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Phytoplankton Productivity in the Tidal Regions of four Chesapeake Bay (U.S.A.) Tributaries

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ABSTRACT

Monthly and annual phytoplankton productivity rates of four Virginia tidal rivers were determined based on a 12-year monitoring study that included sampling stations from tidal freshwater, oligohaline, and mesohaline regions in these rivers. The mean monthly rates and range at these locations were 5.52 (Dec.) to 175.12 (Aug.) mg C m^{-3} h^{-1} for tidal freshwater, 12.21 (Jan.) to 149.90 (May) mg C m^{-3} h^{-1} in oligohaline regions, and 16.20 (Jan.) to 151.33 (May) mg C m^{-3} h^{-1} for the mesohaline. The estimated mean annual 12 year productivity for the different Virginia river sites in this study ranged from 49 g C m^{-2} yr^{-1} to 230 g C m^{-2} yr^{-1}. The dominant phytoplankton during periods of high productivity included a changing seasonal dominance of flora among the different salinity regions. At least one station from each river experienced a significant decrease in productivity rates during the 12 years of this analysis. In comparison to an earlier segment of this study, the results indicate the value of long term monitoring to more accurately characterize the productivity dynamics in estuarine locations.

INTRODUCTION

The four rivers in this study are tidal tributaries of the Chesapeake Bay drainage basin in Virginia, with tidal ranges ca. <0.5-1.0 m. These are the James, Pamunkey, York, and Rappahannock rivers, with the Pamunkey representing one of two smaller rivers forming the York (Fig. 1). The James, York, and Rappahannock rivers flow southeasterly through predominantly forest, crop-land, and pasture prior to entering Chesapeake Bay. Each river is included in the Chesapeake Bay Phytoplankton Monitoring Program, with emphasis placed on phytoplankton composition, abundance, and productivity measurements. Several previous reports associated with this program have described phytoplankton composition and abundance in these rivers (Marshall and Alden 1990; Marshall and Burchardt 1998, 2003, 2004, 2005; Marshall and Nesius 1993). These studies identified a diverse and generally similar phytoplankton flora within these rivers, with freshwater diatoms, chlorophytes, and cyanobacteria the dominant flora upstream, yielding in dominance and abundance to a more varied estuarine population of diatoms, dinoflagellates, and cryptophytes downstream. Seasonal variations also exist in productivity contributions among the phytoplankton categories, with diatoms the predominant component and contributor to productivity in spring, and the autotrophic picoplankton among other phytoplankton groups as the major contributors during the summer and early autumn (Marshall and Nesius 1993). Characteristic phytoplankton assemblages were discussed by Marshall et al. (2006) regarding salinity regions and water quality parameters in the Chesapeake Bay

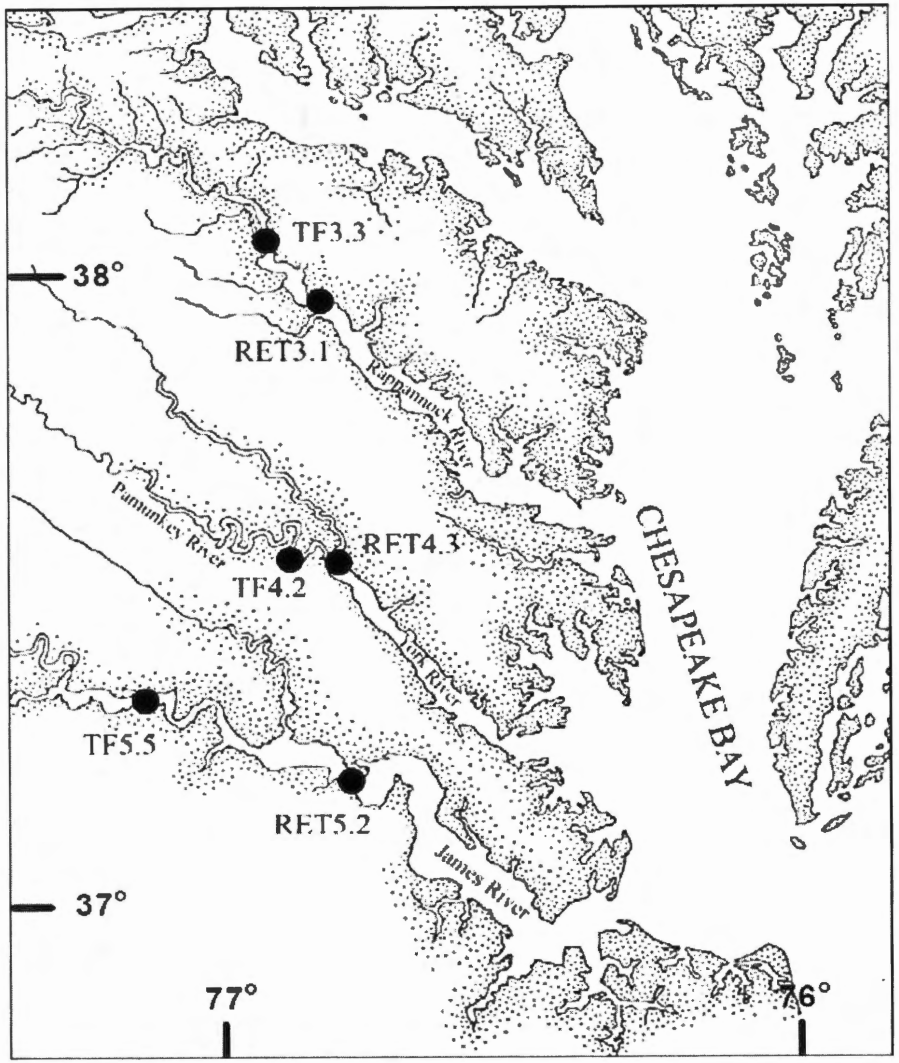

FIGURE 1. Lower Chesapeake Bay indicating location of monitoring stations in the Rappahannock, York, Pamunkey, and James Rivers.

estuarine system. These and other factors that have been associated with productivity in these rivers include long term trends of increasing total suspended solids, decreasing concentrations of total nitrogen and dissolved inorganic nitrogen, plus increasing trends in total phosphorus and dissolved inorganic phosphorus (Marshall and Nesius 1998; Marshall et al. 2002). Although diatoms remain the dominant flora within these rivers, there is evidence for increased abundance of cyanobacteria, plus concern regarding the frequent dinoflagellate blooms occurring in the lower reaches of these rivers (Marshall et al. 2002).

The major objective of this study is to provide a 12-year (1989-2001) synopsis of phytoplankton productivity within the tidal freshwater, oligohaline, and mesohaline regions of four river basins in southeastern Virginia. The rivers are the James, York, Pamunkey, and the Rappahannock. Additional relationships to phytoplankton composition and several water quality parameters during this period are also discussed.

METHODS

Field and laboratory methods

Monthly productivity measurements were taken from stations in tidal freshwater (<0.5 ppt), oligohaline (0.5-5.0 ppt), and mesohaline (>5.0-18.0 ppt) regions of these rivers from July 1989 through June 2001 (Fig. 1). The tidal freshwater stations were located in the Pamunkey (TF4.2) and James (TF5.5) rivers. The oligohaline stations were in the Rappahannock (TF3.3) and James (RET5.2) rivers, with the mesohaline stations in the Rappahannock (RET3.1) and York (RET4.3). Although the Rappahannock River TF3.3 station has long been given the classification (TF), a designation for tidal freshwater, salinity readings over this time period indicated salinity intrusion was common and that it was more appropriately considered an oligohaline site in this study (Marshall and Burchardt 2003).

Two sets of 3 L water samples were taken over a vertical series of 5 depths at each station between the surface and pycnocline and placed in two separate carboys as 15 L composites (Marshall and Nesius 1993). Immediately after mixing, 2-1 L water samples are taken from each of the two carboys and stored in an ice cooler in the dark for transportation to the laboratory. In the absence of a pycnocline the series of water samples were collected from the surface to the lower depth of the photic zone as determined by Secchi depth readings. In the laboratory, after gentle mixing, two 100 mL aliquots were taken from each 1 L sample for productivity analysis, with another 100 mL aliquot having a 15 mL sub-sample filtered immediately for time zero ^{14}C-incorporation. For productivity the sub-samples were placed in 250 mL acid washed dilution bottles, inoculated with 5 µCi $NaH^{14}CO_3$ (specific activity 50-58 µCi µmole^{-1}), and incubated 2-3 hours under saturated light conditions. The time zero ^{14}C incorporation sample was filtered immediately after inoculation with 5 µCi $NaH^{14}CO_3$. Water temperatures in the incubator were the same as when the samples were collected. After incubation, 15 mL sub-samples from each dilution bottle were filtered through 0.45 µm Millipore filters, fumed over concentrated HCl under a vacuum of less than 5 cm Hg pressure and placed in a scintillation vial containing 7 mL scintillation fluid. The ^{14}C-activity was determined using a Beckman LS1701 liquid scintillation counter. Alkalinity was determined from station samples to calculate available inorganic carbon present. Carbon fixation rates (mg C m^{-3} h^{-1}) were determined according to Strickland and Parsons (1972).

From the same 15 L carboys two additional 500 mL and 125 mL samples were obtained. One set (500 mL samples) was processed for phytoplankton analysis using a modified Utermöhl method (Marshall and Alden 1990). The other sub-set (125 mL samples) was examined by epifluorescence microscopy to determine autotrophic picoplankton abundance (Marshall 1995). During these collections, or within a 3-day window of opportunity, water samples were collected and analyzed by the Virginia Department of Environmental Quality (VDEQ) and the Old Dominion University Department of Chemistry for determining the water quality parameters. These include

TABLE 1. Mean Secchi depth, total suspended solids (TSS), total nitrogen (TN), total phosphorus (TP), and surface temperatures (Temp.) for July 1989 to June 2001. A practical salinity scale was used to determine salinity regions: Tidal fresh (TF) stations (<0.5 ppt) are TF5.5 and TF4.2; Oligohaline (Olig.) stations (0.5-5.0 ppt) RET5.2 and TF3.3; Mesohaline (Mes.) stations (>5.0-18 ppt) RET 3.1 and RET4.3 (1989-2001).

Stations	Secchi (m)	TSS (mgL^{-1})	TN (mgL^{-1})	TP (mgL^{-1})	Temp. (°C)
James River					
TF5.5 (TF)	0.53	28.8	1.10	0.100	19.0
RET5.2 (Olig)	0.45	39.7	0.85	0.097	18.3
York/Pamunkey					
TF4.2 (TF)	0.70	16.5	0.71	0.063	18.2
RET4.3 (Mes)	0.50	36.5	0.77	0.098	17.7
Rappahannock					
TF3.3 (Olig)	0.43	38.9	0.89	0.098	18.3
RET3.1 (Mes)	0.42	46.6	0.86	0.090	17.8

total nitrogen (TN), total phosphorus (TP), and total suspended solids (TSS), which are referred to in this study. Secchi depth, water temperature, and salinity measurements were determined on station during plankton collections. The US Geological Survey (USGS) records were the basis of annual river discharge periods in this region.

Data analysis

Average yearly productivity rates were compared between stations using ANOVA and the REGWF post hoc analysis (SPSS for Windows 14.0). To test for a long term trend from 1989 to 2001 and still account for seasonal variability, the data was divided into 3-month seasonal averages (e.g. the spring months as March, April, and May, with summer, autumn, and winter following respectively each in subsequent 3-month segments). A Pearson Correlation analysis was performed for each station between the seasonal productivity averages and years to test the significance of long term trends.

RESULTS

Station relationships

The mean station Secchi depths ranged from 0.53 m to 0.70 m in tidal freshwater (TF), and from 0.42 m to 0.50 m at the oligohaline (Olig) and mesohaline (Mes) stations (Table 1). Seasonally, low Secchi depths and high total suspended solids (TSS) were common during spring which included months of increased precipitation and river flow. In general, average Secchi depths decreased and the TSS increased moving down stream from the tidal freshwater stations. There were generally similar annual mean surface water temperatures at each river station and when comparing the three salinity regions. These were 18.2 & 19.0, 18.0 & 18.3, and 17.7 & 17.8 °C respectively for stations classified in the tidal fresh, oligohaline, and mesohaline regions.

The mean annual TN and TP concentrations for these river segments ranged from 0.71 to 1.10 mg L^{-1} for TN, and 0.063 to 0.100 mg L^{-1} for TP (Table 1). The mean TN and TP levels were greater at tidal freshwater stations in the James R. and Rappahannock R. and decreased downstream. In contrast, TN and TP were lower at the tidal freshwater station (TF4.2) in the Pamunkey R. compared to the downstream mesohaline station (RET4.3) in the York R. The mean TN and TP levels in the Pamunkey R. (TF4.2) were the lowest of the six river stations. In the Rappahannock the oligohaline and mesohaline regions showed little change in TN, TP, and Secchi readings, with TSS increasing downstream. Seasonally, greater nutrient concentrations were associated with winter/spring months and spring rains, however, rainfall and river flow varied annually. The periods of reduced river discharge (dry years) occurred in 1991, 1995, 1999, and 2001, in contrast to years of increased river discharge (wet years) of 1993, 1994, 1996 and 1998 (USGS). Marshall and Burchardt (2003, 2004) reported seasonal changes of phytoplankton development within these rivers were associated with the onset and duration of these wet and dry periods. These relationships included community abundance, a changing community structure, and a seasonal expression of dominant taxa during the year.

TABLE 2. Annual range and averages of river productivity rates from stations from 1989-2001. Tidal freshwater (TF), Oligohaline (Olig). Mesohaline (Mes).

	Range of annual productivity (mg C m^{-3} h^{-1})	Average annual productivity (mg C m^{-3} h^{-1})
Rappahannock River		
TF3.3 (Olig)	38.51-87.33	64.68
RET3.1 (Mes)	28.20-95.66	62.42
Average		63.55
York River		
TF4.2 (TF)	8.93-37.06	19.65
RET4.3 (Mes)	27.58-78.55	52.19
Average		35.92
James River		
TF5.5 (TF)	43.75-132.97	89.70
RET5.2 (Olig)	37.20-172.93	76.79
Average		83.24

Seasonal productivity

The yearly range and 12 year averages of the productivity rates and mean annual productivity at the 6 stations in these rivers are given in Table 2. There were significant differences ($p<0.05$) between stations in yearly average productivity (Fig. 2). The Pamunkey R. TF4.2 had the lowest average productivity of 19.65 mg C m^{-3} h^{1}, while the James R. TF5.5 had the highest average of 89.70 mg C m^{-3} h^{1}. Closer similarity in productivity occurred in the oligohaline sites with a broader range of high productivity extending from mid-spring to mid-autumn. These were 64.68 and 76.79 mg C m^{-3} h^{-1} at stations in the Rappahannock R. (TF3.3) and James R. (RET5.2). In the

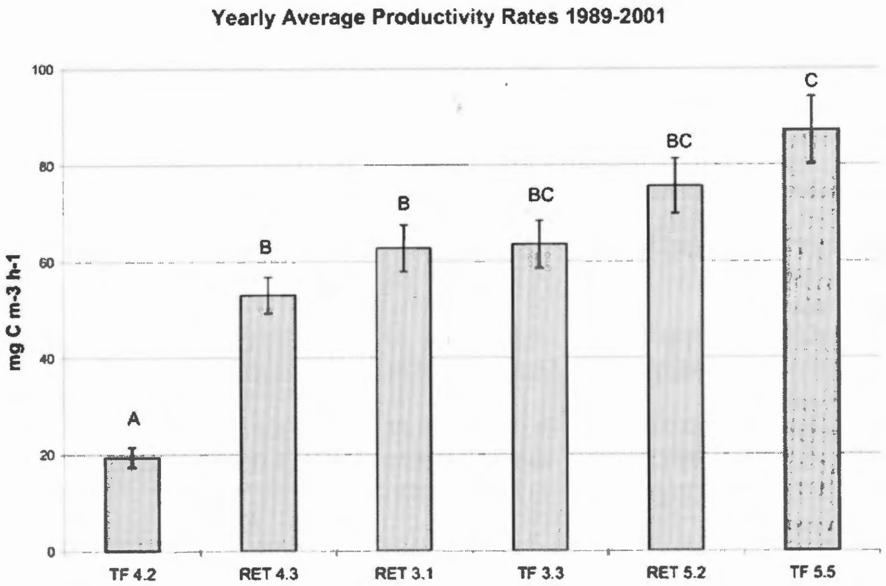

FIGURE 2. Average yearly primary productivity (mg C m^{-3} h^{-1}) of six tributary stations 1989-01. Results of ANOVA post hoc REGWF test identified by letters A-C. Stations in significantly different (α <0.05) groups identified by different letters.

mesohaline, the average yearly productivity rates for the Rappahannock R. (RET3.1) and York R. (RET4.3) were 62.42 and 52.19 mg C m^{-3} h^{-1} respectively. Monthly productivity rates increased from winter into spring and summer; then declined during autumn into winter (Figs. 3-5).

These river patterns showed mean productivity decreased slightly downstream in the James R. and Rappahannock R., but increased from the Pamunkey to the York R. Decreasing productivity was associated with increased total suspended solids and lower Secchi depths moving from the tidal freshwater to mesohaline regions. These conditions and productivity levels were likely influenced by the degree of river flow and subsequent entry of nutrients, light availability, and suspended solids carried in these waters. Such variability in flow and its influence on productivity would be expected, and this influence is generally recognized in long-term studies. For instance, compared to what is considered normal flow years (4), there were 4 years of high and 4 years of low river discharge interspaced during the 12 years of this study.

Monthly productivity

The mean monthly productivity rates at each of these stations are given in Figs. 3-5. Although these varied, the lowest productivity occurred during winter, with increased productivity often beginning in late winter, and continuing to reach highest levels during spring, summer, or early autumn. The mean monthly productivity among the stations seasonally varied over a wide range of values. In the James R. these were from 9.03 to 175.12 mg C m^{-3} h^{-1} at TF 5.5 for January and July, and 16.28 to 133.58 mg C

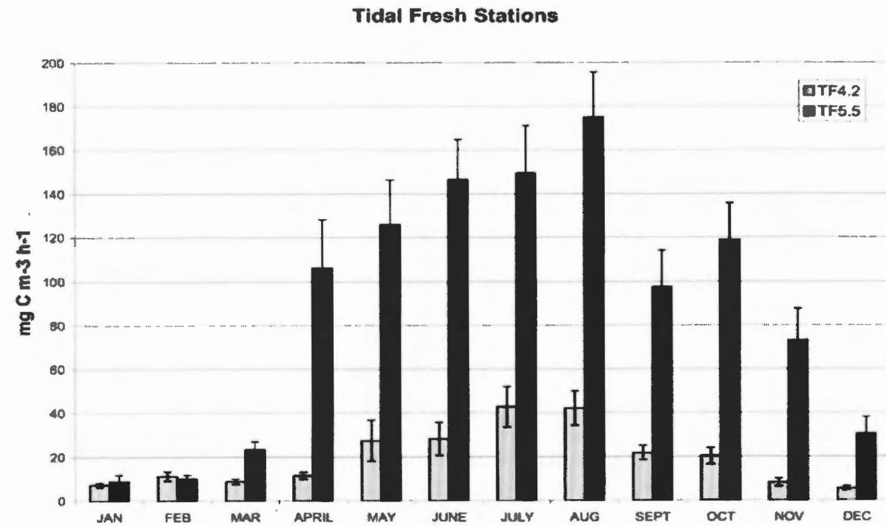

FIGURE 3. Average monthly productivity (mg C m^{-3} h^{-1}) for tidal freshwater stations 1989-2001, (Pamunkey River station TF4.2, and James River station TF5.5).

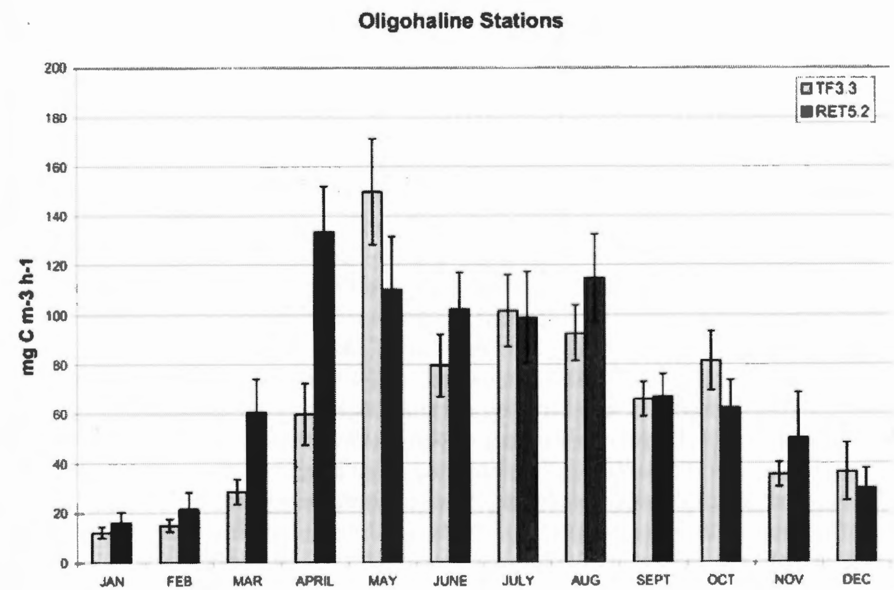

FIGURE 4. Average monthly productivity (mg C m^{-3} h^{-1}) for oligohaline stations 1989-2001, (Rappahannock River station TF3.3, and James River station RET5.2).

$m^{-3} h^{-1}$ at RET 5.2 for January and April. The Pamunkey/York R. monthly productivity means were from 5.52 to 42.94 mg C $m^{-3} h^{-1}$ at TF 4.2, for December and July, and 16.26 to 94.73 mg C $m^{-3} h^{-1}$ for January and March at RET 4.3. The greatest range in monthly means occurred between January and May at both stations in the Rappahannock R., with rates from 12.21 to 149.90 mg C $m^{-3} h^{-1}$ at TF 3.3, and from 19.92 to 151.33 mg C $m^{-3} h^{-1}$ at RET 3.1.

Annual productivity

Subsequent conversion of the productivity rates to estimates of total annual production indicates a range from the least productive site in the Pamunkey R. (TF4.2) at ca. 49 g C $m^{-2} yr^{-1}$, and the highest in the James R. (TF5.5), at ca. 230 g C $m^{-2} yr^{-1}$. The annual production varied from ca. 159 to 190 g C $m^{-2} yr^{-1}$ for the oligohaline and 126 to 153 g C $m^{-2} yr^{-1}$ in mesohaline waters. Results from the initial 2 year segment of this study were reported by Marshall and Nesius (1993) and which also included stations bordering the Chesapeake Bay. When comparing these 2 year productivity means to the 12 year averages at similar stations they show both comparable and widely different rates. Similar values of least productivity occurred in the Pamunkey R., with highest productivity in the James R. However, mean production varied from 298.9 to 190 g C $m^{-2} yr^{-1}$ at RET5.2 (James R.), and 109.2 to 153 g C $m^{-2} yr^{-1}$ at RET3.1 (Rappahannock R.), for the earlier and present study respectively. More consistent was the productivity at the Pamunkey R. station TF4.2, with the rates of 44.7 and 49 g C $m^{-2} yr^{-1}$ in comparison. These results over the longer period of analysis produced a more representative appraisal of productivity in these rivers compared to the shorter period (1-2 yrs) of study.

Trends

Over the 12 year period of this study (1989-2001), significant long term decreasing trends were present at four of the six stations, occurring in spring, summer, and autumn, with none during winter (Table 3). In spring, these were at the tidal fresh Pamunkey R. station (TF4.2) and the oligohaline site of the James R. (RET5.2). However, productivity had the largest reduction in terms of degree and number of stations affected during the summer season. These occurred in both tidal fresh (TF4.2) and mesohaline (RET4.3) sites in the Pamunkey/York R. series, and the oligohaline stations in the Rappahannock R. (TF3.3) and James R. (RET5.2). The two decreasing trends in autumn were in the tidal fresh Pamunkey R. (TF4.2) and the mesohaline York R. (RET4.3). No trends were noted at the tidal fresh station in the James R. (TF5.5), or at the Rappahannock R. mesohaline station (RET3.1). Although not significant at $\alpha = 0.05$ level, stations TF5.5 and RET4.3 had increasing long term trends during winter, and these represented the only increasing trends in productivity for the period analyzed. Using the combined seasonal data set, the tidal fresh station in the Pamunkey (TF4.2) and the oligohaline stations in the Rappahannock (TF3.3) and James (RET5.2) rivers had significant annual trends which indicated decreasing productivity. The largest number of seasonal decreasing productivity trends occurred in this fresh station in the Pamunkey R. and the oligohaline station in the James R. These decreasing trends were accompanied by mean Secchi readings of generally < 1 m, and increasing TSS downstream.

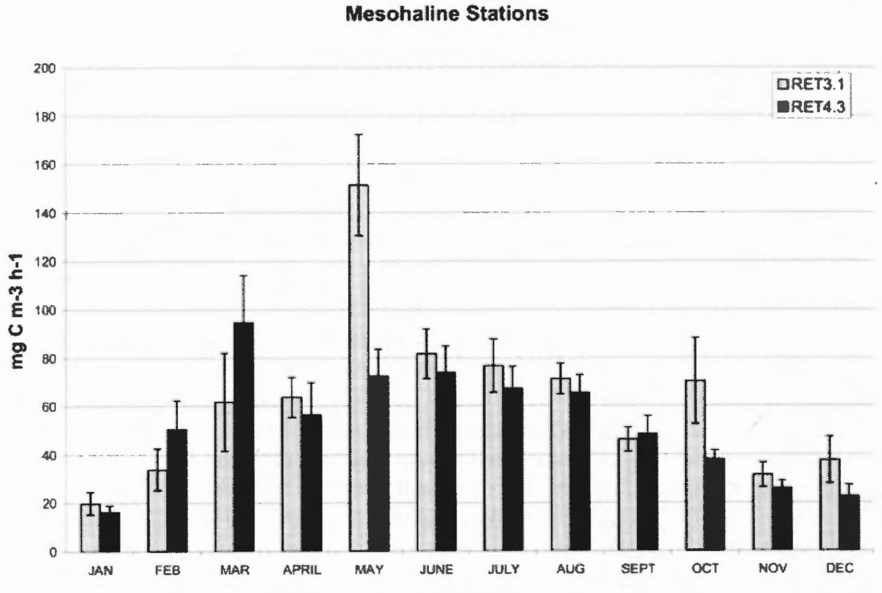

FIGURE 5. Average monthly productivity (mg C $m^{-3} h^{-1}$) for mesohaline stations 1989-2001, (Rappahannock River station RET3.1, and James River station RET4.3).

Associated phytoplankton

Peak algal productivity occurred from mid-spring to early autumn, and coincided with the periods of maximum phytoplankton abundance. The river stations contained a diverse representation of taxa characterized by seasonal succession patterns and a changing species assemblage, with other algae ubiquitous throughout the year. These transitions begin with the spring bloom of diatoms, followed by a summer assortment of diatoms, cyanobacteria, and chlorophytes. In tidal freshwater the dominant diatoms were *Skeletonema potamos* (Weber) Hasle, *Asterionella formosa* Hass., *Aulacoseira granulata* (Her.) Sim., *Cyclotella meneghiniana* Kütz., *Cyclotella striata* (Kütz) Grun., and a variety of small pennates. A diverse composition of cyanobacteria (e.g. *Microcystis aeruginosa, Chroococcus* spp., *Merismopedia* spp.), chlorophytes (*Ankistrodesmus falcatus*, *Scenedesmus* spp.), and cryptophytes (*Cryptomonas erosa*) were also present. In addition to these taxa the oligohaline and mesohaline regions contained an increase in abundance of estuarine diatoms that included *Skeletonema costatum* (Greville) Cleve, *Cerataulina pelagica* (Cleve) Hendy, *Leptocylindrus minimus* Gran, *Thalassionema nitzschioides* (Grun.) Grun., and several *Cyclotella* spp. Dinoflagellates were more common downstream in late spring, including high concentrations of *Prorocentrum minimum* (Pavillard) Schiller, *Heterocapsa triquetra* (Ehr.) Stein, and *Heterocapsa rotundata* (Lohmann) Hansen. The most ubiquitous components throughout the year were autotrophic picoplankton. They represented a major contributor to the summer productivity maximum in each river (Marshall and Nesius 1998), and were composed predominantly of isolated or colonial cyanobacteria,

TABLE 3. Results of Pearson Correlation analysis comparing seasonal productivity rates for years 1989-2001. Slope indicates direction (negative denotes decreasing) and amplitude of trend. Significant trends indicated by bold font.

Spring (n=36)

	Station	Slope	R^2	Significance
Tidal Fresh	TF4.2	-2.40	0.135	**0.028**
	TF5.5	-6.27	0.073	0.112
Oligohaline	TF3.3	-2.80	0.016	0.460
	RET5.2	-6.95	0.098	**0.039**
Mesohaline	RET3.1	-2.41	0.011	0.541
	RET4.3	-2.07	0.014	0.491

Summer (n=36)

	Station	Slope	R^2	Significance
Tidal Fresh	TF4.2	-3.70	0.150	**0.020**
	TF5.5	-6.82	0.086	0.082
Oligohaline	TF3.3	-6.18	0.176	**0.011**
	RET5.2	-14.70	0.588	**0.000**
Mesohaline	RET3.1	-3.48	0.107	0.052
	RET4.3	-6.02	0.342	**0.000**

Autumn (n=36)

	Station	Slope	R^2	Significance
Tidal Fresh	TF4.2	-1.34	0.115	**0.043**
	TF5.5	-1.06	0.003	0.737
Oligohaline	TF3.3	-1.06	0.009	0.588
	RET5.2	-9.70	0.404	**0.000**
Mesohaline	RET3.1	-1.41	0.011	0.550
	RET4.3	-2.21	0.115	**0.044**

Winter (n=36)

	Station	Slope	R^2	Significance
Tidal Fresh	TF4.2	-0.56	0.103	0.056
	TF5.5	1.81	0.104	0.054
Oligohaline	TF3.3	-0.84	0.010	0.562
	RET5.2	-1.16	0.024	0.368
Mesohaline	RET3.1	-1.59	0.029	0.331
	RET4.3	2.76	0.084	0.087

Yearly (n=144)

	Station	Slope	R^2	Significance
Tidal Fresh	TF4.2	-0.0056	0.0869	**0.000**
	TF5.5	-0.0091	0.0193	0.064
Oligohaline	TF3.3	-0.0075	0.026	**0.041**
	RET5.2	-0.0223	0.1723	**0.000**
Mesohaline	RET3.1	-0.0057	0.0157	0.143
	RET4.3	-0.0049	0.019	0.140

Bold= Significance at < 0.05 level

in addition to lesser numbers of eukaryotes. Their development and contribution to total production in these rivers increased during periods of reduced river flow and greater residency time associated with late summer and early autumn (Marshall and Burchardt 1998). A diverse phytoplankton assemblage characterized the summer and autumn flora, with major representation by diatoms, cyanobacteria, chlorophytes, dinoflagellates, and cryptophytes. The lower concentrations during winter were mainly dominated by diatoms, which continued to increase into the spring diatom bloom

(Marshall and Burchardt 2003, 2004). The primary algal biomass and carbon producers in these rivers were diatoms throughout the year, with a variety of eukaryote and prokaryote taxa in abundance and composition. These changing and diverse populations were collectively responsible for often variable monthly productivity levels that occurred within these waters.

DISCUSSION

Phytoplankton productivity within river systems is known to vary seasonally and inter-annually (e.g. Admiraal et al. 1994; Cole and Cloern 1984, 1987; Dokulil 1994; Malone 1976; Joint and Pomeroy 1981; Peterson and Festa 1984). The productivity and species composition will also be influenced by a variety of conditions including differences associated with light availability, nutrient concentrations, residency time and degree of river flow, among combinations with other factors (Peterson et al. 1985; Jassby et al. 2002; Lehman 1992, 2000; Sellers and Bukaveckas 2003). The common pattern in temperate regions is for lower productivity during winter, with increased productivity associated with spring, summer and autumn. The estimated mean annual 12 year productivity for the different Virginia river sites in this study ranged from 49 g C m^{-2} yr^{-1} to 230 g C m^{-2} yr^{-1}. In comparison, Boynton et al. (1982) reviewed the primary production at 43 estuarine sites (North Carolina, USA) and reported a mean value of 190 g C m^{-2} yr^{-1}. Further regional comparisons from North Carolina in the Neuse River include a 4-year study by Boyer et al. (1993), with productivity ranging from 395 to 493 g C m^{-2} yr^{-1}. In a 2-year study in the lower River Spree (Germany), Köhler (1995) indicated station rates of 310-358 g C m^{-2} yr^{-1}, whereas, Jassby et al. (2002) in a 9 year monthly study for the Sacromento-San Joaquin River (California) gave an annual production range of 39-131 g C m^{-2} yr^{-1} and a mean of 70 g C m^{-2} yr^{-1}. They also noted seasonal differences and stress the importance of extended studies for obtaining a more accurate appraisal of annual productivity within aquatic systems. For example, the seasonal productivity in the Loire River estuary (France) was given by Relexans et al. (1988) as between <0.1 to 1.6-7.3 g C m^{-2} day^{-1} for winter and summer months respectively. A wide productivity range would also be expected with different site locations within an estuary as was noted from 32 North Carolina estuarine locations with rates that ranged from 16 to 153 g C m^{-2} y^{-1} (Thayer 1971). In their study of the Neuse River (North Carolina) Mallin and Paerl (1992) stress the influence of seasonal and daily mixing patterns within a river's water column (river flow, tidal periods, etc.) that would effect turnover conditions, light attenuation and re-suspension of substances and their influence to algal productivity. In another study of a Chesapeake Bay tributary, Stross and Stottlmyer (1966) sampled stations in the Patuxent River (Maryland, USA), and reported primary productivity between 384.8 to 647.2 g C m^{-2} yr^{-1}. In another comparison, the Gun Powder River (Maryland, USA) had a range of 3.1 to 142.4 mg C m^{-3} h^{-1} (Sellner 1983), whereas, Köhler (1995) reported a mean 2-year value of ca. 58.6 mg C m^{-3} h^{-1} in the River Spree (Germany). The Virginia river stations had annual mean values that ranged from 19.6 to 89.70 mg C m^{-3} h^{-1} (Table 2).

Compared to other river and estuarine locations, the productivity results from the Virginia rivers were generally comparable, but not grossly higher, or characteristic of increased eutrophic status. However, these results were applicable to this 12 year period, and with future single year, or more extended periods of study (and changes in trophic status) the productivity may likely vary in degree and possibly direction. For example, this long-term data base included years of variable rainfall within the individual watersheds and subsequent flow within these rivers. These events and accompanying conditions will vary in future years, but continue to influence the structure of the phytoplankton composition and their productivity in these rivers. Although intrinsic differences were present within each watershed and tidal sections of these rivers, the general seasonal expression of phytoplankton development and productivity followed similar developmental patterns for the region. The results also indicated the value of long-term monitoring studies to more accurately characterize specific productivity dynamics in these estuarine habitats.

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