College of Humanities and Sciences
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This is to certify that the thesis prepared by Laura E. Barry entitled ZOOPLANKTON ABUNDANCE, COMMUNITY COMPOSITION AND GRAZING IN THE JAMES RIVER ESTUARY (VIRGINIA, USA) has been approved by his or her committee as satisfactory completion of the thesis requirement for the degree of Master of Science (Biology).

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ZOOPLANKTON ABUNDANCE, COMMUNITY COMPOSITION AND GRAZING IN THE JAMES RIVER ESTUARY (VIRGINIA, USA)

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

by

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Abstract

ZOOPLANKTON ABUNDANCE, COMMUNITY COMPOSITION AND GRAZING IN THE JAMES RIVER ESTUARY (VIRGINIA, USA)

By Laura E. Barry, B.A.

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

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This study examined the extent to which zooplankton in the James River Estuary (Virginia, USA) exploit the available algal-food resources. Zooplankton abundance, community composition and grazing rates were assessed at three locations which included a site with high algal production (near the VCU Rice Center) and two sites where algal production was lower. Grazing rates were measured by determining the rate of phytoplankton decline (as chlorophyll *a*) during 48-hour incubation experiments in the presence and absence of zooplankton. Significant differences in zooplankton abundance were observed among the three sites, with the greatest average zooplankton density (434 ±

69.04 ind/L) occurring at the phytoplankton maxima. There were no significant differences in zooplankton filtration or ingestion rates among the three sites. The amount of chlorophyll *a* consumed was low at all sites (< 5%), suggesting that only a small proportion of primary production was directly passed to higher trophic levels. Low grazing rates were attributed to poor food quality owing to the presence of non-algal particulate matter and a predominance of cyanobacteria comprising the phytoplankton community. These findings are consistent with prior studies showing that cyanobacteria are a poor quality food source for zooplankton and that non-algal particulates may interfere with grazing rates. Further, this study lends support to the hypothesis that food quality is an important determinant of trophic transfer efficiency in aquatic food webs.

Introduction

Consumers face variability in the quantity and quality of food resources within their environment (Soetaert & Rijswijk 1993; Kim *et al.* 2000, Islam *et al.* 2005; Lampman *et al.* 2005; Lehman 2007; Murrell *et al.* 2007; Hoffman *et al.* 2008). This variability has implications for understanding trophic level production and energy transfer between trophic levels (Griffin and Rippingale 2001; Cuker & Watson 2002; David *et al.* 2006; Kimmel *et al.* 2006; Lehman 2007). The ability of consumers to exploit food resources determines the proportion of available production that is transferred upwards (Gosselain *et al*. 1998; Griffin and Rippingale 2001; Cuker & Watson 2002; Kimmerer 2002; Murrell *et al*. 2002; Tackx *et al.* 2003; Lionard *et al*. 2005; Azemar *et al.* 2007). In aquatic systems, zooplankton serve as a key link between phytoplankton production and higher trophic levels (*i.e.* fish) (Soetaert & Rijswijk 1993; Kimmel *et al.* 2006; Lehman 2007; Hoffman *et al.* 2008). Understanding trophic transfer efficiency is one of the reasons for continued interest in zooplankton grazing and its impact on and exploitation of phytoplankton production (Soetaert & Rijswijk 1993; Park & Marshall 2000; Kimmerer 2002; David *et al.* 2006; Lair 2006; Hoffman *et al.* 2008).

Consumers respond to variation in both the quantity and quality of food resources (Sellner *et al.* 1993; Kim *et al.* 2000; Cambell *et al.* 2001; Boersma and Kreutzer 2002;

Acharya *et al*. 2006; Hoffman *et al.* 2008). For zooplankton, food quantity is based on the amount of available phytoplankton and allochthonous matter in the water column (Hoffman *et al.* 2008). Food quality is determined by multiple factors including the proportion of phytoplankton relative to non-algal particulate matter (Tackx *et al.* 2003; Hoffman *et al.* 2008), the palatability of the available phytoplankton (Sellner *et al.* 1993; Pietsch *et al.* 2001; Rohrlack *et al.* 2005) and the size of the food particles (Burkill & Kendall 1982). Both food quantity and quality affect zooplankton production (Cambell *et al.* 2001; Boersma and Kreutzer 2002; Tackx *et al.* 2003; Acharya *et al*. 2005; Acharya *et al*. 2006). For example, Islam *et al.* (2005) found that zooplankton production in the lower Chikugo estuary was greater than in the upper estuary due to greater phytoplankton contributions which improved food quality.

Aquatic environments are often characterized by variation in food quantity and quality arising in part from spatially-variable rates of phytoplankton production (Tackx *et al.* 2003; Marshall *et al.* 2009). In lakes, phytoplankton production varies along a vertical (depth) gradient whereas in estuaries, it varies along a longitudinal gradient (Sellner *et al.* 1993; Murrell and Lores 2004; Islam *et al.* 2005; Lehman 2007; Murrell *et al.* 2007). In estuaries, a zone of maximum production is often observed at a mid-point where turbid, nutrient-rich river water mixes with clear, nutrient-poor marine water (Kim *et al.* 2000; Roman *et al.* 2001; Murrell *et al.* 2007). The transition from light limiting to nutrient limiting conditions favors high rates of phytoplankton production. The estuarine transition zone is often associated with increased turbidity (Soetaert & Rijswijk 1993; Islam *et al.* 2005; Lehman 2007), zooplankton abundance (Soetaert & Herman 1994; Kim *et al.* 2000;

Rossetti *et al.* 2009), and juvenile fish production (Soetaert & Rijswijk 1993; Roman *et al.* 2001).

In this study, I examined zooplankton exploitation of food resources in the zone of maximum phytoplankton production in the James River Estuary (Virginia, U.S.A.). To assess the level of exploitation, zooplankton abundance, community composition and grazing rates were quantified at three sites located along a longitudinal gradient in the James River estuary. Spatial variation in abundance, community composition and grazing rates were evaluated by comparing sampling locations landward and seaward of the zone of peak phytoplankton production. I hypothesized that the high phytoplankton production at the chlorophyll *a* maxima would result in greater exploitation by zooplankton via increased abundance and grazing relative to sites landward and seaward of the maximum production zone.

Methods and Materials

Study Sites and Sampling Design

This study was conducted from June to November 2007 when the estuary was warm, river discharge was low and phytoplankton abundance was at its maximum. This combination of environmental factors is favorable for zooplankton production. The community was evaluated at three sites located at navigational river miles 99, 75 and 21 (hereafter designated as James River Mile (JRM); Figure 1). These sites were chosen to capture the range of zooplankton community types and food resource conditions occurring within the estuary. JRM 99 and 75 are within the tidal-freshwater segment of the estuary. JRM 99 is located below the city of Richmond, Virginia. This segment of the estuary is characterized by short transit times, a deep, narrow channel and low levels of phytoplankton abundance (Lederer 2008). JRM 75, located near Hopewell, Virginia and the VCU Rice Center, is characterized by a deep main channel with shallow lateral areas. This site characteristically exhibits high levels of phytoplankton abundance due to greater light availability, longer water residence time and elevated nutrient concentrations (Lederer 2008). JRM 21 is located near Newport News, Virginia in the mesohaline segment of the estuary (mean salinity = 12.8‰) where nutrient concentrations and phytoplankton abundance are low. Long-term monitoring data for these sites were available through the

Virginia Department of Environmental Quality (VADEQ) Chesapeake Bay Program (CBP). Additionally, historical zooplankton abundance and community composition data were available for JRM 75 during the years 2000-2002 through the CBP.

Zooplankton were sampled from one meter below the surface using a hand pump to collect the water which was then filtered through a 63 μm plankton net. Forty liters of water were collected for each of three replicate samples. The samples were fixed in the field with a 12% formaldehyde solution. Zooplankton samples were stained with Rose Bengal solution to aid in identification. Animals were enumerated to their lowest identifiable taxonomic level using Thorp and Covich (2001). The results of these counts were reported as number of animals per liter. *In situ* salinity, temperature, dissolved oxygen, and pH were measured at the time of sample collection using a Hydrolab Multiprobe Minisonde 4a.

Water samples were collected to characterize food resources based on the amount of total suspended solids (TSS), chlorophyll *a*, and the carbon and nitrogen content of suspended particulate matter. Chlorophyll *a* samples were filtered through Whatman GF/A glass filters and placed in a freezer with an acetone/buffer solution for 18 hours prior to analysis on a Turner Design TD-700 Fluorometer (Lederer 2008). The carbon and nitrogen content of suspended particulate matter was determined using a Perkin-Elmer CHN Analyzer. TSS was determined gravimetrically using pre-weighed, pre-combusted filters.

Grazing Rates

Zooplankton grazing was measured in the laboratory using one liter cultures containing natural phytoplankton and zooplankton communities collected at each of the three sites. Grazing rates were determined by comparing the rate of phytoplankton decline in the presence and absence of grazers (*sensu* Frost 1972). Changes in phytoplankton abundance during the 48 hour experiments were quantified by measuring chlorophyll *a* at the beginning and end of the incubation period. The difference in the rate of decline in chlorophyll *a* between enclosures with and without grazers represented the amount ingested by the zooplankton. Ingestion rates were measured for both total chlorophyll *a* and the less than 20 μm fraction to assess feeding selectivity. Ingestion rates of particulate organic carbon (POC) and total suspended solids (TSS) were also measured to assess selectivity for phytoplankton relative to other organic particulates and to total particulates, respectively. Zooplankton abundances were determined at the start and end of the incubation so that grazing rates could be expressed per capita. These per capita rates were used in conjunction with zooplankton densities measured at each of the sampling locations to infer *in situ* grazing rates.

A total of eight grazing experiments were performed among the three sites. Three experiments were run using seston and zooplankton from the site with relatively high chlorophyll *a* concentrations (JRM 75) and five experiments were run using seston and zooplankton from sites with lower chlorophyll *a* concentrations (JRM 21 and JRM 99). Before the start of the experiment, water collected from each site was filtered through 63 μm Nitex screening to remove zooplankton and the inedible seston fraction (Burkill &

Kendall 1982). For each experiment, zooplankton were separated into three size classes consisting of macrozooplankton (>210 μm), mesozooplankton (63-210 μm) and microzooplankton (20-63 μm). The animals were separated using a descending series of Nitex screening until the desired fractions were obtained. Incubating these size classes separately allowed for the determination of their relative contribution to community grazing rates. Three replicates were used for each size fraction resulting in a total of 9 grazing enclosures per experiment. The enclosures were incubated in dark one liter polycarbonate bottles for 48 hours in a Conviron Growth Chamber at the river temperature, as measured at the time of collection. The bottles were rotated every 12 hours to ensure the suspension of the particulate matter. Six bottles without zooplankton were simultaneously incubated in the same manner to measure the loss rate of chlorophyll *a* in the absence of grazers. At the end of the incubation period, the zooplankton were removed by filtering through Nitex screening. The animals were counted and identified to determine abundance and species composition using the same procedures as for samples collected from the estuary. Subsequent analysis of the microzooplankton fraction revealed this group had significantly lower (ANOVA, $n=72$, $p<0.01$) grazing rates than the two larger fractions. Considering this, and the taxonomic challenges of enumerating the very small zooplankton, it was decided to focus the study on the two larger size fractions.

Grazing Rate Calculations

The grazing rate was calculated using the method outlined by Frost (1972). The phytoplankton growth rate (k) in the absence of grazers was calculated as:

$$k = \ln (C_{48}/C_0)/t$$

where C_{48} was the chlorophyll *a* concentration after 48 hours, C_0 was the initial chlorophyll *a* concentration and t was the incubation time. Note that in these experiments, the phytoplankton growth rate was negative because the enclosures are incubated in the dark. This was to prevent differences in phytoplankton growth rates between control and grazer enclosures due to nutrient recycling by zooplankton. The grazing coefficient (g) was calculated as:

$$g = - (\ln (C_{48}/C_0) + k)/t$$

where C_{48} and C_0 represented the final and initial chlorophyll concentrations, respectively, measured in enclosures with grazers. The grazing coefficient therefore represented the additional mortality experienced by phytoplankton in enclosures where grazers were present. The per capita ingestion rate within the enclosures (I_e) was calculated as:

$$I_e = (g \times C_e)/Z_e$$

where C_e and Z_e were the average of initial and final chlorophyll *a* concentrations and zooplankton densities during the incubation. The ingestion rate was expressed as mass of particulate matter (*i.e.* chlorophyll *a*, POC or TSS) consumed by an individual per unit of time (*i.e.* µg chl *a*/d).

The filtration rate represented the 'volume swept clear' (*sensu* Frost 1972) and was expressed as the volume of water an animal would have to filter in one day (*i.e.* mL/d) in order to attain a given ingestion rate. The per capita filtration rate (F_e) was calculated as:

$$F_e = I_e/C_e$$

These per capita rates were multiplied by zooplankton densities measured at each of the sampling locations to estimate the *in situ* community ingestion and community filtration rates expressed as percentage chlorophyll *a* ingested per day and percent volume filtered per day.

Statistical Analyses

A one-way ANOVA (α=0.05) was used to determine whether inter-site differences in food resource conditions (chlorophyll *a*, TSS, POC, PON) were statistically significant. A one-way nested ANOVA (α=0.05) was used to determine if differences existed between number and types of zooplankton at the three sites. In this model, date was nested within site to increase the test's power. Regression analyses were used to determine whether chlorophyll *a* was a significant predictor of zooplankton abundance. One-way ANOVAs (α=0.05) were used to determine if differences existed between the per capita filtration, community filtration and community ingestion rates among sites. The tests were run for the animal size fractions 63-210 μm and >210 μm and for chlorophyll *a* fractions <20 μm and total. Zooplankton densities measured in this study were compared with prior data (VADEQ Chesapeake Bay Program) to assess whether abundances observed during this study were within historical expectations. During the year 2000-2002, the bay monitoring program collected monthly zooplankton samples at river mile 75, 42, and 0 using a 200 μm tow net. The historical data were averaged for June through August in each of the three years to compare with data from our study. Finally, the feeding rates of zooplankton on

chlorophyll *a* <20 μm, total chlorophyll *a*, total suspended solids, and particulate organic carbon were compared using a one-way ANOVA test (α=0.05).

Results

Water Quality and Food Resources

Differences in water quality among the three sites followed expected trends based on site location (Table 1). Salinity at JRM 21 (mean= 12.8 ‰) was higher than at JRM 99 or 75 (mean = 0.01 ‰ for both) as would be expected based on its proximity to the Chesapeake Bay. JRM 75 occurs within the Estuarine Turbidity Maximum (mean = 18.0 NTU) whereas JRM 99 and 21 are above and below, respectively, the Estuary Turbidity Maximum (mean = 9.6 and 10.5 NTU, respectively). Water temperature during the study was similar at all three sites with average values ranging from 26-29ºC. Mean dissolved oxygen at all sites was above 5.0 mg/L indicating well-oxygenated conditions within the surface layer. The pH at the three sites ranged from 7.5 to 8.4.

Zooplankton food resources (*i.e.* chlorophyll *a* and suspended particulate matter) varied significantly among the three sites (Figure 2). The highest average chlorophyll *a* concentration was observed at JRM 75 (mean= 71.2 μg/L) followed by JRM 99 (mean= 12.7 μg/L) and JRM 21 (mean= 10.4 μg/L). Chlorophyll *a* concentrations at JRM 75 were consistently higher than the other two sites and inter-site differences were statistically significant ($p<0.01$; Table 2). The quantity of suspended solids was lowest at JRM 99 (mean= 6.27 mg/L). TSS levels at JRM 75 and 21 (mean= 22.5 mg/L and 27.6 mg/L) were

significantly higher (p= 0.01). Average concentrations of particulate organic carbon (POC) and nitrogen (PON) were also significantly higher at JRM 75 (mean= 2.93 mg/L and 0.53 mg/L, respectively) than at JRM 99 and 21 ($p<0.01$). JRM 75 consistently had between double and triple the POC and PON than the other two locations. There were no significant differences in the percentage of carbon or nitrogen in particulate matter among the three study sites (p= 0.11 and p= 0.17, respectively).

Zooplankton Abundance and Community Composition

JRM 75 had the highest average density of zooplankton (434 ind/L) followed by JRM 99 (274 ind/L) and JRM 21 (92.5 ind/L). Differences among the three sites were statistically significant ($p<0.01$) with 'site' accounting for 84% of the variation in density. Community composition was dominated by small-bodied animals (63-210 μm; Figure 3). Rotifers, primarily *Brachionus* spp. (57% - 90% of all rotifers), and copepod nauplii constituted most of the animals identified at JRM 99 and 75. Nauplii and barnacle larvae dominated the community at JRM 21. The number of rotifers found at JRM 99 and 75 was significantly higher than the number found at JRM 21 ($p<0.01$, Table 3). There were also significant differences in the abundance of copepod nauplii at each station ($p<0.01$). JRM 75 had the highest mean number of nauplii (73 ind/L) followed by JRM 21 (mean= 38 ind/L) and JRM 99 (mean= 6 ind/L). Cladocerans, primarily *Bosmina longirostris (*55% - 86% of total cladocerans), had highest abundance at JRM 75 (mean= 19 ind/L) and were significantly more abundant than at either JRM 99 (mean = 5 ind/L) or JRM 21 (none found). The calanoids found at JRM 99 and 75 (mean = < 1 ind/L and 2 ind/L,

respectively) were mostly *Eurytemora affinis* (>90%) whereas the calanoids at JRM 21 (mean = 24 ind/L), were exclusively composed of *Acartia tonsa*. The calanoid density at JRM 21 was significantly higher than at JRM 99 or 75 ($p<0.01$). The highest cyclopoid density was at JRM 75 (mean= 6 ind/L) with lower densities observed at JRM 21 (mean = 4 ind/L) and JRM 99 (mean= 1 ind/L). Barnacle larvae were only found at JRM 21 but were among the dominant zooplankton at this site (mean= 24 ind/L).

To assess the relationship between zooplankton abundance and phytoplankton abundance, zooplankton densities were regressed against chlorophyll *a*. These regressions revealed that densities for four of the major taxonomic groups were correlated with chlorophyll *a* (Figure 4). Nauplii abundance was the most strongly correlated with chlorophyll *a* ($p<0.01$, $R^2=0.42$) followed by calanoids and cyclopoids ($R^2= 0.50$ and $R^2= 0.42$, respectively). Cladoceran abundances were not related to chlorophyll *a* ($p=0.10$, $R^2= 0.28$). Rotifer densities were not significantly related to chlorophyll *a* and because rotifers comprised the majority of zooplankton abundance, total densities were also not correlated with chlorophyll *a*.

Grazing Rates

Per capita filtration rates of macrozooplankton (>210 μm) averaged 1.5 mL/ind/d and were not significantly different among the three sites ($p= 0.5$; Figure 5). Per capita filtration rates of mesozooplankton (63-210 μm) were ten-fold lower than for macrozooplankton (mean= 0.17 mL/ind/d) and also did not differ among sites ($p= 0.34$; Table 4 and 5). Per capita ingestion rates followed the same pattern with the >210 μm

animal fraction ingesting (mean= 0.013 μg chl *a*/ind/d) more than the 63-210 μm fraction (mean= 0.001 μg chl *a*/ind/d). Despite their low per capita rates, total grazing rates by the smaller size fraction were comparable to those of the larger size fraction owing to their higher densities (Figure 6). On average, the community ingestion rate was greater for the smaller size fraction (mean= 0.21 μg chl *a*/L/d) relative to the large size fraction (mean= 0.09 μg chl *a*/L/d; Table 4 and 5). At one site (JRM 99) the mean community filtration for the 63-210 μm animals (3.8 % vol/day) exceeded the mean filtration of the >210 μm fraction (mean= 1.8 % vol/day). There were no significant differences in community filtration or ingestion rates among the study locations for either the mesozooplankton or macrozooplankton communities (Table 4 and 5).

Zooplankton grazing rates on chlorophyll *a*, POC, and TSS were compared to assess feeding selectivity. A one-way ANOVA test revealed significant differences in ingestion rates among the dietary components suggesting that zooplankton were feeding selectively ($p < 0.01$). Ingestion rates for the small algal size fraction (chlorophyll *a* <20 μm) were consistently higher than ingestions rates of total chlorophyll *a*, POC and TSS (see Figure 7; note points are above 1:1 ratio line). The animals selected chlorophyll *a* bearing particles <20 μm in size over all other particles.

Discussion

The purpose of this study was to assess the extent to which zooplankton exploit food resources within a zone of high algal abundance in the James River estuary. It was expected that zooplankton abundance and grazing would increase in response to greater food resources at the estuary's chlorophyll *a* maxima. The results only partially supported this hypothesis. There were significantly more animals at the site of the chlorophyll *a* maxima (JRM 75) compared to the two other sampling locations. However, grazing rates at JRM 75 were low and not significantly different from the other sites. The ability of zooplankton to exploit the food resources at the chlorophyll *a* maxima may have been constrained by either resource-related (*e.g.,* food quality) or non-resource factors (*e.g.,* residence time, predation). The following discussion presents suggestions as to why zooplankton abundance was correlated with food resources while grazing rates were not.

Low grazing rates could potentially arise if methodological issues resulted in an under-estimation of *in situ* densities or if actual abundances were unusually low during the period of study. The abundance and composition of zooplankton observed in this study were similar to previously reported values for the James River estuary. The summer (June-August) abundance averages were compared to Chesapeake Bay Program summer data for

2000-2002 (Figure 8). The two studies report similar abundances of cladocerans and calanoids. However, more nauplii, cyclopoids, and barnacle larvae were found during my (2007) study. Differences in densities of these small-bodied animals can be attributed to differences in sampling equipment given the large mesh size used to collect the animals for the CBP study (200 μm) relative to my study (63 μm). Rotifer abundances could not be compared directly because the CBP study did not enumerate this phylum. However, Park and Marshall (2000) reported rotifer densities in the James River estuary during 1994 and 1995. Their annual rotifer densities at the site of the chlorophyll *a* maxima (JRM 75) (mean= 675 ± 157 ind/L) were larger than the mean density in this study for the same location (mean= 333 ± 67.4 ind/L). However, Park and Marshall (2000) noted that the rotifer abundances during the summer of 1994 had a peak that was not present in 1995 which increased the annual mean density. Overall, the abundance and community composition observed in this study were generally similar to previously reported values for this site. This similarity indicates that the low grazing rates obtained in my study were not a result of under-estimating zooplankton densities due to methodology or unusually low densities during the study period. Following is a consideration of some factors that may explain why grazing rates were low.

Low grazing rates may relate to methodological factors in laboratory determinations of per capita rates or to other factors that influence zooplankton feeding behavior such as the quantity and quality of food resources. The measured per capita filtration rates from this study were compared to previously published species-specific values to determine if the rates observed in the experimental enclosures were reasonable

(Figure 9). The per capita filtration rate for the macrozooplankton species were comparable to previously published rates for the dominant species occurring at these sites (*i.e*. calanoids, nauplii and *Bosmina spp.*) (Bogdan & Gilbert 1984; Sierzen & Frost 1990). The mesozooplankton per capita filtration rates were also comparable to previously reported values (Bogdan & Gilbert 1984; Sierzen & Frost 1990; Lionard *et al.* 2005) but were at the lower range. There are several possible reasons why the mesozooplankton grazing rates were low. First, this could be an artifact of the laboratory experiment. Roman and Rublee (1980) found that enclosure experiments often underestimate zooplankton grazing. The available food quantity and quality changes as phytoplankton settles to the bottom of enclosures during the experiment despite the "mixing" or rotation of the enclosures (Roman and Rublee 1980; Lair 2006). Crowding effects may also influence feeding behavior. In order to quantify grazing rates, a quantifiable change in chlorophyll *a* must occur in the enclosures. To ensure this happens the animals are concentrated from their natural densities and this may cause increased predation among the zooplankton therefore reducing grazing pressure on phytoplankton (Lair 2006; Azemar *et al.* 2007). Alternatively, the lower filtration rates seen in this study may be a reflection of the zooplankton's response to food quality. Sellner *et al.* (1993) reported similar zooplankton per capita filtration rates in the Potomac River during a cyanobacteria bloom (204 million cells/L) in early August of 1993. Cyanobacteria are considered to be a low quality food resource due to their low nutritional value and, in some cases, the presence of toxins (Sellner *et al.* 1993; Pietsch *et al.* 2001; Rohrlack *et al.* 2005). Cyanobacteria blooms are common in the tidal freshwater James River (Marshall et al. 2009). During the

summer of 2007, the density of cyanobacteria averaged 157 million cells/L at JRM 75 comprising 70% of the phytoplankton community (H. Marshall, unpubl. data).

Another aspect of food quality that may influence zooplankton grazing rates is the presence of non-algal particulate matter. The highest concentrations of total suspended solids were found at the chlorophyll *a* maxima (JRM 75) and the estuarine site (JRM 21). Non-algal particulate matter has been shown to inhibit the grazing behavior of zooplankton in estuarine habitats despite the ability of zooplankton to preferentially select food particles bearing chlorophyll *a* (Soetaert & Herman 1994; Tackx *et al.* 2003). The quality of suspended particulate matter as indicated by its C and N content was not significantly different at JRM 75 compared to the other study sites. These two factors indicate that the quality of food resources for zooplankton at the site of the chlorophyll *a* maxima may have been similar to that of other sites despite the increased quantity of phytoplankton. The ability of zooplankton to exploit food resources at the chlorophyll *a* maxima may have been constrained by low food quality due to the dominance of undesirable phytoplankton taxa (*i.e.* cyanobacteria) and the greater abundance of non-algal particulate matter.

Based upon the findings of this study, most of the phytoplankton production at the site of the chlorophyll *a* maxima is not directly transferred to higher trophic levels via zooplankton grazing. This begs the question, what is the fate of the phytoplankton biomass? A portion of the phytoplankton production can be lost due to advection (*i.e.* transported down the estuary). During low river discharge in summer, the importance of fluvial-driven advective loss declines but advective forces associated with tidal exchange could account for algal export from the site of the chlorophyll *a* maxima (Kimmerer 2002;

Murrell *et al.* 2007). Phytoplankton biomass can also be lost due to sedimentation despite the influence of tidal mixing (Cole *et al.* 1992). Finally, a portion of the phytoplankton biomass may be incorporated into the microbial food loop as senescing phytoplankton are colonized and decomposed by bacteria (Beckwith 2009).

Prior studies have reported variable rates of zooplankton grazing in estuaries. Zooplankton in the Suwannee River estuary consume as much as 83% of the primary production per day (Quinlan *et al.* 2009). Similarly, Gosselain *et al.* (1998) found that the zooplankton community in the River Meuse fully exploited the phytoplankton community, grazing up to 113% per day during the summer months when discharge was low, temperatures were high and phytoplankton production peaked. Significant grazing pressure on phytoplankton was also seen in the Schelde estuary (Lionard *et al.* 2005). In contrast, zooplankton in the Pensacola Bay estuary were unable to exploit phytoplankton resources such that phytoplankton growth rates were greater than the grazing rates by a factor of two (Murrell *et al.* 2002). The grazing rates of zooplankton in the James River estuary are low in comparison to most other estuaries but the cause for this remains unknown.

Tables

Table 1. Average water quality conditions at three sampling locations in the James River estuary during June-August 2007.

	River Mile		
Parameter	99	75	21
Salinity (‰)	0.01	0.01	12.8
Temperature (°C)	28.5	28.3	26.3
Dissolved Oxygen (mg/L)	6.7	7.4	5.7
pH	8.3	8.4	7.5
Turbidity (NTU)	9.6	18.0	10.5

Table 2. Mean values (with standard error) and statistical analysis (one-way ANOVA) of food resource conditions at three sampling locations in the James River estuary. 'ns' indicates there were no significant differences; R^2 is the proportion of the variation in the dependent variables explained by the factor site.

Parameter	JRM 99	JRM 75	JRM 21	p	R^2	N	Significant
Chlorophyll *a* (*μ*g/L)	12.7 ± 1.28	71.2 ± 10.0	10.4 ± 1.07	<0.01	0.76	11	75 > 99=21
Total Suspended Solids (mg/L)	6.27 ± 0.18	22.5 ± 3.02	27.6 ± 4.08	0.01	0.70	11	75=21>99
Particulate Organic Carbon (mg/L)	0.84 ± 0.10	2.93 ± 0.10	0.92 ± 0.25	<0.01	0.96	11	75 > 99=21
Particulate Organic Nitrogen (mg/L)	0.17 ± 0.02	0.53 ± 0.02	0.15 ± 0.01	<0.01	0.95	11	75 > 99=21
% Carbon	13 ± 1.5	15 ± 2.8	3.7 ± 1.5	0.11	0.42	11	ns
% Nitrogen	2.7 ± 0.4	2.7 ± 0.5	0.6 ± 0.2	0.07	0.49	11	ns

Table 3. Average zooplankton densities and statistical analysis (nested one-way ANOVA) for the three sampling locations in the James River estuary.

Zooplankton	JRM 99	JRM 75	JRM 21	p	R^2	N	Significant
Rotifers	263 ± 76.2	333 ± 67.4	1.16 ± 0.73	<0.01	0.88	33	75=99>21
Nauplii	5.95 ± 4.00	73.3 ± 8.63	38.4 ± 10.2	<0.01	0.75	33	75>21>99
Cladocerans	5.04 ± 1.08	19.2 ± 4.76	0.00 ± 0.00	<0.01	0.77	33	75>99=21
Calanoids	0.25 ± 0.20	2.16 ± 0.32	24.0 ± 22.6	<0.01	0.95	33	21>75=99
Cyclopoids	0.72 ± 0.57	6.47 ± 1.19	3.81 ± 1.69	<0.01	0.72	33	75=21, 75>99, 21=99
Barnacle Larvae	0.00 ± 0.00	0.00 ± 0.00	24.3 ± 6.55	<0.01	0.98	33	21> 75=99
Total	274 ± 78.4	434 ± 69.04	92.5 ± 23.2	<0.01	0.84	33	75>99>21

Table 4. Average grazing rates and statistical analysis (one-way ANOVA) by mesozooplankton (63-210 µm) in the James River estuary.

Parameter	JRM 99	JRM 75	JRM 21	p	R^2	N	Significant
Per Capita Filtration (mL/ind/d)	0.21 ± 0.14	0.04 ± 0.03	0.25 ± 0.07	0.34	0.35	8	ns
Community Filtration Rates (% vol/d)	3.84 ± 1.55	0.81 ± 0.46	1.62 ± 0.31	0.20	0.92	8	ns
Community Ingestion Rates (µg Chl *a*/L/d)	0.21 ± 0.09	0.27 ± 0.15	0.07 ± 0.00	0.63	0.17	8	ns

Table 5. Average grazing rates and statistical analysis (one-way ANOVA) by macrozooplankton (>210µm) in the James River estuary.

Parameter	JRM 99	JRM 75	JRM 21	p	R^2	N	Significant
Per Capita Filtration (mL/ind/d)	2.78 ± 2.19	0.37 ± 0.12	1.35 ± 0.07	0.51	0.24	8	ns
Community Filtration Rates (% vol/d)	1.78 ± 0.83	1.11 ± 0.44	2.78 ± 2.42	0.17	0.17	8	ns
Community Ingestion Rates (µg Chl *a*/L/d)	0.09 ± 0.04	0.42 ± 0.24	0.09 ± 0.07	0.32	0.04	8	ns

Figures

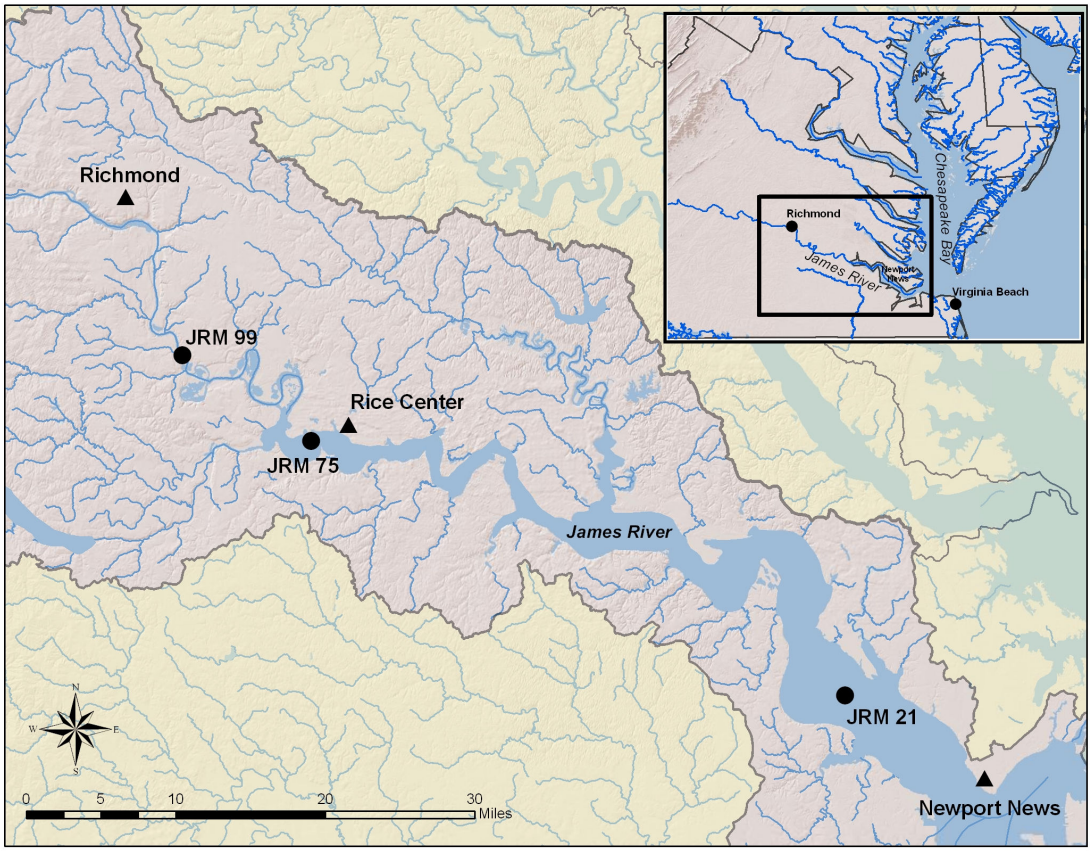

Figure 1. Map of the James River Estuary (Virginia, USA) showing sampling locations in the tidal freshwater (river mile 99 and 75) and mesohaline (river mile 21) segments. Map courtesy of R. Scott Williams.

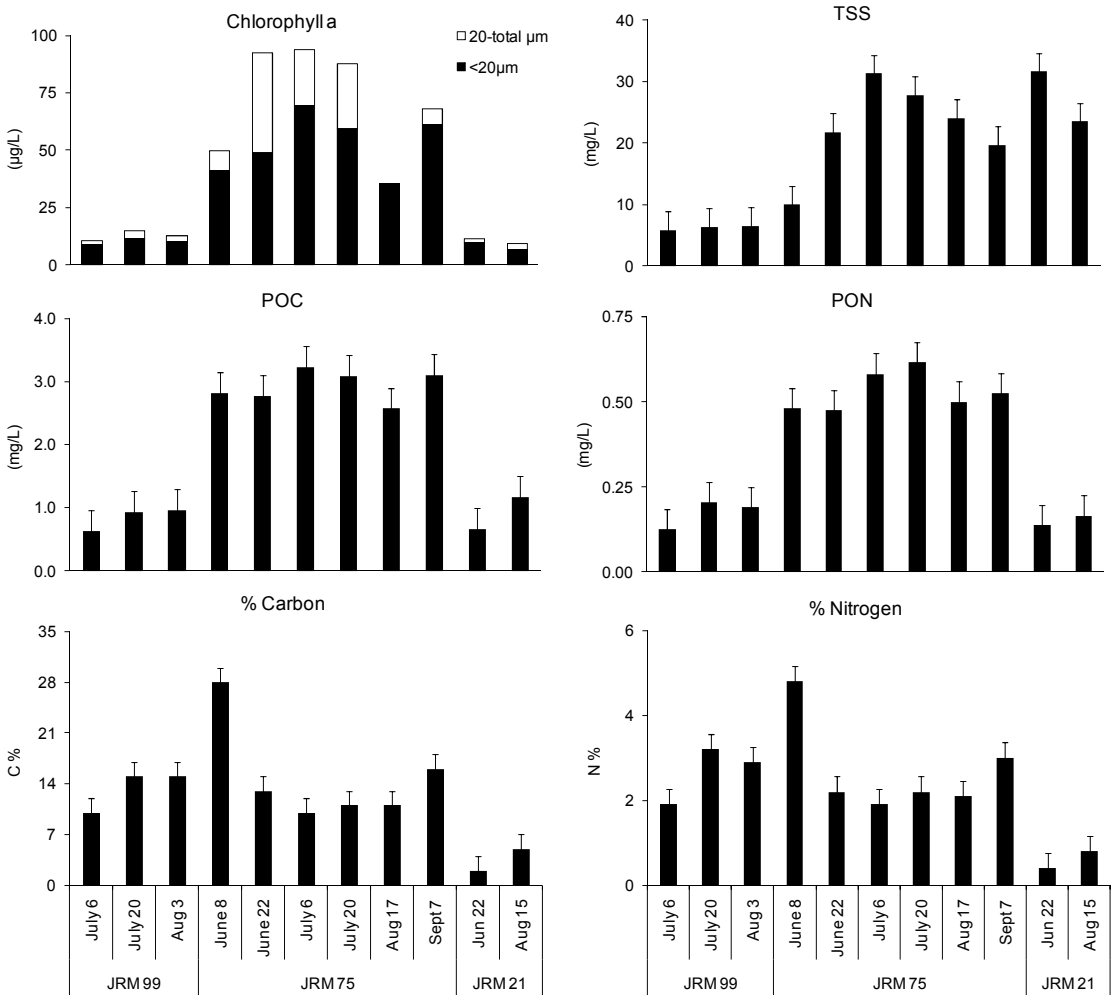

Figure 2. Food resource conditions at three sampling locations in the James River estuary during 2007. Each bar represents the mean of three replicate samples with its associated standard error.

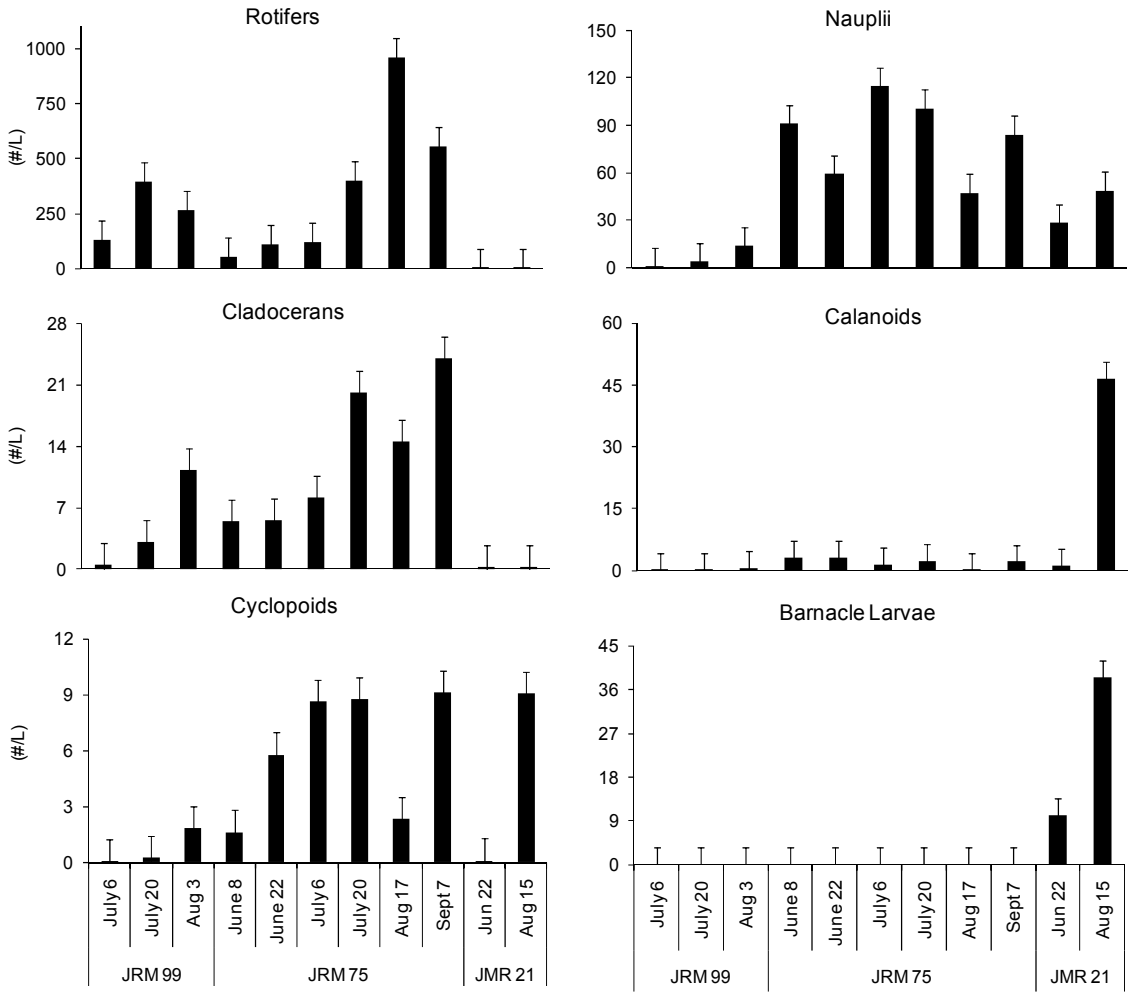

Figure 3. Zooplankton abundances at three sampling locations in the James River estuary during 2007. Each bar represents the mean of three replicates with its associated standard error.

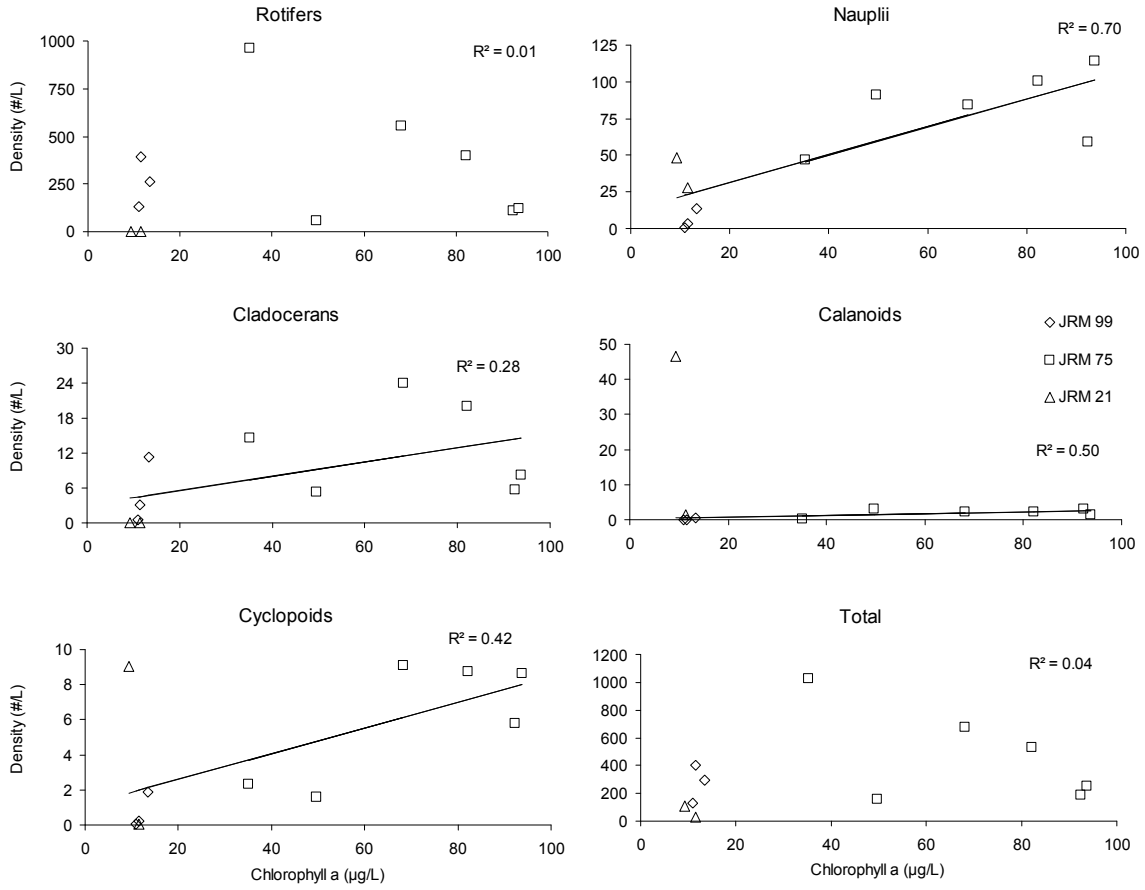

Figure 4. Relationships between zooplankton densities and chlorophyll *a* concentrations based on a pooled dataset from three sampling locations in the James River estuary.

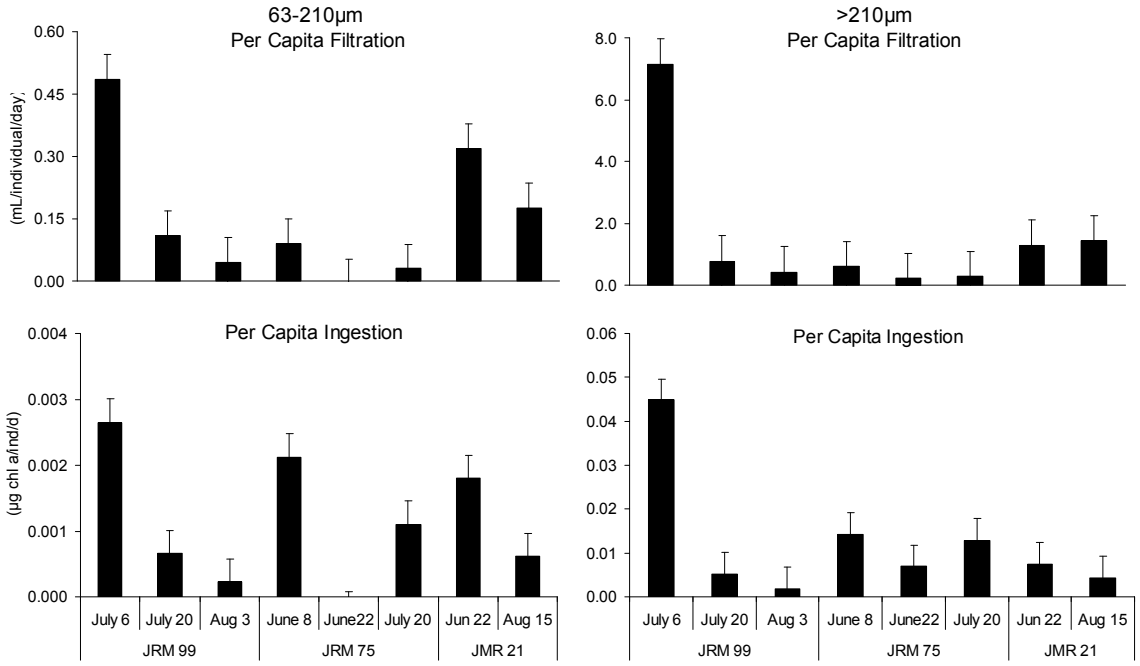

Figure 5. Per capita filtration and ingestion rates of chlorophyll *a* < 20 µm for two size fractions of zooplankton (63-210 and >210 µm) from the James River estuary. Each bar represents the mean of three replicates with its associated standard error.

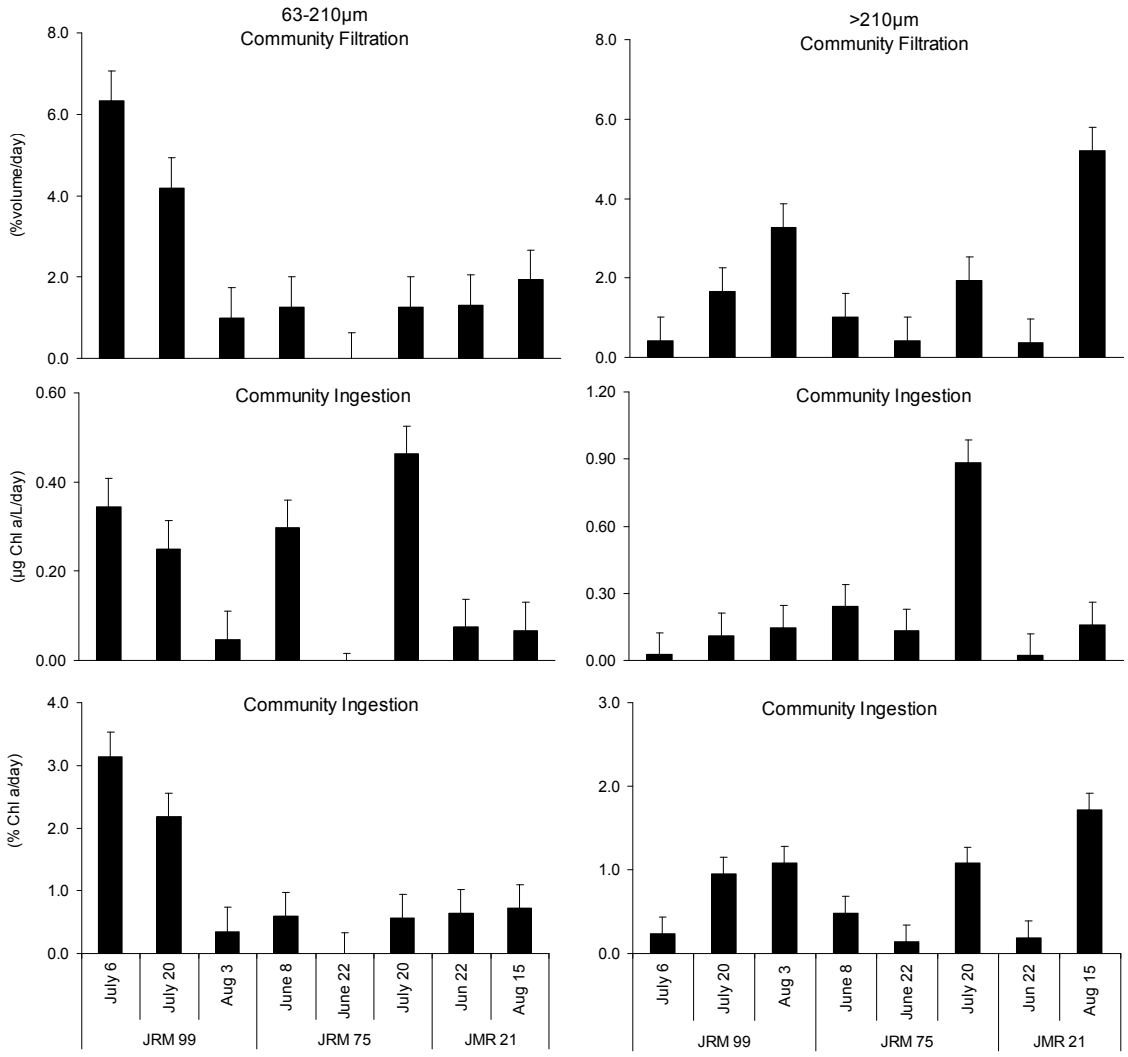

Figure 6. Community filtration and ingestion rates of chlorophyll *a* < 20 µm for two size fractions of zooplankton (63-210 and >210 µm) from the James River estuary. Each bar represents the mean of three replicates with its associated standard error.

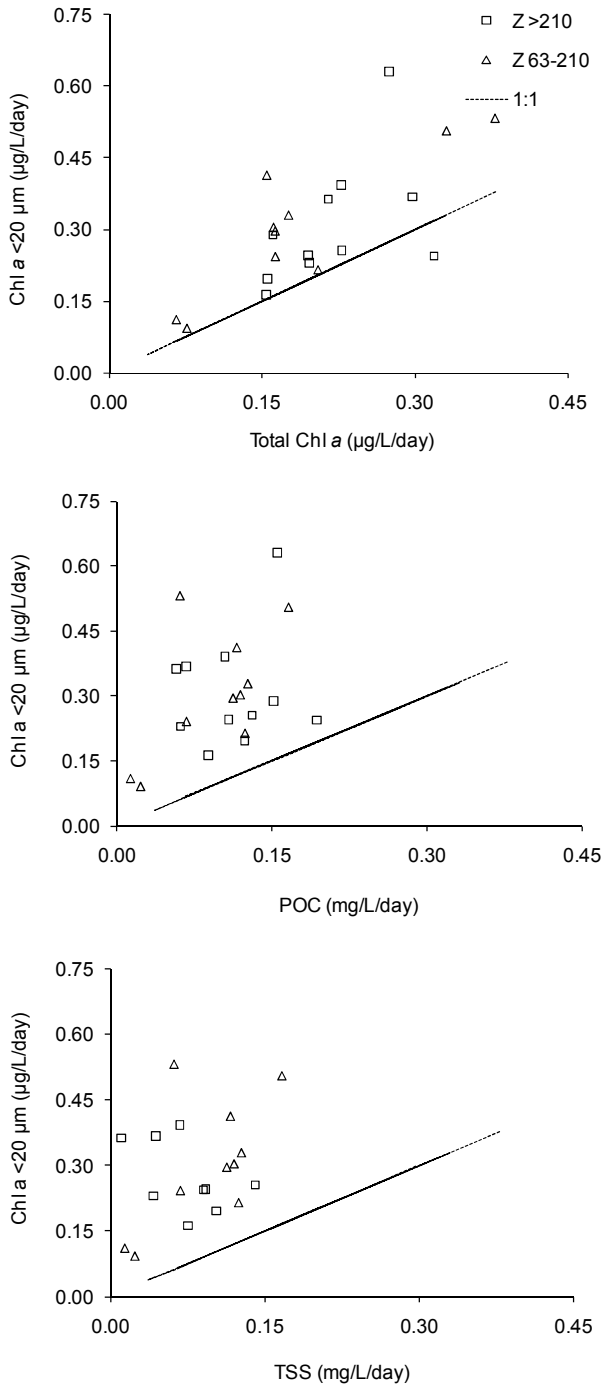

Figure 7. Ingestion rates of chlorophyll *a* <20 µm, total chlorophyll, particulate organic carbon (POC) and total suspended solids (TSS) by zooplankton from the James River estuary. Lines shown (1:1) are the expected relationship in the absence of feeding selectivity; values above the line demonstrate a preference for the dietary factor on the y-axis.

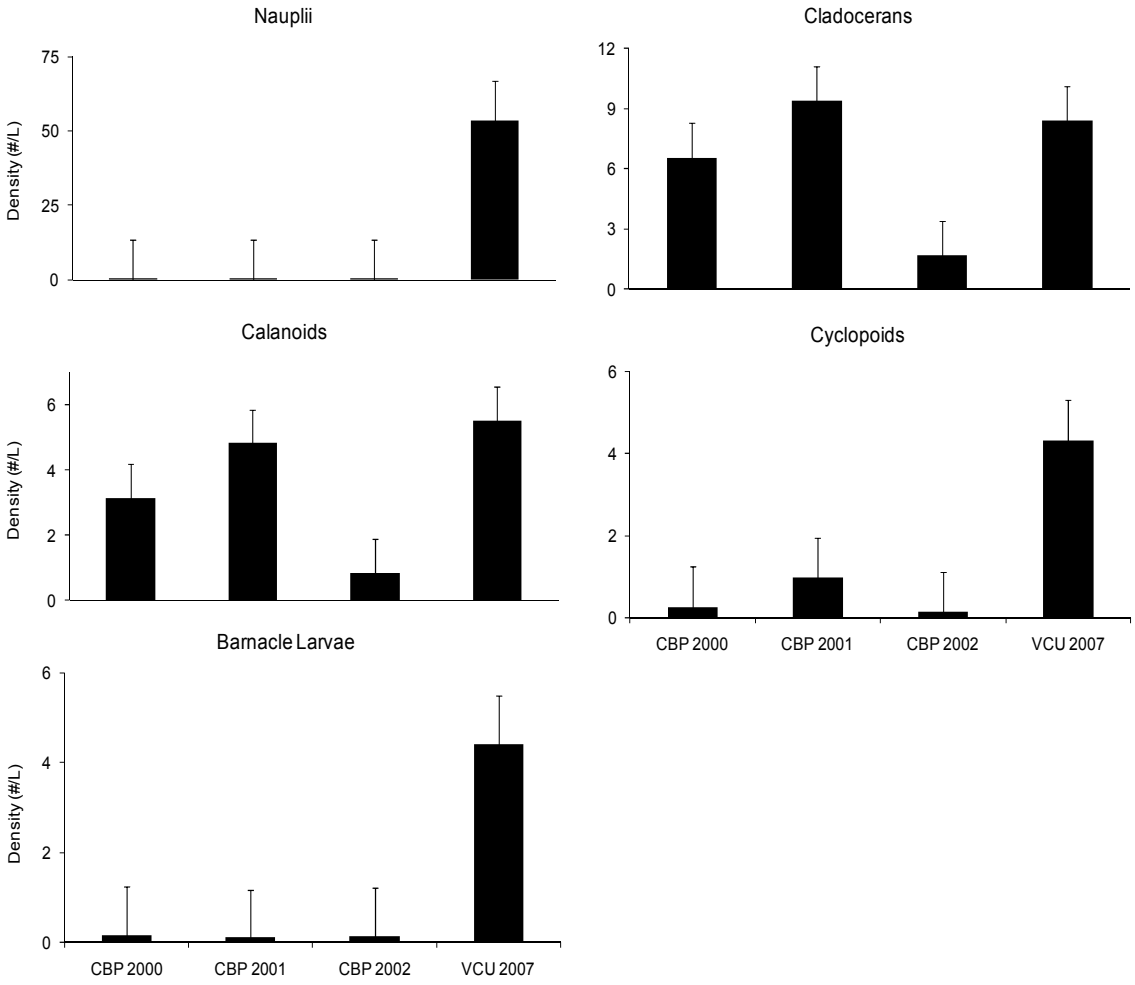

Figure 8. Comparison of average zooplankton densities in the James River estuary reported in this study (VCU 2007) with historical data collected by the Chesapeake Bay Program (CBP 2000-2002). For comparison purposes, only summer data (June-August) were used from the CBP monitoring. Each bar represents the mean abundance with its associated standard error.

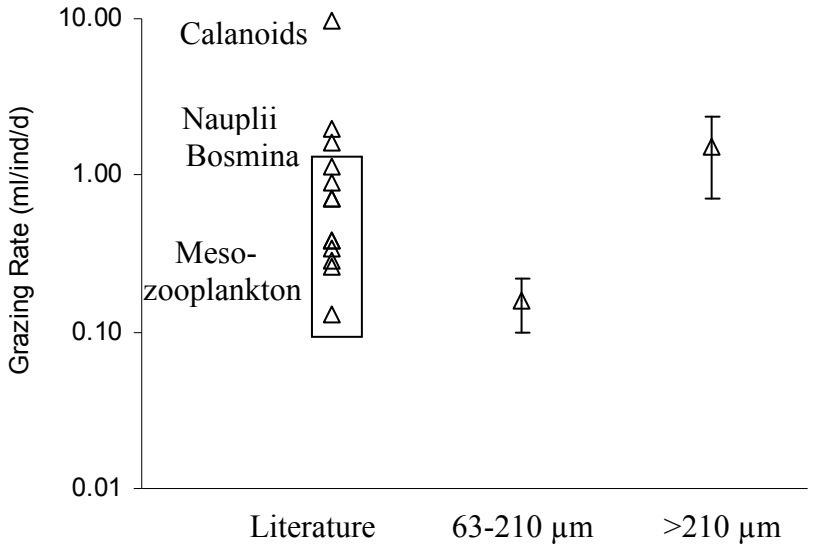

Figure 9. Comparison of measured per capita grazing rates obtained in this study with previously published values for taxa common to the James River estuary. Average values for the two size fractions measured in this study are shown separately (mean + SE).

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