.2[a]	14.5[a,b]	14.6[a,b]	15.2[c]	<.0001	0.005	<.0001	0.86
SOD	µg/mg C/d	57.3	66.4[a]	55.6[a]	14.0[b]	102[c]	54.7[a,b]	72.0[a]	73.9[a]	36.9[b]	<.0001	0.006	<.0001	0.86

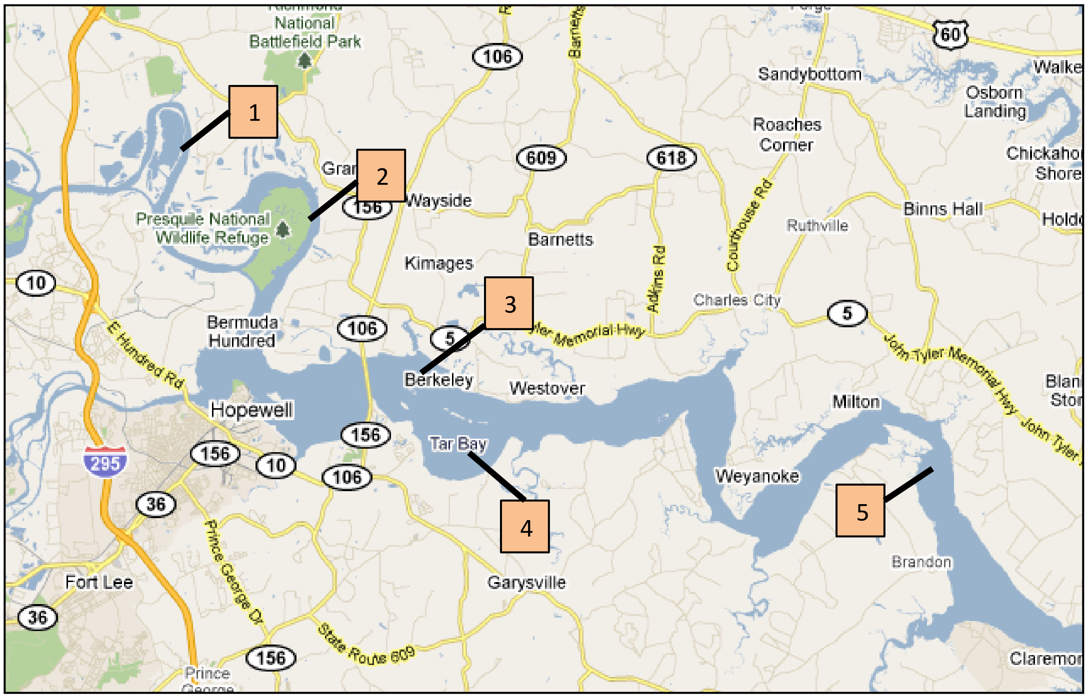


Figure 1. Map of tidal freshwater James River showing sampling locations. 1 = Jones Neck (JN); 2 = Presquile (PQ); 3 = Rice; 4 = Tar Bay (TB); 5 = JMS56. Sites 1 and 5 are approximately 70 river kilometers (navigation kilometers) apart. Rice is approximately 120 river kilometers from the confluence with the Chesapeake Bay. Map obtained from maps.google.com.

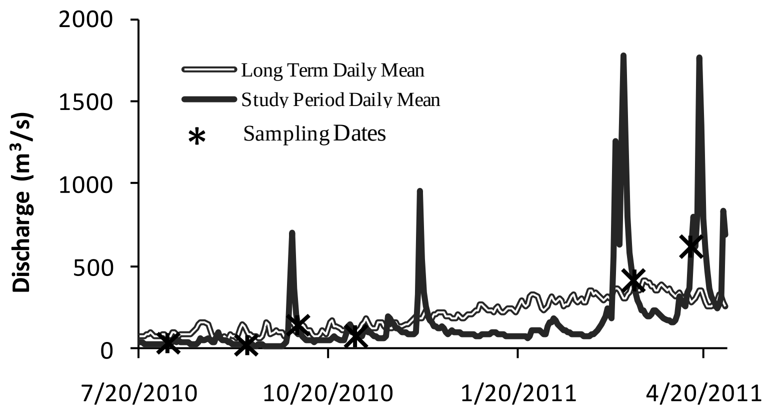


Figure 2. Daily mean discharge of the James River at USGS site 02037500 (near Richmond, VA).

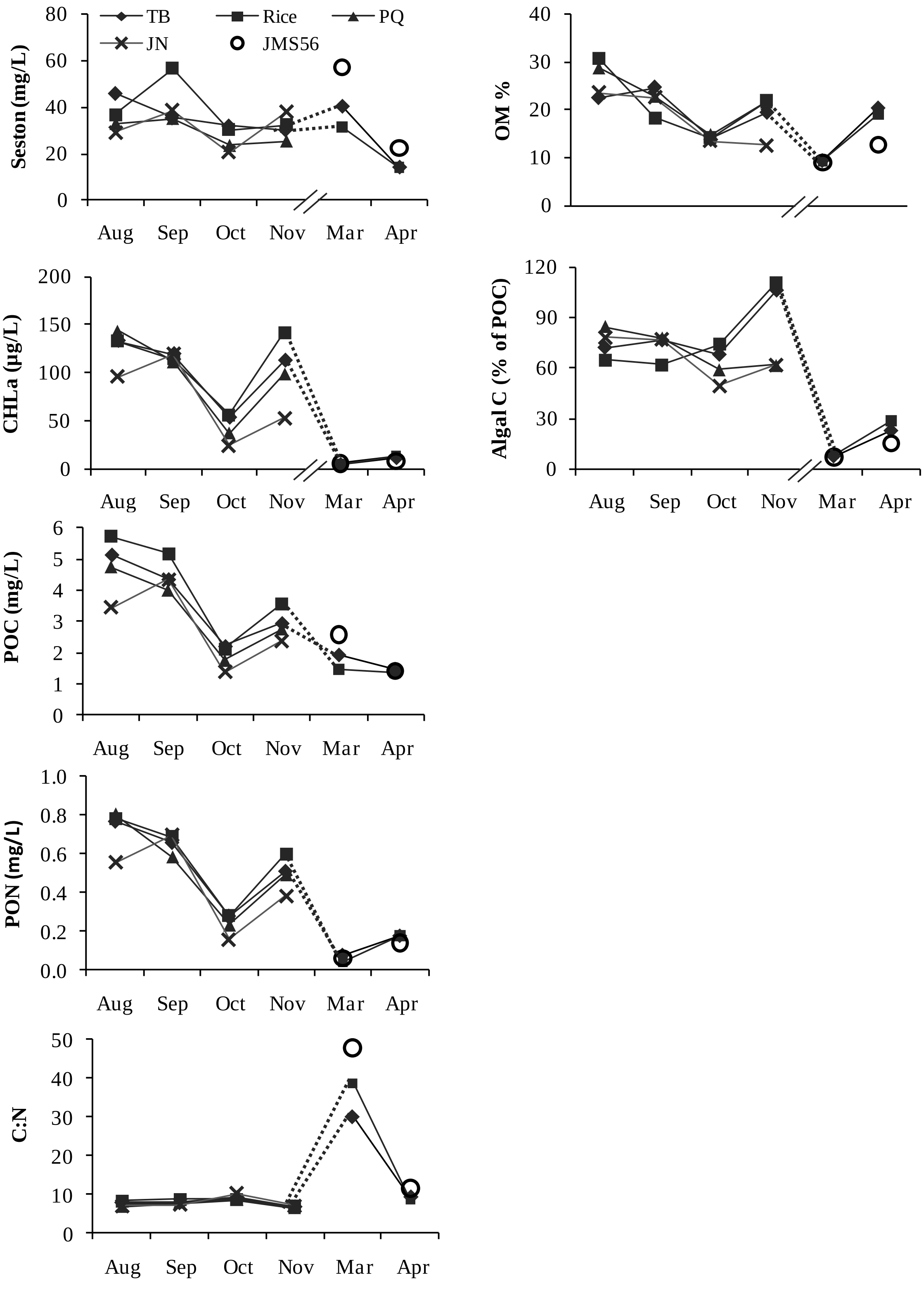


Figure 3. Temporal variation in the mass and composition of suspended particulate matter at five sites in the tidal freshwater James River. Similar seasonal patterns were observed among all sites.

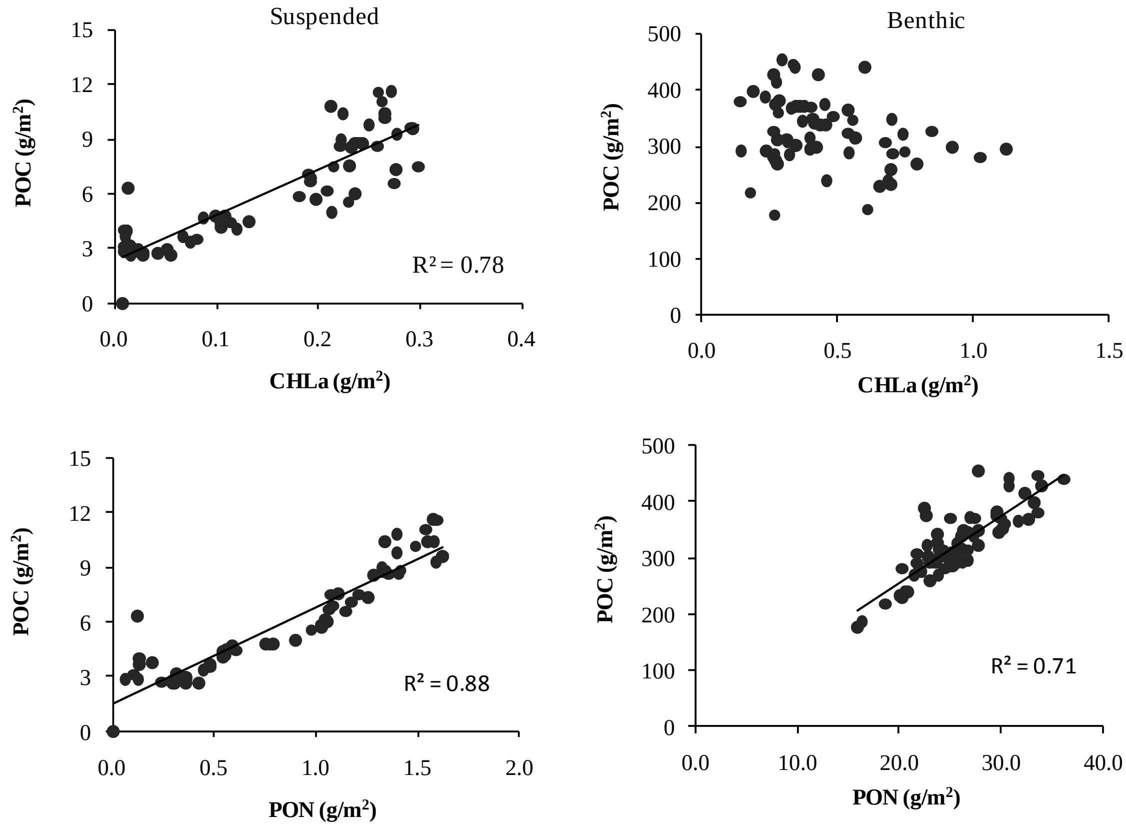


Figure 4. A) The positive correlations between suspended POC and CHLa suggest that phytoplankton is a significant contributor to organic matter in the tidal freshwater James River. B) POC and PON were well correlated for both suspended and benthic sediments. Overall, the larger scales on the x and y axes of the benthic plots indicate increased constituent masses in the benthos relative to suspended masses. Linear regressions are significant ($P < .05$).

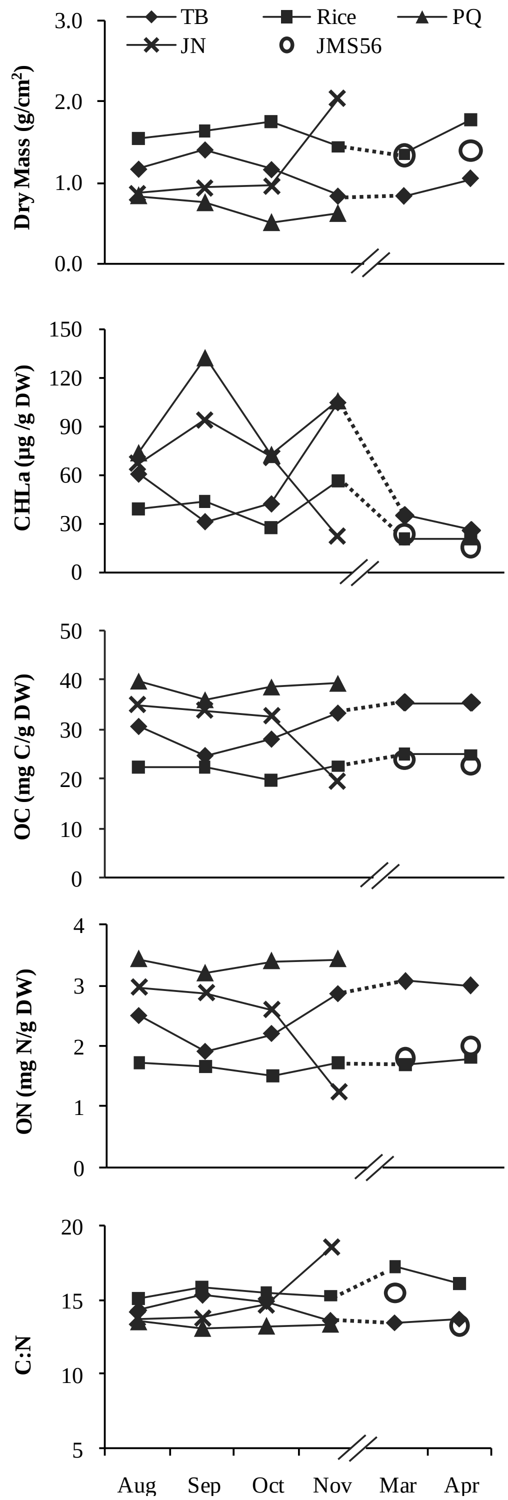


Figure 5. Spatial variation of benthic sediment constituents was greater than temporal variation at five sites in the tidal freshwater James River. Dry mass (g/cm^2) was greater at the lower sites (Rice, TB, JMS56) and organic constituents normalized to sediment dry mass were greater at the upper sites (JN and PQ).

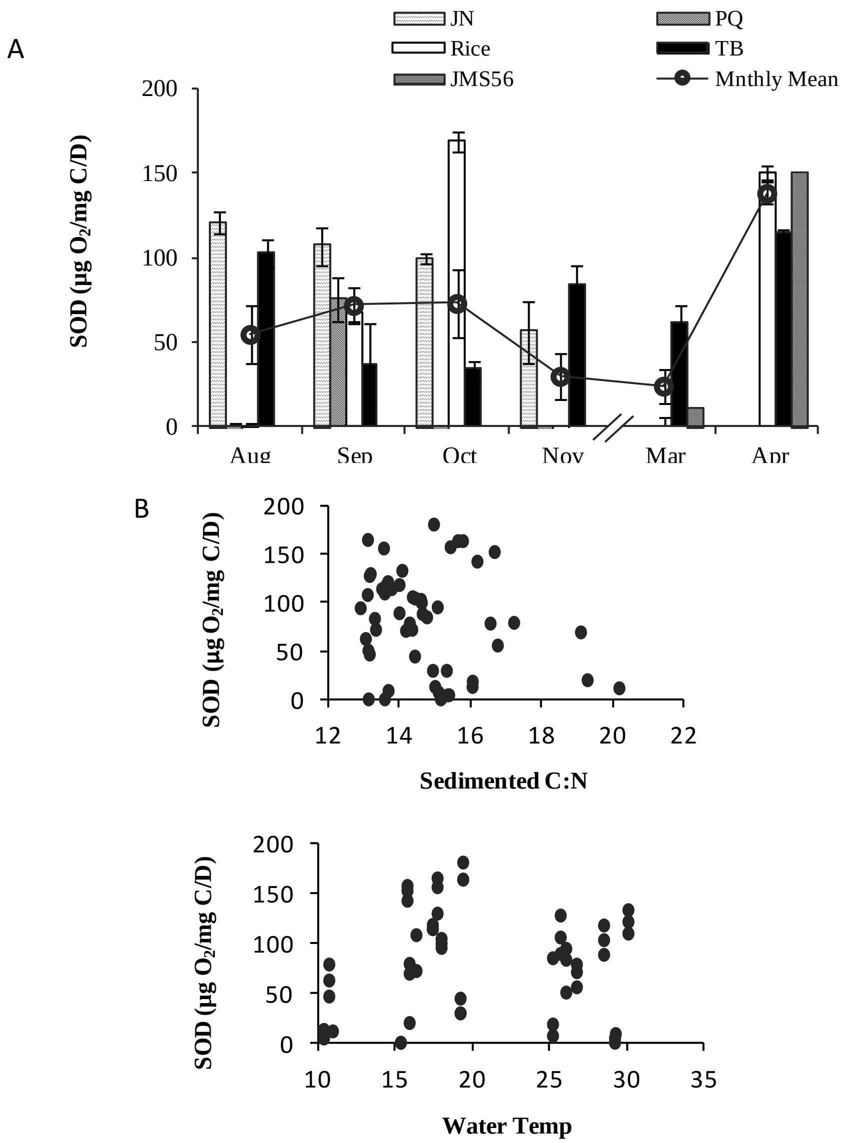


Figure 6. A) Sediment oxygen demand (SOD) by site and month. (Error bars are standard error.) B) The relationship between SOD and water temperature and SOD and sediment C/N.

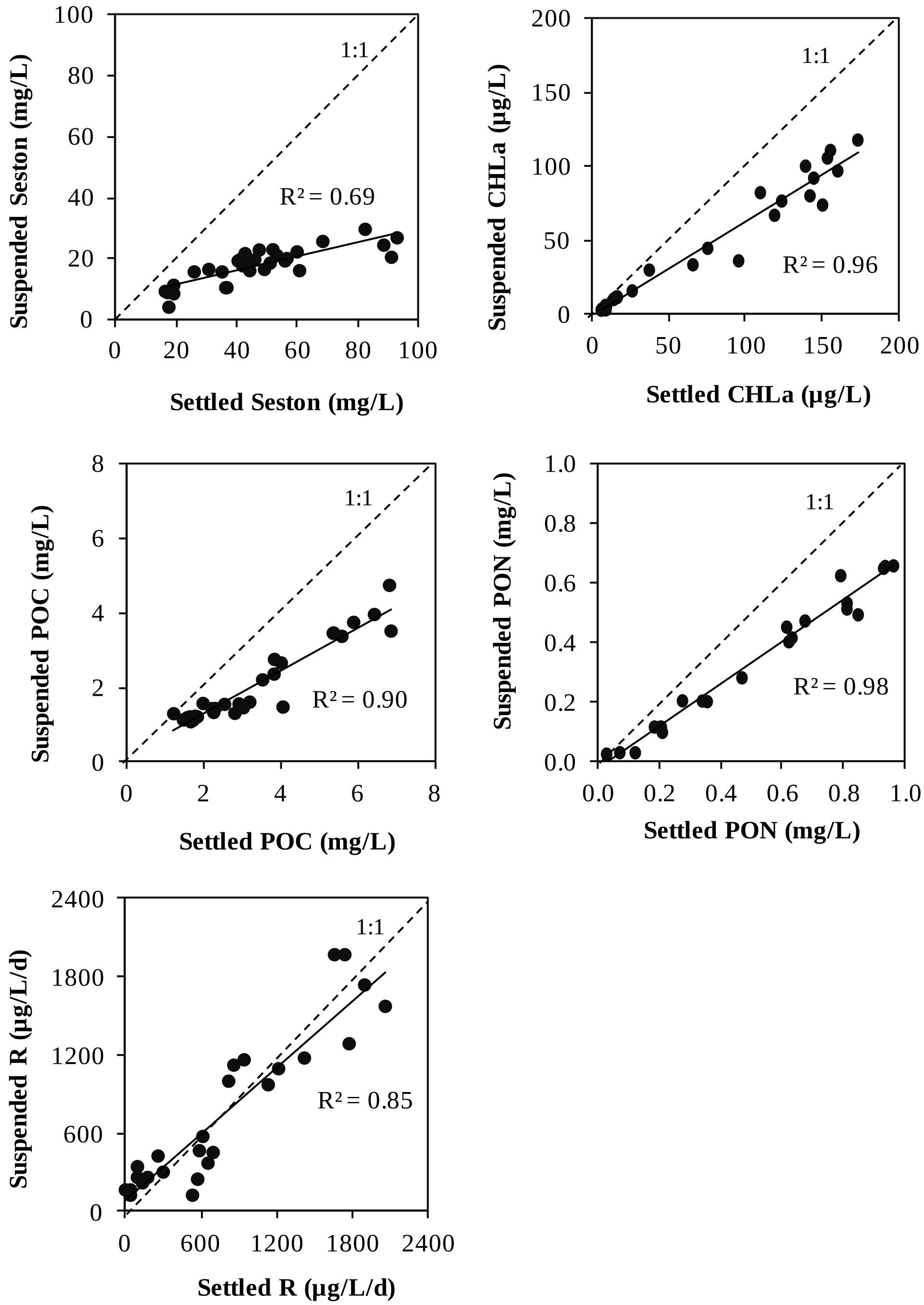


Figure 7. Constituent concentrations in the upper (suspended) and lower (settled) halves of the settling tubes after 240 minutes. Seston, CHLa, POC, and PON all had measurable differences between the two halves as is evidenced with data points falling below the 1:1 line. The exception was respiration - differences between the upper and lower halves were indistinguishable.

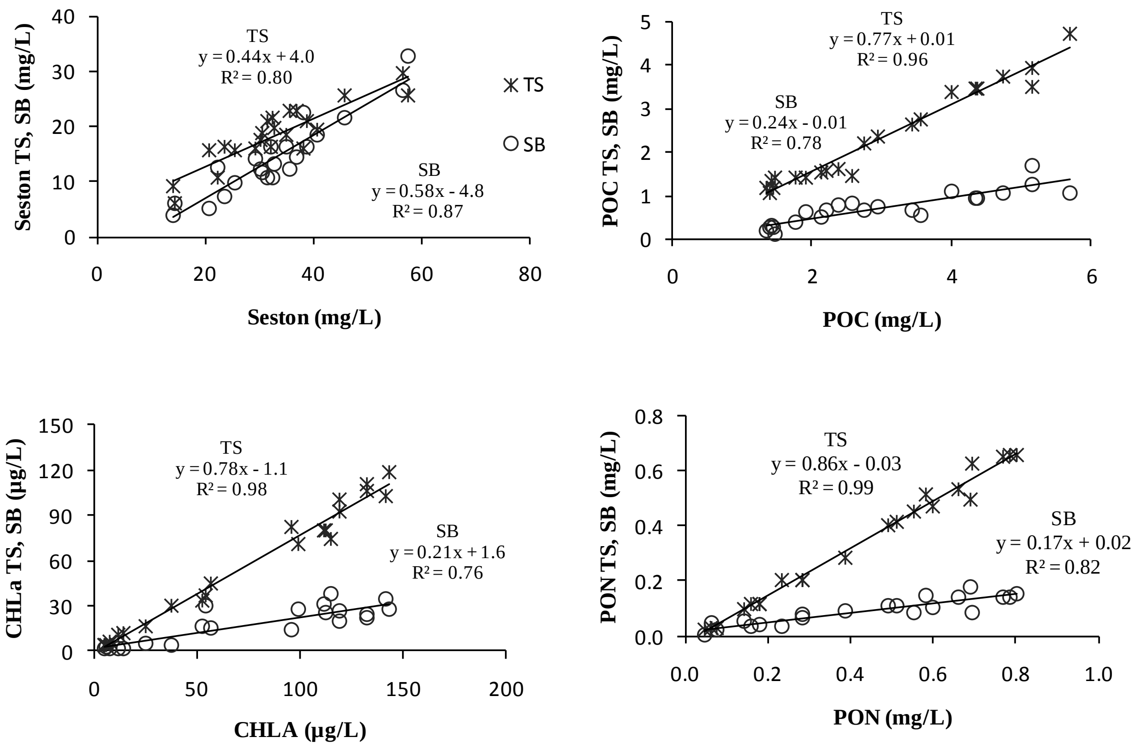
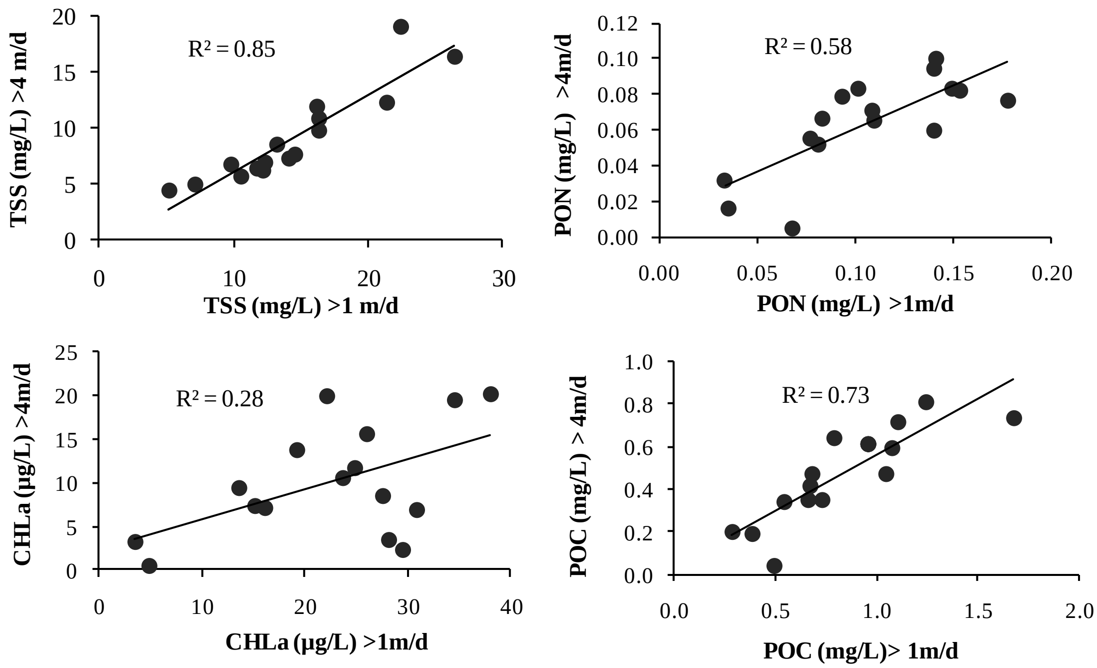


Figure 8. Constituent concentrations of the truly suspended (TS) and settleable (SB) fractions as a function of total concentrations. Proportional contributions of CHLa, POC, and PON to the TS and SB fractions are similar across constituent concentrations but proportional contributions of seston to the TS fraction decreased with increasing concentrations. All linear regressions are significant ($P < .05$).

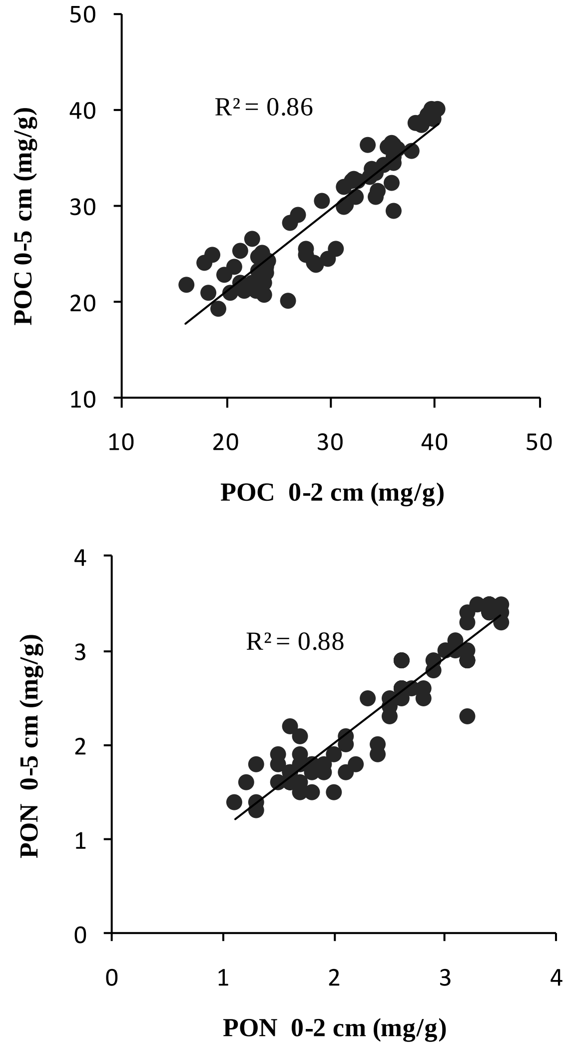
APPENDIX

Appendix Table 1. Tidal stage for each sampling date and site in the tidal freshwater James River. Falling tide = FT; rising tide = RT. Sampling that occurred within 30 minutes of slack tide is designated as 'slack'.

Date	Site				
	JN	PQ	TB	Rice	JMS56
8/3/2010	FT	FT	FT	FT	-
9/10/2010	FT	Slack	RT	RT	-
10/5/2010	RT	RT	RT	Slack	-
11/2/2010	RT	RT	Slack	FT	-
3/17/2011	-	-	RT	RT	RT
4/14/2011	-	-	RT	Slack	RT



Appendix Figure 1. Concentrations of constituents in the settleable fraction for two time trials (60 and 240 minutes). Concentrations in the settleable fraction of the 240 minute time trial (settling rate > 1 m/d) were greater than the 60 minute time trial (settling rate > 4 m/d) but correlations show strong predictability between time trials for each constituent. Because the 240 minute time trial provided a closer approximation to the daily loss from the water column given typical depths (1 - 2 m) in the study area, results presented in this study use the 240 minute time trial.



Appendix Figure 2. Relationship between 0-2 and 0-5 cm cores for POC and PON. Proportional differences between 0-2 and 0-5 cm cores are minimal. Therefore all results reported in this study are based on the 0-2 cm cores. Linear regressions are significant ($P < .05$).

Vita

Anne Schlegel was born in Raleigh, North Carolina and later relocated to Richmond, Virginia with her family. She received a Bachelor of Science degree in Psychology with a minor in Business Administration from Longwood College in 1986. Following college, she worked primarily in the insurance industry as a computer programming analyst. In 2007, she began taking undergraduate prerequisites in order to apply to the Masters program in Biology at Virginia Commonwealth University. In that program, she received a teaching assistantship and has focused her studies in aquatic ecology.