

# Factors Determining the Location of the Chlorophyll Maximum and the Fate of Algal Production within the Tidal Freshwater James River

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**Abstract** Longitudinal variation in factors affecting phytoplankton production were analyzed to better understand the mechanisms that cause the formation of a chlorophyll maximum within the tidal freshwater James River. Phytoplankton production was two- to threefold higher in the region where persistent elevated chlorophyll concentrations occurred. Near this site, the morphology of the James transitions from a narrow, deep channel to a broad expanse with shallow areas adjoining the main channel. Shallower depths resulted in greater average irradiance within the water column and suggest that release from light limitation was the principal factor accounting for the location of the chlorophyll maximum. Grazing rates were low indicating that little of the algal production was directly consumed by zooplankton. Low exploitation by zooplankton was attributed to poor food quality due to high concentrations of non-algal particulate matter and potential presence of cyanobacteria. Metabolism data suggest that two thirds of net primary production was respired in the vicinity of the chlorophyll maximum and one third was exported via fluvial and tidal advection. Comparison of water column and ecosystem metabolism indicates that the bulk of respiration occurred within the sediments and that sedimentation was the dominant loss process for phytoplankton.

**Keywords** Phytoplankton · Nutrients · Rivers · Estuaries · Algal blooms · Tidal freshwaters · James River · Chesapeake Bay

## Introduction

Freshwater estuaries occur where tidal forces extend inland beyond the influence of marine waters. Though estuarine in their dominant mode of hydrodynamics, tidal freshwaters share a number of features in common with rivers including aspects of their geomorphology, hydrology and water chemistry. Their cross-sectional morphology is often narrow (constricted) and lacking the extensive shallow areas that occur along the lateral margins of the saline estuary. Their hydrodynamics are dominated by bi-directional flow but are subject to considerable fluvial forces resulting in short transit times during periods of elevated river discharges. Water chemistry is also discharge-dependent and therefore highly variable in concentrations of nutrients and suspended particulate matter. This combination of features results in unique conditions that have been under study in comparison to the lower, saline segments of estuaries.

Tidal freshwaters typically constitute a small proportion of estuarine surface area, but studies suggest they play an important role in ecosystem energetics and biogeochemistry (Lampman et al. 1999; Lionard et al. 2008). A number of studies have reported high levels of phytoplankton biomass occurring in tidal freshwaters (Moon and Dunstan 1990; Cole et al. 1992; Vincent et al. 1996; Muylaert et al. 2005). As food quality for consumers is enhanced where phytoplankton constitute a greater proportion of suspended particulate matter (Sobczak et al. 2005; Martineau et al. 2004; Hoffman et al. 2008), zones of elevated chlorophyll *a*

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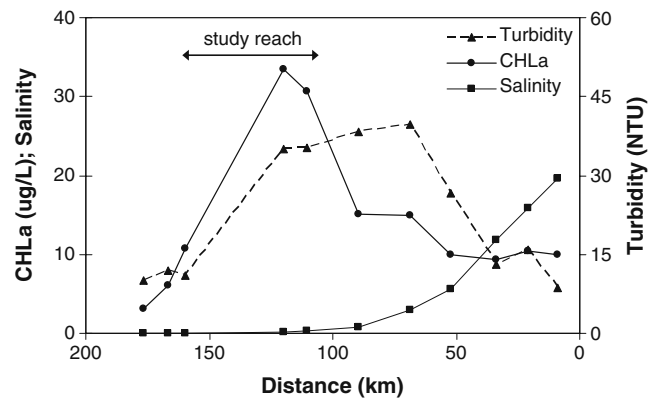
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concentrations (hereafter, CHL $a$  maxima) may have a disproportionate influence on secondary production relative to their areal extent. Local exploitation of autochthonous food sources benefits consumers in the region of the CHL $a$  maximum (North and Houde 2001, 2003; Islam et al. 2006); export of these resources subsidizes food webs in adjacent areas (Cloern 2007). Enhanced primary production alters the balance between autotrophic and heterotrophic activity thereby influencing dissolved oxygen and C metabolism. In addition, tidal freshwaters act as “hot spots” of biogeochemical activity where assimilative uptake by autotrophs and heterotrophs enhance nutrient removal from the dissolved phase (Arndt et al. 2009). Nutrients contained in particulate matter may be sequestered through sedimentation and burial or, in the case of nitrogen, lost through denitrification.

The occurrence of CHL $a$  maxima in estuaries is variously attributed to localized conditions that favor enhanced growth rates or reduced loss rates. The latter include retention effects whereby entrainment of exogenous phytoplankton promotes their accumulation despite low localized growth rates. Circulation patterns in some estuaries are characterized by a surface layer of low-salinity water flowing seaward over a bottom layer of higher salinity water moving landward. Hydrodynamic entrainment occurs as dense particles sink into the landward bottom current (Moon and Dunstan 1990; Simons et al. 2006; Lapierre and Frenette 2008). Where CHL $a$  maxima co-occur with the estuarine turbidity maximum, retention has been invoked as a mechanism to explain high phytoplankton abundance despite low light availability (Cole et al. 1992; Kocum et al. 2002; Muylaert et al. 2005). Alternatively, localized areas of high CHL $a$  may reflect enhanced growth rates in response to favorable light and nutrient conditions. In estuaries, the transition from turbid, nutrient-rich riverine waters to clear, nutrient-poor marine waters favors peak production at a transition point where release from light limitation allows phytoplankton to maximize nutrient utilization. For example, rates of primary production in the tidal freshwater portion of the Schelde Estuary were nearly an order of magnitude higher than in the saline zone (Muylaert et al. 2005). Thus, both growth- and loss-related processes have been invoked as mechanisms accounting for the occurrence and magnitude of CHL $a$  maxima in estuaries.

Monitoring of the James River Estuary revealed persistently elevated CHL $a$  at a site within the tidal-freshwater segment (station “JMS75”; Fig. 1). We selected this area of high algal abundance to investigate factors that determine the location of the CHL $a$  maxima. Specifically, we related variation in CHL $a$  and net primary production to longitudinal trends in dissolved nutrients and light availability. We also assessed the fate of algal biomass by measuring



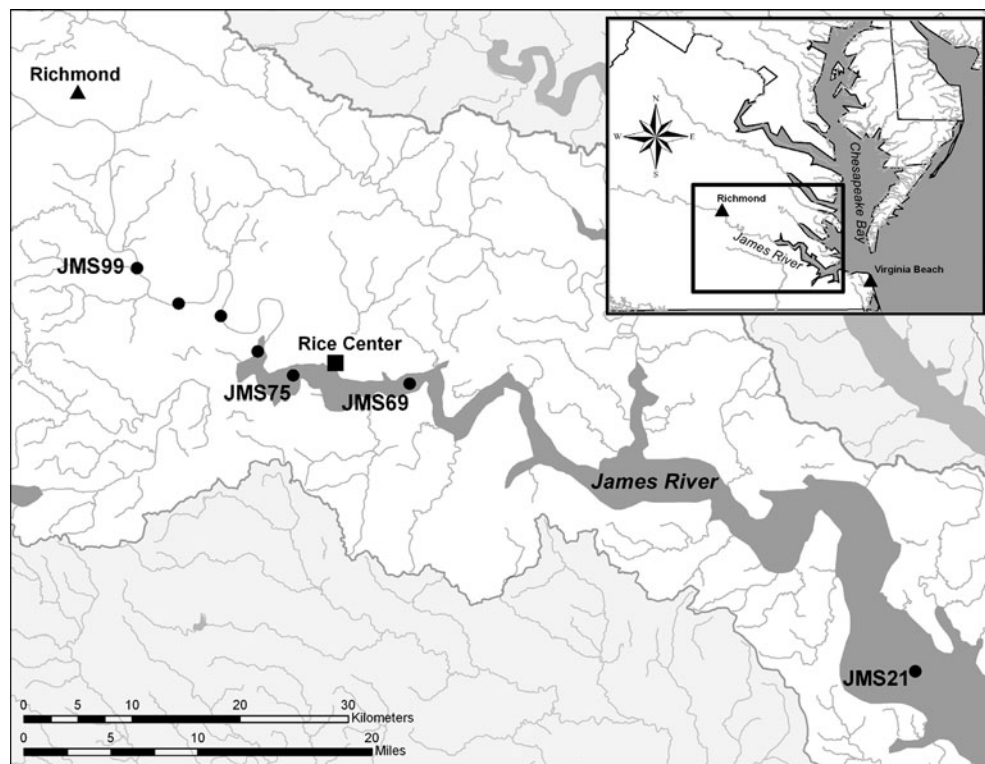
**Fig. 1** Longitudinal patterns in turbidity, salinity and CHL $a$  in the James River Estuary (distance is from the confluence with Chesapeake Bay). Data are average values for 1999–2004 based on monthly sampling for the Chesapeake Bay Program by the Virginia Department of Environmental Quality (<http://www.deq.state.va.us/bay/cbpmn.html>)

zooplankton grazing and water column and ecosystem respiration. Our objective was to address the following questions related to the occurrence and importance of CHL $a$  maxima in estuaries: What does the location of the CHL $a$  maximum reveal about the mechanisms regulating phytoplankton production in estuaries? To what extent is autochthonous production in the CHL $a$  maximum utilized locally through grazing and heterotrophic respiration?

## Methods

**Study Site** The James River is a tributary of Chesapeake Bay with a length of 545 km and a drainage area of 26,165 km<sup>2</sup> (Smock et al. 2005). The watershed is comprised of 71% forest, 7% agriculture, 5% urban and 3% wetland (Smock et al. 2005). Discharge during the period of study (April–November 2007) was 96 m<sup>3</sup> s<sup>-1</sup> and below the 10-year average for these months (155 m<sup>3</sup> s<sup>-1</sup>; USGS 2008). The James River Estuary begins below the Fall Line at Richmond, VA and extends 180 km to the confluence with Chesapeake Bay. The uppermost portion of the tidal zone is characterized by a deep (>5 m) and narrow (>1 km) channel which transitions abruptly to a more estuarine morphology with broad shallow areas (<1 m depth) lateral to the main channel (Fig. 2). Our study reach was a 50-km section within the tidal-freshwater zone encompassing the site of peak CHL $a$  concentrations and extending 40 km above and 10 km below. The study reach was bounded by Chesapeake Bay Program monitoring stations JMS99 and JMS69. The average tidal amplitude during the period of study was 1.1 m at JMS99 and 0.8 m near JMS69. The dominance of the tidal prism over the mean freshwater discharge results in a vertically well-mixed

**Fig. 2** Map of the James River Estuary showing sampling locations for this study. Four of the sites are long-term monitoring stations and identified by their Chesapeake Bay Program designation. Sites JMS99 to JMS69 are within the tidal freshwater segment and correspond to river km 100 to 160 (distance from mouth). A mesohaline site (JMS21) was included in the zooplankton component of the study



system. The study reach receives nutrient inputs from multiple point sources, including four major waste water treatment plants (WWTP) within the study reach (combined discharge=93 mgd or  $3 \text{ m}^3 \text{ s}^{-1}$ ) and one (City of Richmond WWTP: 53 mgd or  $1.7 \text{ m}^3 \text{ s}^{-1}$ ) which discharges ~10 km above our uppermost sampling location (discharges from EPA database for facilities holding National Pollutant Discharge Elimination System permits). The Appomattox River joins the James within this segment contributing an annual mean discharge of  $9 \text{ m}^3 \text{ s}^{-1}$ .

**Sampling** Longitudinal variations in CHL<sub>a</sub>, light availability, dissolved nutrients (N–NH<sub>4</sub>, N–NO<sub>3</sub> and P–PO<sub>4</sub>), bacterial abundance, suspended particulate matter and plankton production and respiration were characterized at six sites located at river-kilometer 160 (JMS99), 145, 136, 128, 120 (JMS75) and 110 (JMS69; Fig. 2). Water samples obtained for constituent analyses and plankton metabolism measurements were collected at a depth of 1 m below the surface. Periodic checks of surface and near-bottom parameters (conductivity, temperature and dissolved oxygen) did not reveal consistent differences. Data were collected on 12 sampling dates at 2- to 3-week intervals from April to November 2007. Zooplankton abundance and community grazing rates were determined on a subset of these dates at three sites—two located in the tidal freshwater segment (JMS99 and JMS75) and one located ~75 km seaward in the mesohaline region of the estuary (JMS21). The mesohaline site (salinity=9–20) was included in the zooplankton

component of the study to provide a broader representation of community types and food resource conditions within the estuary.

Irradiance (PAR) was measured with a LI-COR model LI-1400 data logger equipped with underwater and surface quantum sensors (Li-192SA and LI-190SA, respectively). Underwater irradiance measurements consisted of vertical profiles at 0.5-m intervals with two or more replicates profiles obtained at each site. Light attenuation coefficients ( $K_d$ ;  $\text{m}^{-1}$ ) were derived from a regression of the downwelling irradiance versus depth (Kirk 1994). We estimated the average daily underwater irradiance at each site taking into account light attenuation and the average (cross-sectional) depth of the channel (Gosselain et al. 1994):

$$I_{x\text{-sec}} = I_s / (K_d \times z_{x\text{-sec}})$$

where  $I_s$  is daily incident solar radiation ( $\text{E m}^{-2} \text{ day}^{-1}$ ), and  $z_{x\text{-sec}}$  is the cross-sectional average depth of the channel (m). The daily incident solar radiation was a region-specific average value for May to November ( $40 \text{ E m}^{-2} \text{ day}^{-1}$ ; Fisher et al. 2003). The average underwater irradiance ( $I_{x\text{-sec}}$ ;  $\text{E m}^{-2} \text{ day}^{-1}$ ) was used to characterize inter-site variation in light availability and to establish appropriate light levels for incubating primary production samples.

Turbidity was measured with a HACH model 2100 Turbidimeter. Dissolved nutrients were measured on a Skalar Autoanalyzer using standard methods for colorimetric reactions (APHA 1998). Total nitrogen and phosphorus were measured monthly at three of our sampling locations

(JMS99, JMS75 and JMS69) by the Virginia Department of Environmental Quality. Suspended particulate matter was analyzed for CHL $a$ , particulate C and N (POC and PON, respectively) and total suspended solids (TSS). CHL $a$  samples were filtered thru Whatman GF/A glass filters (0.5  $\mu\text{m}$  nominal pore size), extracted for 18 h in buffered acetone and analyzed on a Turner Design TD-700 Fluorometer (Sellers and Bukaveckas 2003). TSS was determined gravimetrically using pre-weighed, pre-combusted filters. A subsample was analyzed on a Perkin–Elmer CHN analyzer for determination of the C and N content of particulate matter. Bacterial abundance was determined using acridine orange direct counts (Hobbie et al. 1977). Three replicate samples from each site were preserved with pre-filtered formaldehyde. Following sonication, samples were vigorously vortexed, stained and filtered through a 0.2- $\mu\text{m}$  black polycarbonate membrane filters (Millipore). Filters were fixed to slides using non-fluorescing immersion oil and viewed under an epifluorescence microscope.

*Oxygen Metabolism* Estimates of production, respiration and net metabolism were derived for both the water column (plankton) and the whole ecosystem. Hereafter, we use the terms NPP $_p$ ,  $R_p$  and NPM for plankton production, respiration and net metabolism. Corresponding ecosystem terms are NPP $_e$ ,  $R_e$ , and net ecosystem metabolism (NEM). Plankton metabolism was determined using the light/dark bottle dissolved oxygen method (Carignan et al. 1998). Three to four replicate BOD bottles (60 ml) were incubated in a Conviron growth chamber at ambient (in situ) light and temperature for 8 h (NPP $_p$ ) and 24 h ( $R_p$ ). Light intensities during incubations were derived from average daily solar radiation for this region, average cross-sectional depth at the sampling location, and measured in situ light attenuation on the date of sample collection (see above). Initial and final dissolved oxygen concentrations were determined by the Winkler technique to obtain a precision  $\sim 0.01$  mg O $_2$  L $^{-1}$  (Carignan et al. 1998).

Whole-ecosystem metabolism was inferred from diel O $_2$  data. Continuous measurements of dissolved O $_2$  were obtained for JMS99 and JMS75 from the National Estuarine Research Reserve (NERR) network of automated monitoring stations (Caffrey 2003, 2004). Diel patterns were analyzed for the subset of dates corresponding to light/dark bottle incubations. Dissolved O $_2$  measurements recorded at 15-min intervals were smoothed to 30-min averages for O $_2$  flux analyses. We derived NPP $_e$  from the sum of daytime O $_2$  fluxes,  $R_e$  from the sum of nighttime O $_2$  fluxes extrapolated to a 24 h period, and GPP $_e$  from NPP $_e$  plus  $R_e$  occurring during daylight hours (Caffrey 2003, 2004). NEM was calculated by subtracting total (24 h)  $R_e$  from GPP $_e$ . Derivation of NPP $_e$  and  $R_e$  from diel data require correction for atmospheric exchange. Air–water O $_2$

fluxes were estimated using two approaches: (1) assuming that atmospheric exchange varied only in response to O $_2$  saturation, and (2) assuming that exchange varied in response to both O $_2$  saturation and wind speed. The former approach follows Caffrey (2003, 2004) whereby a fixed estimate of the exchange coefficient ( $k$ ) yields a potential range of atmospheric exchange from  $-0.5$  to  $+0.5$  g O $_2$  m $^{-2}$  h $^{-1}$  for 0–200% saturation. The latter approach used daily average wind speeds obtained from a nearby meteorological station (NERR site at Taskinas Creek) and the regression of Marino and Howarth (1993) relating  $k$  to wind speed. The wind-correction method yielded a similar range of exchange values ( $-0.3$  to  $+0.3$  g O $_2$  m $^{-2}$  h $^{-1}$ ) to those derived using a fixed estimate of the exchange coefficient because wind speeds were low at these sites (i.e. in a range where  $k$  was comparable to the constant value). We report values derived with no wind-speed correction. A second factor complicating assessments of metabolism based on single-station diel O $_2$  data is the potential for advection of super- or under-saturated water to affect local O $_2$  concentrations. After de-trending the diel data for a 24-h cycle we did not find that tidal intervals explained a significant fraction of the residual variation at either of the two monitoring stations.

*Zooplankton* Zooplankton grazing was measured in the laboratory using natural assemblages from each of the three sites. Zooplankton were collected near the surface (1–3 m) using a hand pump to transfer water through a 63  $\mu\text{m}$  plankton net. Forty litres of water were collected for each of three replicate samples which were preserved in the field and used for density determinations. Grazing rates were estimated by comparing phytoplankton growth rates in the presence and absence of zooplankton (Lionard et al. 2005). Zooplankton were separated from phytoplankton using 63  $\mu\text{m}$  mesh Nitex netting. Exploratory tests revealed that this did not significantly affect CHL $a$ . Zooplankton were separated into two size classes: macrozooplankton ( $>210$   $\mu\text{m}$ ) and mesozooplankton (63–210  $\mu\text{m}$ ). Incubating these size classes separately allowed for the determination of their relative contribution to community grazing rates (Kim et al. 2000). Three replicates of each size fraction were incubated in dark 1 L polycarbonate bottles for 48 h in a Conviron growth chamber at ambient (in situ) temperature. Six bottles without zooplankton were simultaneously incubated to measure the loss rate of chlorophyll  $a$  in the absence of grazers. Bottles were gently inverted twice per day to resuspend sedimented materials.

A total of eight grazing experiments were performed: six at the tidal freshwater sites (three each at JMS99 and JMS75) and two at the mesohaline site (JMS21). Ingestion and filtration rates were calculated assuming they followed

an exponential model with time (Frost 1972). The phytoplankton growth rate ( $k$ ) was calculated as:

$$k = \ln(C_f/C_i)/t$$

where  $C_i$  and  $C_f$  are the initial and final CHL $a$  in enclosures without zooplankton. Phytoplankton growth rates were negative in these experiments because the enclosures were incubated in the dark to prevent differences in growth rates due to nutrient recycling by grazers. The grazing coefficient ( $g$ ) was calculated as:

$$g = -(\ln(C_f/C_i) + k)/t$$

where  $C_f$  and  $C_i$  represent the final and initial CHL $a$  in enclosures with grazers. Zooplankton abundances were determined at the start and end of the incubation to derive per capita ingestion and filtration rates. The per capita ingestion rate ( $I_{pc}$ ) was calculated as:

$$I_{pc} = (g \times C_m)/Z_m$$

where  $C_m$  and  $Z_m$  are the mean of initial and final CHL $a$  and zooplankton densities within the enclosures (assuming an exponential model). The per capita filtration rate ( $F_{pc}$ ):

$$F_{pc} = I_{pc}/C_m$$

represents the ‘volume swept clear’ (sensu Frost 1972). These per capita rates were multiplied by in situ zooplankton densities to estimate community ingestion and filtering rates ( $I$  and  $F$ , as micrograms of CHL $a$  L $^{-1}$  day $^{-1}$  and percent volume day $^{-1}$ , respectively).

## Results

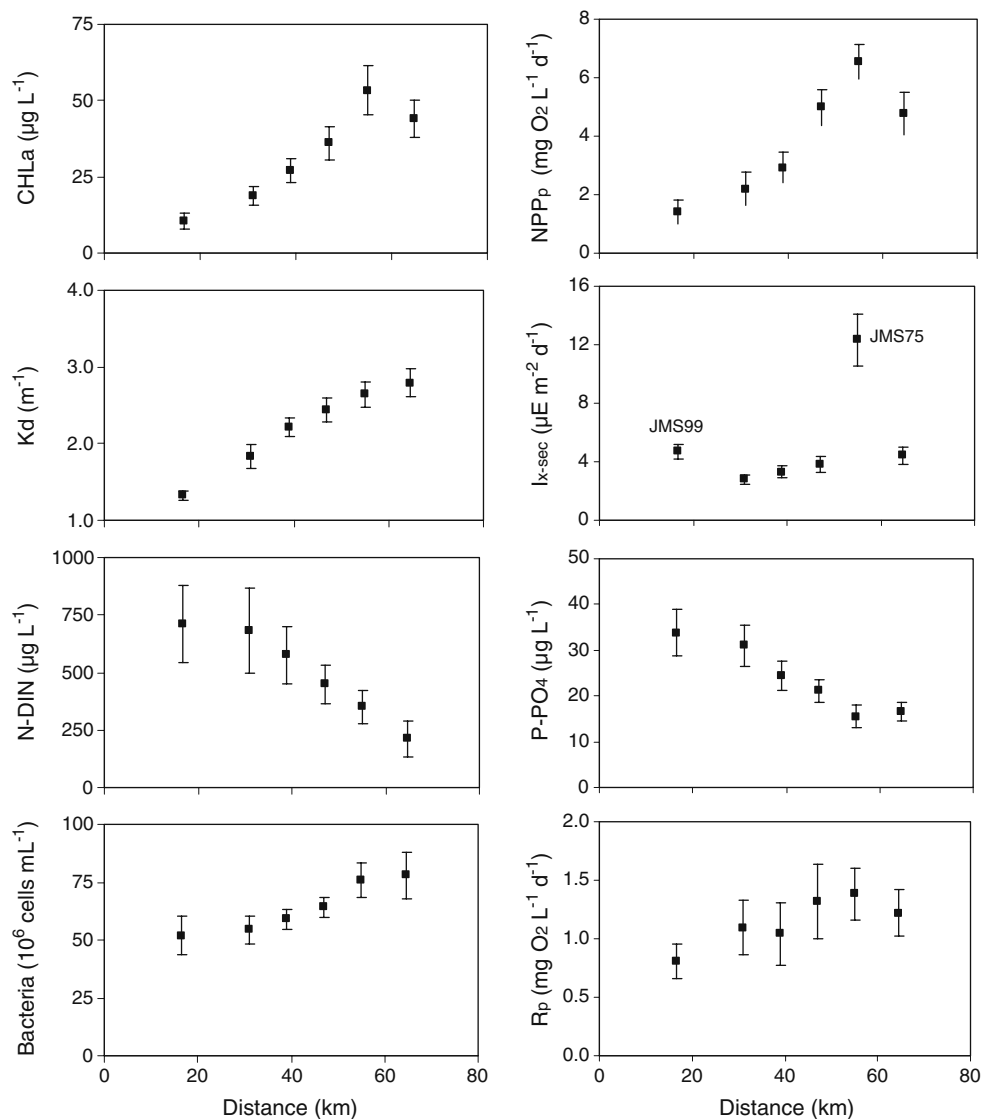
Longitudinal patterns were characterized based on average values among the six sampling locations during April to November (Fig. 3). Mean CHL $a$  varied fivefold with lowest values at the uppermost site (JMS99=10.5±2.6 μg L $^{-1}$ ) and peak values at JMS75 (53.3±8.0 μg L $^{-1}$ ). NPP $_p$  closely followed trends in CHL $a$  with average values ranging from 1.40±0.40 mg O $_2$  L $^{-1}$  day $^{-1}$  at JMS99 to 6.53±0.59 mg O $_2$  L $^{-1}$  day $^{-1}$  at JMS75. Variation in NPP $_p$  was principally determined by CHL $a$  ( $R^2=0.62$ ;  $N=65$ ;  $p<0.0001$ ) such that biomass-specific production was similar among sites (mean=12.6±1.2 μg O $_2$  μg $^{-1}$  CHL $a$  h $^{-1}$ ). Light attenuation ( $k_d$ ) increased longitudinally from 1.32±0.21 m $^{-1}$  at JMS99 to 2.67±0.62 m $^{-1}$  at JMS75. However, inter-site differences in average underwater irradiance ( $I_{x-sec}$ ) were largely determined by channel depth not attenuation. In the constricted landward segment, cross-sectional average depth ranged between 4.4 and 8.2 m resulting in low values of  $I_{x-sec}$  (range=2.8–4.7 E m $^{-2}$  day $^{-1}$ ). The CHL $a$

maximum at JMS75 occurred in a zone of shallow cross-sectional depth (1.3 m) and high  $I_{x-sec}$  (mean=12.3±1.7 E m $^{-2}$  day $^{-1}$ ). DIN concentrations decreased longitudinally from 711±166 μg L $^{-1}$  at JMS99 to 212±78 μg L $^{-1}$  at JMS69. A similar pattern was observed for P–PO $_4$  which decreased from 34±5 μg L $^{-1}$  (JMS99) to 17±2 μg L $^{-1}$  (JMS69). Bacterial abundance and  $R_p$  also exhibited consistent longitudinal trends though inter-site variation was less than that for CHL $a$ , and NPP $_p$ . Bacterial abundance increased from 52±8×10 $^6$  cells mL $^{-1}$  at JMS99 to 76±8×10 $^6$  cells mL $^{-1}$  at JMS75. Corresponding rates of respiration were 0.81±0.15 mg O $_2$  L $^{-1}$  day $^{-1}$  and 1.38±0.22 mg O $_2$  L $^{-1}$  day $^{-1}$  at JMS99 and JMS75, respectively.  $R_p$  was significantly related to temperature with linear models accounting for 78% (JMS75) and 42% (JMS99) of the variation ( $p<0.01$ ). Net plankton metabolism was positive at all sites (GPP $_p > R_p$ ). Production in excess of respiration was greatest at the CHL $a$  maximum (5.84 mg±0.50 O $_2$  L $^{-1}$  day $^{-1}$ ) and lowest at JMS99 (1.17±0.38 mg O $_2$  L $^{-1}$  day $^{-1}$ ).

Seasonal variation in longitudinal trends was assessed by comparing time series from the most landward station (JMS99) and the site of the CHL $a$  maximum (JMS75; Fig. 4). The two sites exhibited consistent and large differences in CHL $a$  and NPP $_p$  during May to October. Smaller differences were observed in April and November. Average cross-sectional irradiance was always greater at the site of the CHL $a$  maximum despite higher light attenuation. Differences in nutrient concentrations between the two sites were more variable than for CHL $a$  and NPP $_p$  though the upriver site (JMS99) generally exhibited higher DIN and P–PO $_4$ . During late summer differences in P–PO $_4$  concentrations were >20 μg L $^{-1}$  and DIN differed by >1,000 μg L $^{-1}$ . Bacterial abundance and  $R_p$  were typically higher at the site of the CHL $a$  maximum (JMS75) through differences between the two sites were smaller and more variable than those for CHL $a$  and NPP $_p$ .

Diel O $_2$  data from JMS99 and JMS75 were analyzed to assess differences in ecosystem metabolism above and within the zone of the CHL $a$  maximum. Diel amplitudes for dissolved O $_2$  were consistently larger at the site of the CHL $a$  maximum (mean=3.8 mg L $^{-1}$ ) relative to the upriver site (mean=1.4 mg L $^{-1}$ ). Atmospheric exchange was a small component of O $_2$  fluxes at both sites with average values corresponding to 2% and 19% of biologically driven O $_2$  fluxes. Atmospheric exchange was greater at JMS75 due to its shallower depth (0.08±0.02 mg L $^{-1}$  day $^{-1}$  and –1.27±0.29 mg L $^{-1}$  day $^{-1}$  at JMS99 and JMS75, respectively); negative fluxes at this site were a result of persistent supersaturation. By comparison, the upriver site was typically under-saturated except in late summer during the afternoon O $_2$  peak. Ecosystem production and respiration values derived from diel O $_2$  data were also higher at JMS75 relative

**Fig. 3** Longitudinal gradients of chlorophyll *a* (*CHLa*), net primary production (*NPP<sub>p</sub>*), light attenuation (*K<sub>d</sub>*), average cross-sectional irradiance (*I<sub>x-sec</sub>*), dissolved inorganic N (*N-DIN*), orthophosphate (*P-PO<sub>4</sub>*), bacterial abundance and plankton respiration (*R<sub>p</sub>*) in the tidal freshwater James River. Data shown are average values (with standard error) for the period April–November 2007. Long-term monitoring stations are denoted by CBP designations JMS99 and JMS75

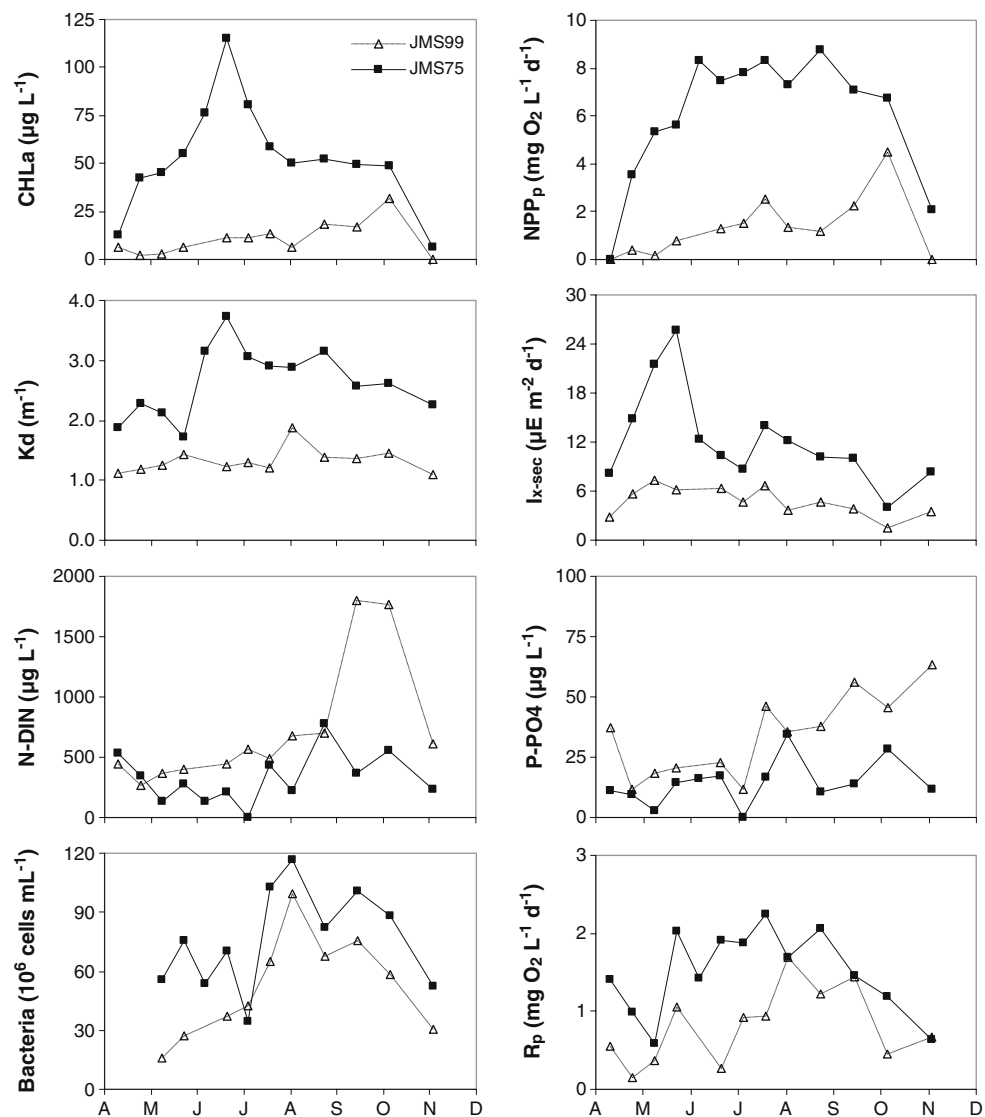


to JMS99 (Fig. 5). At JMS75,  $NPP_e$  was on average three times higher ( $3.98 \pm 0.46 \text{ mg L}^{-1} \text{ day}^{-1}$  vs.  $1.11 \pm 0.19 \text{ mg L}^{-1} \text{ day}^{-1}$ ) and  $R_e$  was twofold higher ( $5.18 \pm 0.62 \text{ mg L}^{-1} \text{ day}^{-1}$  vs.  $2.31 \pm 0.42 \text{ mg L}^{-1} \text{ day}^{-1}$ ) relative to JMS99 over the period of study (Table 1). Net ecosystem metabolism was positive at JMS75 ( $1.39 \pm 0.62 \text{ mg L}^{-1} \text{ day}^{-1}$ ) but near zero at JMS99 ( $-0.17 \pm 0.62 \text{ mg L}^{-1} \text{ day}^{-1}$ ). Spatial and temporal variation in  $NPP_e$  was strongly related to average underwater irradiance with a non-linear model (Jassby and Platt 1976) accounting for 89% of the variation in  $NPP_e$  ( $N=22$ ;  $p < 0.0001$ ). The model depicted a saturation response when  $I_{x\text{-sec}}$  exceeded  $10 \text{ E m}^{-2} \text{ day}^{-1}$ . *CHLa* was the best predictor for both  $R_e$  and NEM ( $R^2=0.46$  and  $0.45$ , respectively;  $p < 0.01$ ).

The quantity and composition of suspended particulate matter varied longitudinally (Fig. 6). TSS increased from  $8.1 \pm 1.6 \text{ mg L}^{-1}$  to  $28.6 \pm 3.1 \text{ mg L}^{-1}$  between JMS99 and

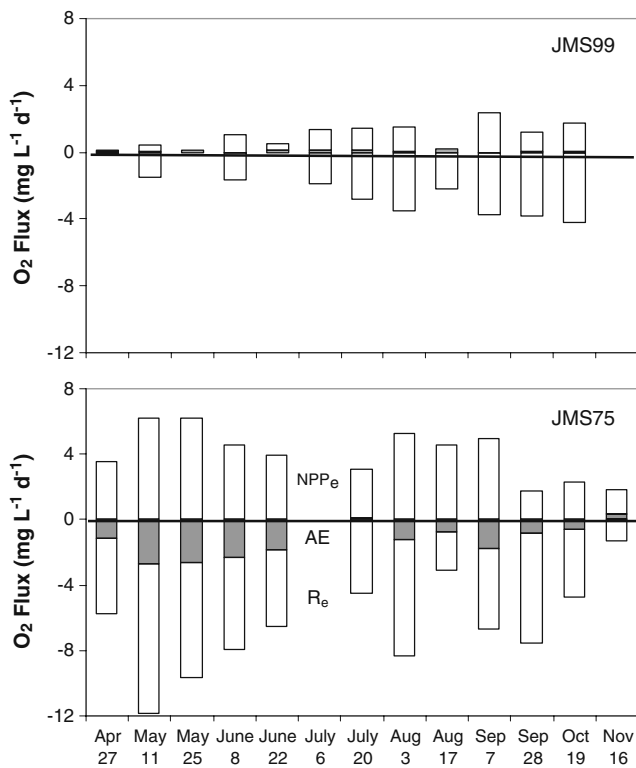
JMS69. Trends in POC and PON were similar to those for TSS with lowest average concentrations at the most upriver site and highest concentrations at the lowermost site. Because trends in POC tracked TSS, the proportion of organic C in suspended particulate matter was relatively uniform across sites (range of means=10–15%). *CHLa* was a significant predictor of the C and N content of particulate matter accounting for 71% and 68% of the variation in POC and PON ( $N=86$ ;  $p < 0.001$ ). POC and PON were themselves strongly correlated ( $R^2=0.91$ ) such that C/N ratios were similar among sites (range of means=5.9 to 6.5 M). The relationship between POC and *CHLa* was used to derive an average C/*CHLa* ratio ( $39 \pm 2 \text{ µg/µg}$ ) from which the algal contribution to POC was estimated. The algal C fraction of POC ranged from  $37 \pm 2\%$  at JMS99 to  $72 \pm 8\%$  at the *CHLa* maximum (JMS75). In contrast, the algal fraction of total particulate matter was similar among sites (range of means=5–8%) due to co-occurring increases in *CHLa* and TSS.

**Fig. 4** Seasonal variation in chlorophyll *a* (CHL*a*), net primary production (NPP<sub>p</sub>), light attenuation (*K<sub>d</sub>*), cross-sectional average irradiance (*I<sub>x-sec</sub>*), dissolved inorganic N (*N-DIN*) orthophosphate (*P-PO<sub>4</sub>*), bacterial abundance and plankton respiration (*R<sub>p</sub>*) at two stations in the tidal freshwater James River during April–November 2007



Zooplankton abundance and grazing were measured at two sites in the tidal freshwater segment (JMS99 and JMS75) and at one site in the mesohaline zone (JMS21; Fig. 7). Total zooplankton densities were higher at the tidal freshwater sites, particularly at the CHL*a* maxima (mean=434±69 ind L<sup>-1</sup> and 274±45 ind L<sup>-1</sup> at JMS75 and JMS99, respectively) and lower at the mesohaline site (93±23 ind L<sup>-1</sup>). Inter-site differences were largely determined by mesozooplankton which were significantly more abundant at the freshwater sites ( $p < 0.01$ ;  $N = 33$ ). Mesozooplankton were dominated by rotifers (principally *Brachionus*) and copepod nauplii. Among macrozooplankton, cladocerans (principally *Bosmina longirostris*) also exhibited greater abundances at the freshwater sites with highest densities occurring at the CHL*a* maxima (11.1 ind L<sup>-1</sup>). Calanoid copepods and barnacle larvae exhibited highest densities at the mesohaline site. Calanoid copepods were principally *Eurytemora affinis* (JMS75 and JMS99) and *Acartia tonsa* (JMS21).

Per capita ingestion rates for the macrozooplankton averaged  $0.0127 \pm 0.0050 \mu\text{g CHL}a \text{ ind}^{-1} \text{ day}^{-1}$  with associated filtration rates averaging  $49.6 \pm 27.9 \mu\text{l ind}^{-1} \text{ h}^{-1}$ . Corresponding values for mesozooplankton were an order of magnitude lower (ingestion= $0.0007 \pm 0.0005 \mu\text{g CHL}a \text{ ind}^{-1} \text{ day}^{-1}$ ; filtration= $4.2 \pm 1.7 \text{ ml}^{-1} \text{ ind}^{-1} \text{ day}^{-1}$ ). Per capita ingestion rates for macrozooplankton were higher at the tidal freshwater sites but inter-site differences were not statistically significant. Community ingestion rates derived from the product of per capita values and in situ densities were highest at the site of the CHL*a* maximum (JMS75= $0.691 \mu\text{g CHL}a \text{ L}^{-1} \text{ day}^{-1}$ ) and lower at JMS99 (mean= $0.272 \mu\text{g CHL}a \text{ L}^{-1} \text{ day}^{-1}$ ) and JMS21 (mean= $0.139 \mu\text{g CHL}a \text{ L}^{-1} \text{ day}^{-1}$ ). Inter-site differences were not significant owing to high intra-site variability (average CV=45%) and low power (two to three dates per site). Ingestion rates expressed as a proportion of in situ CHL*a* ranged from 1.0% to 2.3% with lowest average values at the CHL*a* maxima. Overall, these findings



**Fig. 5** Dissolved O<sub>2</sub> fluxes associated with net ecosystem primary production ( $NPP_e$ ; positive values), ecosystem respiration ( $R_e$ ; negative values) and atmospheric exchange ( $AE$ ; shaded) at two stations in the tidal freshwater James River. Positive  $AE$  values denote the flux of O<sub>2</sub> from air to water; negative  $AE$  values denote the flux of O<sub>2</sub> from water to air

suggest that although zooplankton densities were higher at the CHL $a$  maximum, phytoplankton losses due to grazing were low and similar at all sites.

## Discussion

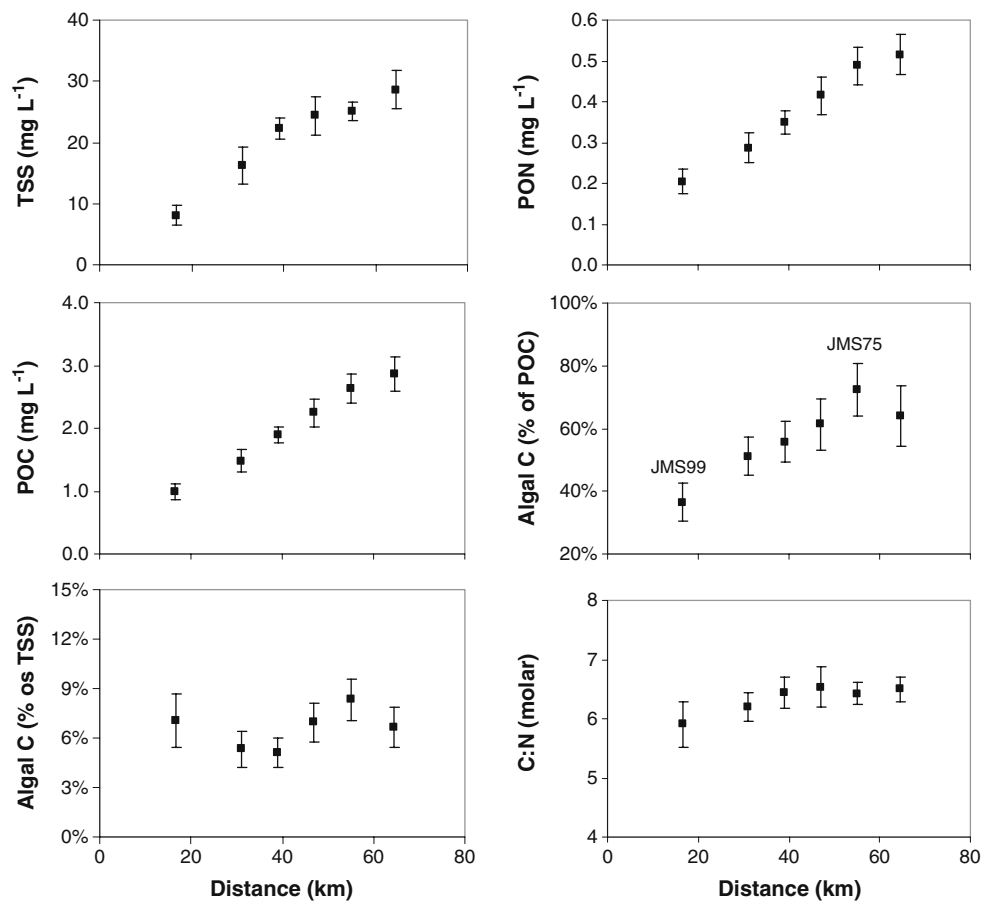
Prior studies have concluded that CHL $a$  maxima in some estuaries arise through retention of exogenous phytoplankton because abundance cannot be explained by local growth where turbidity is high (Cole et al. 1992; Lapierre and Frenette 2008). Our metabolism data suggest that is not the case in the tidal freshwater segment of the James River Estuary. Net plankton metabolism was positive at all sites ( $GPP_p > R_p$ ) with highest values observed at the CHL $a$  maximum.  $NPP_e$  was correlated with the mean irradiance of the water column indicating that light availability determined primary production. Chlorophyll-specific production was similar among sites suggesting that changes in light utilization efficiency (e.g., due to species shifts; Lehman 2007) did not account for inter-site variation in NPP. The CHL $a$  maximum occurred at the transition from a narrow, deep channel to a broad channel with shallow lateral areas. In the narrow upper segment, light availability and NPP were limited by large water depths despite greater water clarity (low turbidity and attenuation). At the site of the CHL $a$  maximum, average values of underwater irradiance were two–threefold higher and exceeded previously reported light limitation thresholds for river and estuarine phytoplankton ( $5\text{--}10 \text{ E m}^{-2} \text{ day}^{-1}$ ; Koch et al. 2004; Oliver and Merrick 2006; Whalen and Benson 2007). The region of elevated

**Table 1** Estimates of ecosystem metabolism derived from diel oxygen data obtained at the upriver sampling location (JMS99) and the site of the CHL $a$  maximum (JMS75)

	$NPP_e$		$R_e$		$GPP_e$		NEM	
	Rm 99	Rm 75	Rm 99	Rm 75	Rm 99	Rm 75	Rm 99	Rm 75
	mg O <sub>2</sub> L <sup>-1</sup> day <sup>-1</sup>							
27 Apr 2007	0.09	3.55	0.09	4.66	0.14	5.88	0.04	1.21
11 May 2007	0.36	6.24	1.49	9.14	1.11	10.81	-0.38	1.67
25 May 2007	n.d.	6.19	n.d.	7.07	n.d.	9.72	n.d.	2.65
8 Jun 2007	1.06	4.57	1.67	5.63	1.90	7.38	0.22	1.75
22 Jun 2007	0.42	3.91	0.00	4.65	0.39	6.23	0.39	1.59
6 Jul 2007	1.26	n.d.	1.86	n.d.	2.19	n.d.	0.33	n.d.
20 Jul 2007	1.32	2.99	2.80	4.47	2.72	5.22	-0.08	0.76
3 Aug 2007	1.46	5.30	3.51	7.09	3.22	8.85	-0.29	1.76
17 Aug 2007	n.d.	4.54	2.20	2.32	0.89	5.70	-1.31	3.38
7 Sep 2007	2.33	4.96	3.71	4.94	4.19	7.43	0.48	2.49
28 Sep 2007	1.12	1.77	3.81	6.78	3.03	5.16	-0.79	-1.62
19 Oct 2007	1.66	2.29	4.22	4.14	3.77	4.36	-0.45	0.22
16 Nov 2007	n.d.	1.49	n.d.	1.29	n.d.	2.14	n.d.	0.85
Mean	1.11	3.98	2.31	5.18	2.14	6.57	-0.17	1.39
SE	0.19	0.46	0.42	0.62	0.62	0.62	0.62	0.62



**Fig. 6** Longitudinal variation in total suspended solids (TSS), particulate organic N (PON) and C (POC), algal contributions to POC and TSS (as%) and the molar ratio of C to N in suspended particulate matter of the tidal freshwater James River. Data shown are average values (with standard error) for the period April–November 2007. Long-term monitoring stations are denoted by CBP designations JMS99 and JMS75

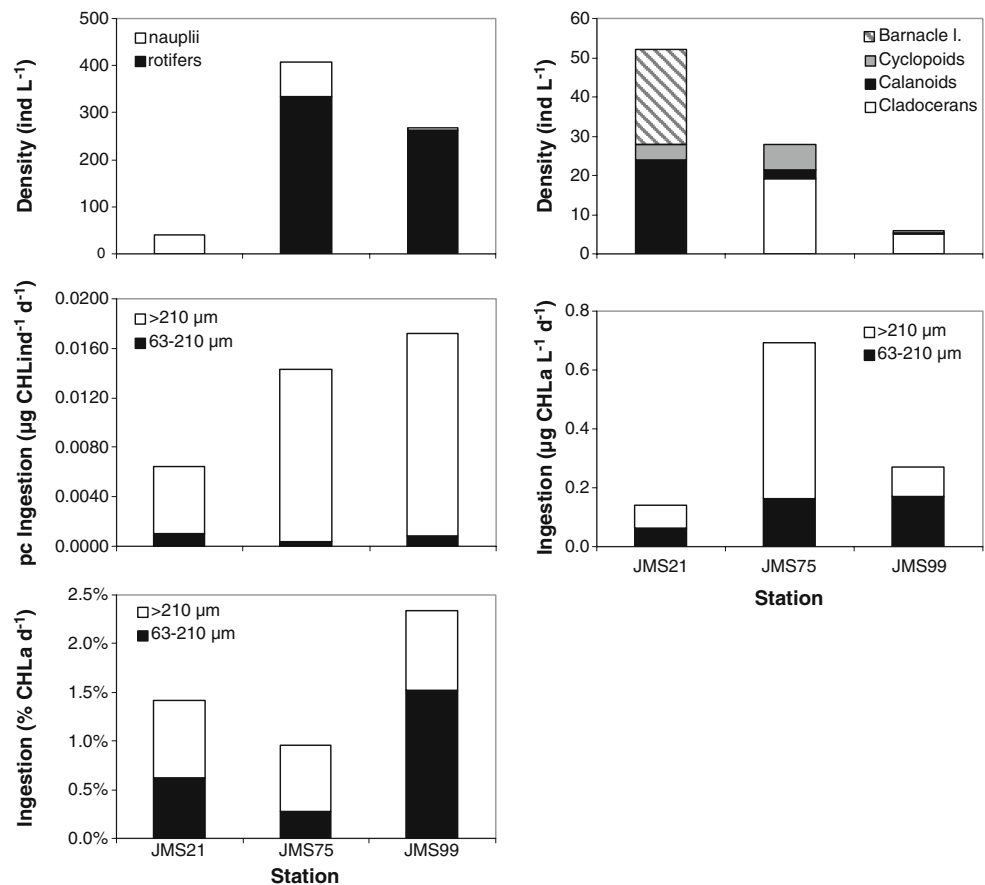


CHL<sub>a</sub> extended outside the zone of highest underwater irradiance suggesting that tidal dispersion propagated localized effects. While longitudinal patterns in CHL<sub>a</sub> showed strong correspondence to variation in underwater irradiance, seasonal patterns were less consistent. For example, a period of rising underwater irradiance (from 8 to 26 E m<sup>-2</sup> day<sup>-1</sup>) occurred in early summer (April 27 to June 8) and was accompanied by large increases in CHL<sub>a</sub> at JMA75 (from 12 to 55 μg L<sup>-1</sup>) but the summer peak in CHL<sub>a</sub> occurred later (115 μg L<sup>-1</sup> on July 6) after irradiance had declined to (10 E m<sup>-2</sup> day<sup>-1</sup>). Irradiances above 5–10 E m<sup>-2</sup> day<sup>-1</sup> are saturating with respect to NPP (see references above) and may explain why CHL<sub>a</sub> and NPP do not track light availability above this range. Overall, our results attest to the importance of light availability in determining the location of the CHL<sub>a</sub> maximum and the importance of considering morphometry (depth) effects on underwater light conditions along with incident solar radiation and attenuation within the water column.

Areal rates of GPP<sub>e</sub> at the CHL<sub>a</sub> maximum (mean=12 g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>) were comparable to summer values at four other NERR sites within Chesapeake Bay (range=9–15 g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>; Caffrey 2004). Net metabolism differed in that NEM was positive at the James River CHL<sub>a</sub> maximum (2.4 g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>) and negative at the other NERR sites

(mean=-3.4 g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>). These patterns are consistent with the theory that autotrophy is favored in shallow systems because underwater irradiance and NPP increase with decreasing depth whereas depth-integrated *R* declines with decreasing depth (Cloern 2007). Similar findings were reported for the Colne and Schelde Estuaries where favorable ratios of photic depth to mixing depth allowed for positive NPP despite high turbidity (Kocum et al. 2002; Muyaert et al. 2005). Phytoplankton production (NPP<sub>p</sub>) was sufficient to account for all of NPP<sub>e</sub> despite the extensive shallow areas which are potential habitat for benthic algae (e.g. Murrell et al. 2009). Phytoplankton experiencing a favorable light regime likely benefited from their proximity to riverine nutrient inputs and to numerous point sources that discharge directly to this segment of the estuary. Nutrient concentrations typically exceeded limitation thresholds based on half-saturation coefficients for N and P uptake (DIN=15–300 μg L<sup>-1</sup>; PO<sub>4</sub>=2–10 μg L<sup>-1</sup>; Hamilton and Schladow 1997). Inter-site differences in nutrient concentrations were inversely related to CHL<sub>a</sub> as both N and P concentrations were lower in the vicinity of the CHL<sub>a</sub> maximum. Lower nutrient concentrations at JMS75 relative to JMS99 (threefold for DIN and twofold for SRP) may reflect autotrophic and heterotrophic assimilation in the region of the CHL<sub>a</sub> maximum as well as

**Fig. 7** Zooplankton abundance and ingestion rates at stations located in the tidal freshwater (JMS99 and JMS75) and mesohaline (JMS21) segments of the James River Estuary. Data shown are average values for two to three sampling dates at each site during June–August 2007. Ingestion metrics shown are for two size fractions (63–210  $\mu\text{m}$  and  $>210 \mu\text{m}$ ) as per capita ('pc') and total (community) ingestion rates



dilution by tidal exchange. Molar ratios of DIN/TP declined from 22 (JMS99) to 8 (JMS75) but remained above threshold values for N limitation (2–5; Ptacnik et al. 2010) indicating that the tidal freshwater James River is P limited where light conditions are favorable. Ratios of CHLa to TP were on average fourfold higher at JMS75 (0.56 mg/mg) relative to JMS99 (0.15 mg/mg) suggesting that the release from light limitation allowed for greater nutrient utilization through enhanced photosynthesis and biomass conversion.

The location of the CHLa maximum is principally attributed to favorable growth conditions following a release from light limitation though we cannot discount the potential importance of factors affecting phytoplankton loss rates. Greater cross-sectional area of the channel near the CHLa maximum would result in lower fluvial and tidal velocities and longer transit times. Simulations with a two-dimensional hydrodynamic model (Shen et al. 1999; Shen and Lin 2006) yielded transit time estimates of 4.6 days in the narrow, upper channel and 10 days in the broader, lower channel. These estimates were based on the long-term annual mean river discharge (200  $\text{m}^3 \text{s}^{-1}$ ) which was twofold higher than observed discharge during the study period (96  $\text{m}^3 \text{s}^{-1}$ ). Thus, actual transit times were likely longer. Longer transit times coupled with higher average

irradiance in shallow waters would enhance nutrient utilization efficiency and biomass accumulation. The predominance of cyanobacteria at this site (see below) may also explain why the CHLa maximum occurs here (JMS75) given their sensitivity to rising salinity (Sellner et al. 1988). For example, *Microcystis* occurs commonly in fresh and brackish waters up to a salinity of 7 ppt (Robson and Hamilton 2003; Lehman et al. 2010). However, salinities in the James River Estuary remain low (<5) up to 50 km seaward from this site (Fig. 1) suggesting that the rapid decline in CHLa cannot be attributed to salinity effects. More likely, elevated suspended solids concentrations coupled with diminishing nutrient concentrations limit biomass accumulation at sites seaward of the CHLa maximum.

Although grazing estimates derived from laboratory feeding experiments must be interpreted with caution, our results suggest low exploitation of phytoplankton production by zooplankton in this system. Zooplankton densities were higher at the CHLa maximum, but community ingestion rates were low at all sites corresponding to less than 5%  $\text{day}^{-1}$  of the standing stock of CHLa. By comparison, a compilation of literature values yielded an average grazing rate of 31%  $\text{CHLa day}^{-1}$  among diverse estuaries (Murrell et al. 2002). As grazing estimates are the

product of laboratory-derived per capita ingestion rates and in situ zooplankton densities, either factor could account for low values. Our estimates of zooplankton abundances were comparable to those previously reported for this system though methodological differences in sample collection complicate direct comparisons. The Chesapeake Bay Program (CBP) monitored macrozooplankton abundance at JMS75 during 2000–2002. Their results show good agreement with our values for large-bodied animals such as Cladocerans (CBP=14.2 ind L<sup>-1</sup>; this study=11.1 ind L<sup>-1</sup>) and calanoids (CBP=1.13 ind L<sup>-1</sup>; this study=1.68 ind L<sup>-1</sup>). Differences in mesh size between these two studies (CBP=200 μm; this study=63 μm) preclude comparisons for small-bodied animals but an earlier study reported rotifer densities for this site during 1994–1995 (Park and Marshall 2000). Their average rotifer densities (675±157 ind L<sup>-1</sup>) were greater than ours (333±67 ind L<sup>-1</sup>); however, their collection method was based on settling of whole water samples and would therefore include rotifers too small to be captured by our 63 μm net. Overall, densities reported in prior studies suggest that low grazing rates during the study period were not a result of unusually low densities.

Our measured per capita grazing rates for meso- and macrozooplankton were generally within the range of previously published estimates. For macrozooplankton our average filtration rate (49.6 μl ind<sup>-1</sup> h<sup>-1</sup>) was comparable to species-specific values for taxa that were common at our sites (e.g. *Bosmina*=31 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>, nauplii=84 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>, Bogdan and Gilbert 1984; *Bosmina*=68 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>, Sierszen and Frost 1990; *Bosmina*=37 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>, Kim et al. 2000) though low in comparison to some published values for adult copepods (e.g. 626 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup> for *Eurytemora*; Tackx et al. 2003). For mesozooplankton, the average filtration rate (4.2 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>) was at the lower range of those reported in other field and lab studies (mean=22.6 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>; Lionard et al. 2005 and references therein). Mesozooplankton were numerically dominant in our samples from the tidal freshwater sites and accounted for on average 30% (JMS75) and 57% (JMS99) of the community grazing rate. A number of factors could account for low per capita grazing rates including food resource conditions and methodological issues. The method we used to determine ingestion rates requires a sufficient density of animals to produce measurable loss of CHLa while avoiding food depletion and other crowding effects. These enclosure and manipulation effects may alter feeding behavior (Roman and Rublee 1980; Lair 2006). However, our average mesozooplankton filtration rate was very similar to the nearby Potomac River (5.4 μl<sup>-1</sup> ind<sup>-1</sup> h<sup>-1</sup>) where low filtration rates were attributed to the presence of cyanobacteria (Sellner et al. 1993). Biomass of cyanobacteria has increased significantly in the tidal freshwater James River during the past 20 years (Marshall et al. 2009). Average densities of cyanobacteria

(principally *Merismopedia*, *Anabaena* and *Microcystis*) at the CHLa maximum were 157 million cells L<sup>-1</sup> during our study (H. Marshall, unpublished data) and exceeded those reported for the Potomac (86 million cells L<sup>-1</sup>; Sellner et al. 1993). Cyanobacteria have been shown to be a poor food source for zooplankton due to issues related to edibility, nutritional sufficiency and in some cases toxicity (Wilson et al. 2006; Brett et al. 2009).

Other aspects of food quality may also contribute to low grazing rates. The CHLa maximum is situated at the head of the estuarine turbidity maximum. Phytoplankton account for a large proportion of POC at JMS75 (mean=72%) but higher CHLa was offset by elevated TSS such that algal contributions to suspended particulate matter were low (<10%) and similar to other sites. These findings suggest that although the quantity of food resources was significantly greater at the CHLa maximum, the quality was not. Prior work has shown that the capacity for selective grazing by zooplankton to compensate for increasing quantities of non-algal particulate matter is diminished when TSS concentrations are on the order of 100 mg L<sup>-1</sup> (Tackx et al. 2003; David et al. 2006). Although TSS at JMS75 was low by comparison (<30 mg L<sup>-1</sup>), our prior work with *Bosmina* has demonstrated life history responses to even small changes (e.g. 3–10%) in the relative contribution of phytoplankton to suspended particulate matter (Acharya et al. 2005, 2006).

Elevated GPP<sub>e</sub> in the region of the CHLa maximum (6.57 mg L<sup>-1</sup> day<sup>-1</sup>) was largely offset by higher R<sub>e</sub> (5.18 mg L<sup>-1</sup> day<sup>-1</sup>) suggesting localized utilization of phytoplankton production via heterotrophic metabolism. High NPP and low grazing at the CHLa maximum indicate that bacterial decomposition may be an important sink for algal biomass. NEM was positive at the CHLa maximum with a net excess of phytoplankton production over local respiration equivalent to 35% of NPP<sub>e</sub>. The bulk of NPP<sub>e</sub> (65%) was respired locally and represents a large autochthonous contribution to heterotrophic metabolism (Oliver and Merrick 2006). This finding is consistent with the quantitative dominance of algal C in particulate organic matter at this site (inferred from C/CHLa ratios). Thus, metabolism data suggest that bacterial decomposition was the dominant fate for primary production in the region of the CHLa maximum. A prior study in the oligohaline segment of the estuary similarly reported that 50% of chlorophyll biomass was utilized locally (Filardo and Dunstan 1985).

In some estuaries, bacterial production is dependent on allochthonous inputs and weakly related to phytoplankton production though exceptions have also been reported (Murrell 2003; Sobczak et al. 2005). Our data suggest that this is not the case at the CHLa maximum of the James River given the strong relationship between bacterial

abundance and CHL<sub>a</sub>. Although bacterial and phytoplankton abundances may be correlated due to other factors (e.g. water residence time), the significant relationship between  $R_e$  and  $NPP_e$  at JMS75 (but not JMS99) suggests that heterotrophic metabolism at the CHL<sub>a</sub> maximum is dependent on algal-derived organic matter. Estimated turnover times of DOC were 3 and 10 days at JMS75 and JMS99 (respectively) based on an assumed algal contribution to the DOC pool equivalent to 13% of NPP (Baines and Pace 1991). C/N analysis of DOC revealed significantly higher N content at the high CHL<sub>a</sub> site (JMS75) indicating more labile dissolved organic matter (Beckwith 2009). Greater contributions of autochthonous carbon at the CHL<sub>a</sub> maximum may in part account for low C/N of DOC, faster DOC turnover, and higher bacterial abundance and community respiration at this site. Stepanauskas et al. (2001) have reported that bacterioplankton community composition in the Sacramento River varied in response to enhancement of DOC quality by autochthonous production and we are presently investigating compositional shifts in the tidal freshwater James River.

Metabolism data suggest that the bulk of respiration occurred within the sediments. The average depth at the CHL<sub>a</sub> maximum (1.7 m) is comparable to daily sinking rates for phytoplankton (mean = 1.6 m d<sup>-1</sup>; Wetzel 2001) suggesting that sedimentation losses are high though depth effects may be offset by positive buoyancy of cyanobacteria which are locally dominant. Furthermore, net sedimentation may be considerably lower than gross sedimentation given the strong mixing forces generated by a large tidal amplitude (0.8 m) relative to overall depth. To assess the proportion of organic matter respired in the water column we derived a mass-specific degradation rate (sensu Wainright and Hopkinson 1997) by converting water column respiration to C equivalents and dividing by the standing stock of organic matter (DOC + POC). Higher average utilization rates at JMS75 (20 ± 4%) relative to JMS99 (14 ± 2%) suggest that autochthonous contributions at the CHL<sub>a</sub> maximum enhance organic matter degradation; but overall, the proportion of decomposition occurring in the water column was low at both sites. Similarly, a comparison of bottle and diel O<sub>2</sub> respiration rates yielded estimates of 31% and 69% for water column and sediment contributions to ecosystem respiration (respectively). Prior work in marine and freshwater systems has reported that 30–60% of NPP is processed by bacterioplankton (Cole et al. 1988; Ducklow and Carlson 1992). Our value is at the low end of this range ( $R_p$  = 40% of  $NPP_e$ ) but consistent with the expectation that high rates of sedimentation would favor benthic respiration. Islam and Tanaka (2006) reported similar findings for the oligohaline portion of the Chikugo River Estuary where the bulk of algal production was transferred to higher trophic levels via detritivory.

In conclusion, our findings suggest that the location of the CHL<sub>a</sub> maximum in the tidal freshwater James River is determined in part by natural geomorphic features of the channel. The transition from a riverine-type (narrow, deep) cross-sectional morphometry to a broad channel with shallow lateral areas provided favorable light conditions and resulted in increased phytoplankton production and abundance. Greater cross-sectional area also likely reduced local water velocities allowing more efficient phytoplankton utilization of nutrients from the catchment and local point sources. Zooplankton grazing rates were low suggesting that other food quality factors may offset high CHL<sub>a</sub> concentrations such as the presence of cyanobacteria and non-algal particulates. Estimates of whole-ecosystem respiration indicate that the bulk of algal production was respired in the region of the CHL<sub>a</sub> maximum and comparisons to water column rates suggest that the bulk of respiration occurred in the sediments. Thus the shallow, high light environment favored net autotrophy within the water column but also likely enhanced the export of chlorophyll biomass to the benthic detrital food web.

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