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Benthic and Planktonic Microalgal Community Structure and Primary Productivity in Lower Chesapeake Bay

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ABSTRACT

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Microalgal populations are trophically important to a variety of micro- and macroheterotrophs in marine and estuarine systems. In Chesapeake Bay, microalgae facilitate the survival and development of ecologically and economically relevant fauna, including shellfish and finfish populations. While regarded as significant components of coastal environments, microphytobenthic communities are historically understudied. In Chesapeake Bay, the importance of phytoplankton to the ecosystem is understood, but the contribution of microphytobenthos remains unclear. This project surveys intertidal microphytobenthic communities, in relation to phytoplankton communities, around lower Chesapeake Bay describing the taxonomic makeup of these populations, coupled with quantification of cell abundance, biomass, and primary production. Whole water samples and sediment cores were collected at eight sites throughout lower Chesapeake Bay for phytoplankton and microphytobenthic community analysis over a two-year period. Over the span of the study, a total of 142 taxa were identified (124 phytoplankton; 95 benthos). Microphytobenthic community composition, abundance and biomass were dominated by diatoms in spring, autumn and winter, while cyanobacteria were dominant during summer. Similarly, within the water column, diatoms were the most diverse group with greatest cell abundance and biomass throughout the sampling period. Algal abundance, biomass, species richness, and productivity rates all differed between the phytoplankton

and benthos. Abundance and biomass values were significantly higher in the benthos than in the phytoplankton throughout the study. Conversely, species richness and productivity rates were significantly higher in the phytoplankton. These results provide evidence that the microphytobenthos are an important, diverse community similar to, but significantly different than neighboring planktonic populations.

This dissertation is dedicated to my parents, Jean and Stan.

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CHAPTER I

INTRODUCTION

Estuaries are among the most productive aquatic ecosystems in the world (van der Wal et al. 2010). Microalgae living in the water column as phytoplankton and the algae of the microphytobenthos growing on intertidal and subtidal sediment are the major sources of this productivity and constitute the initial components of vital food webs in estuaries (Underwood and Kromkamp 1999). Our knowledge of estuarine phytoplankton dynamics is extensive for Chesapeake Bay. The first phytoplankton surveys began with descriptions of community composition by Wolfe et al. (1926) and Cowles (1930), and this has continued into the present century (Marshall et al. 2003, 2005, 2006). In comparison, fewer studies both globally and regionally have focused on the benthic microalgae, which represent a major component in estuarine food webs (Underwood and Kromkamp 1999). For definition, the benthic microalgae, also described as microphytobenthos, are the microscopic algae inhabiting the upper few centimeters of sediment in aquatic ecosystems. They are fast-growing, readily grazed, and may constitute a greater and more stable source of organic matter to higher trophic levels than estuarine macrophytes (Rizzo et al. 1996). The microphtyobenthos are also vital facilitators of carbon cycling in the world's coastal ecosystems, with production estimates of ca. 500 million tons of carbon annually (van der Wal et al. 2010). Production estimates for microphytobenthos in various mid-Atlantic coastal systems range between 29 and 234 g C m^{-2} yr^{-1}, compared to 7 and 875 g C m^{-2} yr^{-1} for phytoplankton (Underwood and Kromkamp 1999). Numerous authors have suggested that benthic microalgal primary

production contributes significantly to the overall production in shallow aquatic environments, and may equal or exceed phytoplankton productivity rates in these waters (Admiraal and Peletier 1980, Leach 1970, Blasutto et al. 2005, Underwood and Kromkamp 1999, Cahoon and Cooke 1992). In some locations, benthic microalgae may contribute up to 50% of the total primary production in estuarine systems (Underwood and Kromkamp 1999).

Along with their importance as a food source to the global carbon cycle, sediments dominated by benthic microalgae exhibit lower rates of ammonium, nitrite, and nitrate release, indicating these communities may also function as nutrient sinks, rather than a source of nutrient release into the water column (Rizzo et al. 1996). Benthic microalgae also influence water quality by stabilizing fine sediments, thereby reducing turbidity in the water column and reducing the release of nutrients from re-suspended sediments (Rizzo et al. 1996). They are generally localized and concentrated in the intertidal regions and shallow subtidal sediments of coastal and estuarine ecosystems. These are euphotic areas that are favorable locations for algal development comprising 23-42% of the estuaries in the U.S. mid-Atlantic region (Rizzo et al. 1996). Although these are mainly surface biofilms of benthic microalgae, other studies have reported between 30% - 50% of the estuarine benthic microagal biomass can be resuspended into the water column (Underwood and Kromkamp 1999). This suggests portions of what has been considered phytoplankton biomass is often of benthic origin.

Benthic algal assemblages have been defined according to differences in their adhesive tendencies and/or their affinity for different sediments. The "epipelic" algae favor fine silty/muddy sediments, whereas sandy sediments support the growth of

"epipsammon", or attached algal cells (Yallop et al. 1994). These terms have typically been applied to only diatoms, often neglecting to include other microalgal groups in the sediment, e.g. cyanobacteria, chlorophytes, cryptophytes, etc. To be more inclusive, MacIntyre and Cullen (1995) used the term microphytobenthos to describe any of these algal organisms associated with the substrate. In this study, all benthos-associated microalgae are referred to as microphytophenthos.

Studies of microphytobenthic populations in Chesapeake Bay are especially sparse, with few studies conducted in the Bay over the last 30 years (Rizzo and Wetzel 1985, Rizzo and Wetzel 1986, Murray and Wetzel 1987, Reay et al. 1995, Rizzo et al. 1996, Wendker et al. 1997, Stribling and Cornwell 1997, Buzzelli 1998). None of these provide a Bay-wide review of microalgal production or species composition, but rather report productivity rates involving small temporal periods and limited spatial ranges. Microphytobenthic studies have also been considered more complex than the phytoplankton since the benthic environment in the intertidal zone is more heterogeneous than the water column, with additional physical forcing interactions operating at different time and spatial scales compared to the pelagic environment (Guarini et al. 2000). Cahoon (1999) summarized these variables and the importance of benthic microalgae in neritic ecosystems and the intrinsic difficulty of measuring the natural properties and responses of these organisms in coastal communities.

Microphytobenthic Community Composition

The majority of microphytobenthic studies treat algal assemblages as a single functional algal component. However, the benthic microalgal communities are typically

composed of a great diversity of taxa, each with unique photosynthetic requirements and behavioral features (Janousek 2009, Underwood and Kromkamp 1999). Previous studies have also noted the general lack of specific taxonomic information available regarding the microphytobenthos composition (Fielding et al. 1998, Janousek et al. 2007, Saburova et al. 1995). When examining these communities, biomass data is generally recorded as chlorophyll *a* measurements, with little or no attention given to species present, their abundances, or diversity. Reporting biomass in terms of a photosynthetic pigment is also questionable, since algal cells in deeper sediment layers may possess lower or greater chlorophyll *a* content than surface cells, even though their true biomass is unchanged. For instance, Fielding et al. (1998) reported diatom biomass at depths below 10 cm in some sediments, emphasizing the inconsistency associated with pigment-only measures of surface algal biomass. While biomass (e.g. as chlorophyll *a*) and abundance measurements provide an instantaneous and general appraisal of existing algal communities, they provide no information regarding community dynamics, such as seasonal species composition and turnover (Pinckney et al. 2003). Furthermore, a quantification of the taxonomic makeup of a benthic algal community can reveal insights into nutrient cycling, sediment stabilization, organic matter content, and the ecological niches that each major algal group may occupy. The value of diversity and abundance studies of microphytobenthic communities are key to a more complete understanding the productive value of these taxa and the habitats in which they reside.

Microphytobenthic Variability

Microphytobenthic community composition and biomass vary widely across and within benthic habitats (Janousek 2009). These communities tend to be heterogeneous on spatial scales ranging from millimeters to kilometers. The environmental factors driving the microphytobenthic composition and biomass are wide-ranging, with general agreement that no single, stand-alone variable is controlling microphytobenthic dynamics. Instead, these populations are influenced by a suite of interacting physical and biological conditions, working in concert to shape these communities. These factors include varying combinations of changing temperatures and salinities, terrestrial elevation gradients, emersion time (intertidal), bathymetry, light intensities, and sediment-nutrient availability. Other factors often involve the presence or absence of deposit and suspension feeders, bioturbation, physical turbulence (wave and current intensity), the shoreline aspect, plus others (Orvain et al. 2012). Several authors have attributed sediment type as being one of the most significant variables driving microphytobenthic algal biomass and community structure in estuarine environments (Jesus et al. 2009; Skinner et al. 2006). Sediment type and porosity will control water content and water residence time, and therefore the rate of allochthonous nutrient delivery to the microalgal community. Viable benthic algae below the sediment's surface layers are also limited in their development due to the extremely small euphotic zone common to benthic habitats, especially those composed of fine sediments. Because of limited light, the majority of microphytobenthic biomass commonly occurs in the surface layer to depths of less than several centimeters.

Microphytobenthic communities are exposed to the interaction of numerous variables that influence their abundance, biomass, photosynthesis, and species composition. The intertidal zone also presents a particularly harsh and dynamic environment for algal communities which respond to a variety of stressors that commonly include sediment scour, varying light gradients during periods of emersion/immersion, extreme temperature variation, and variable salinities. While no single stress factor may be the sole driving force shaping these communities, a select few have been singled out as most significant. Salinity has been considered the main ecological constraint to microphytobenthic composition in some studies (e.g. Blasutto et al. 2005), along with temperature as major factors influencing microphytobenthic biomass (Blanchard et al. 1997). Large daily temperature fluctuations, particularly during low tides often have deleterious effects on microphytobenthic populations and their photosynthetic capacity (Blanchard et al. 1997). Microphytobenthic spatial and temporal patterns of composition and abundance are also attributed to available nutrient concentrations and grazing (Bennett et al. 2000). Though nutrient limitation is often a controlling factor in phytoplankton dynamics, this condition is less prevalent in the benthos where nitrogen and phosphorous are readily available due to remineralization processes in the sediment (MacIntyre et al. 1996). While nutrients and grazing may play a role in shaping the floristic community of the benthos, evidence of nutrient limitation is scarce (Underwood and Kromkamp 1999), and even grazing pressure may not be significant, particularly in areas overlain with thick microbial mats.

Light limitation is a major factor influencing spatial and temporal distributions of the microphytobenthos. Shallow coastal systems are characterized by high surface area to

water volume ratios, leaving a significant benthic habitat within the photic zone. While this appears favorable for benthic algal growth and high production, coastal areas are also characterized by having increased sediment loads. Higher concentrations of suspended matter yields increased turbidity, and reduced light intensity which can negatively affect species composition and production by the microphytobenthos (Blasutto et al. 2005). Steep gradients of irradiance may occur within estuarine sediments, particularly in silty/muddy habitats. These sites are characterized by high organic matter content with intertidal areas subjected to extreme illumination cycles during tidal periods of emersion and immersion. Greater quantities of algal biomass may be found higher in the intertidal zone due to the overall longer exposure times, and higher light levels. In some instances the sediment itself can affect irradiance. In sandy sediments, light intensity at the surface can be higher than incident light, due to backscattering effects, creating increases in light intensity of 200% at the surface (Underwood and Kromkamp 1999), with this effect reduced in more cohesive sediments. Light intensity in the sediment is highly variable, as irradiance values, particularly at the upper end of typical irradiance ranges, may not affect microphytobenthic development. However, there is no evidence of benthic microalgal photosynthetic inhibition at full light intensity. Though photosynthesis/irradiance relationships among the microphytobenthos are well documented, the role of their species composition is rarely explored, and often these communities are simply described as "diatom biofilms", without fully exploring their taxonomic makeup.

Biomass and Productivity Relationships

A review of the benthic algal role as producers in nearshore waters (Cahoon 1999) revealed a wide range of primary production rates (< 1 to > 500 mg C m^{-2} hr^{-1}) worldwide, while in Chesapeake Bay, a smaller, yet still considerable range of rates (1 to 90 mg C m^{-2} hr^{-1}) is reported (Rizzo and Wetzel 1985, Wendker et al. 1997). Observed differences in microalgal biomass and productivity measurements are often attributed to spatial variability of the algae or habitat type. Temporal factors also play a role in establishing these communities. Blanchard et al. (2001) described common small-scale daily oscillations in the microphytobenthos, highlighting the potential rapid increase of sediment surface biomass during daytime exposure. This response is followed by a net decrease in biomass and productivity during immersion, due to resuspension, grazing, and natural mortality. This subsequently produces a high localized turnover leading to major differences in biomass and productivity estimates (Rizzo and Wetzel 1985, Thornton et al. 2002). A series of fluctuating tidal and light regimes may then produce a predictable sequence of biomass and productivity flux as a consequence of these physical and biotic factors. Though small-scale variation is well documented, more studies need to be focused on large-scale, seasonal variations in microphytobenthic biomass and productivity. For example, seasonal biomass-productivity relationships have been documented with conflicting conclusions (Tilman et al. 1996). In temperate microphytobenthic communities, Yallop et al. (2000) found a negative relationship between algal biomass and productivity, particularly in the higher biomass ranges. Others have noted production peaking at various times throughout the year, including the warmer summer and colder winter months (Thornton et al. 2002). In these studies, the

benthic microalgal communities did not follow the often predictable growth patterns occuring in the plankton, which in many estuaries is associated with rising water temperatures, and nutrient delivery via seasonal precipitation and river flow events (Marshall et al. 2006).

In addition to complications associated with high spatial and temporal heterogeneity in measuring productivity of microphytobenthic communities, the methodology followed is also a concern. Caution must be exercised when extrapolating small scale productivity measurements to predict large scale trends. Not only do methods differ, but different approaches yield different measures of production (e.g. gross productivity, net productivity, potential productivity), each of which is not explicitly comparable (Underwood and Kromkamp 1999). Of the microphytobenthic productivity data available for Chesapeake Bay, it is difficult to compare data due to methodological differences. Another common methodological issue is the frequency of sampling. For example, variations in microphytobenthic productivity may occur on scales from hours to days. This variability is not detected by typical month to month (if not longer) sampling designs (Rizzo and Wetzel 1985). This high temporal variation reinforces the hesitancy of extrapolating hourly production to daily, monthly, and annual rates.

Disturbance and Distribution

In estuarine systems, sediment landscapes are altered frequently via temporal events such as seasonal river flow, tidal extremes, and storm events (van der Wal et al. 2010). These recurrent, physical forces, along with the transient and resident meio- and

megafauna in the sediment, subject the physical benthic environment to high levels of disturbance, particularly in the intertidal zones, and affect the distribution and composition of resident flora and fauna. Spatial and temporal heterogeneity of the microphytobenthos is most apparent in the intertidal zone where irradiance, temperature, and turbidity often reach extremes and relate directly to their lengths of exposure. Temporal variations are generally considered on a seasonal basis. However, the intertidal microphytobenthos exhibit high microscale temporal variation of a shorter time scale. This is due to rapid fluctuations in sediment biomass due to both biotic and abiotic disturbances involving rhythmic vertical migrations of the biota within the sediment strata. The depth of algal migrations within the sediment is influenced by emersion time and the sediment grain size. While the majority of the microphytobenthic biomass is within the top few millimeters of the sediment, bioturbation by grazers and sediment mixing (due to wave action) and tidal currents can relocate algal cells to depths of more than 10 centimeters (Middleburg et al. 2000). Despite being buried below the euphotic zone, these displaced cells can maintain some photosynthetic activity (Steele and Baird 1968). Thus, a simple surface sediment sample may be insufficient to collect and characterize these benthic communities.

Microphytobenthic vertical and horizontal (spatial) distributions are also influenced by temporal microalgal migration. Long-term, resident distributions may be attributed to the degree of physical disturbance and sediment grain size. However, it is often difficult to differentiate between the two since currents and turbulence are also major particle sorting mechanisms (Fielding et al. 1998, Saburova et al. 1995). While vertical sampling may be ameliorated by extending the depth of sampling cores,

horizontal variability at the microscale level becomes more problematic. Austen et al. (1999) noted a cross-shore variability in microphytobenthic biomass, with a gradient of high to low biomass along a transect from the upper to lower shore regions in an intertidal zone. This apparent elevation gradient is not only apparent in microphytobenthic biomass, but also common in species composition and distribution. This gradient is suggested as a product of extended exposure/illumination time in the upper reaches, as well as the higher water content of lower and middle shore sediments. Higher water content results in less stable environments, especially during high tidal flow, causing sediment scour and resuspension of loose sediment particles and associated algal cells (Underwood and Kromkamp 1999). Conflicting reports suggest either an equal distribution of microalgal species throughout the intertidal zone, with density differences along elevation gradients, or patterns of heterogeneity on both vertical and horizontal scales (Saburova et al. 1995).

Sediment-Benthic Algal Relationships

Sediment type

In addition to light and temperature among the major drivers of microphytobenthic productivity and biomass, the sedimentary characteristics and the role of granulometry (grain size characteristics) are also significant (Cahoon et al. 1999). Numerous studies have identified substrate type as a major variable driving microphytobenthic composition within estuaries (Riznyk and Phinney 1972, Colijn and Dijkema 1981, Davis and McIntire 1983, Shaffer and Onuf 1983, Fielding et al. 1988,

McIntire and Amspoker 1986, Whiting and McIntire 1985). In reference to grain size and its relationship to microphytobenthos biomass, Cahoon et al. (1999) reviewed the literature noting algal biomass positively correlates with coarse-grained sediments (Skinner et al. 2006; Cahoon et al. 1999; Colijn and Dijkema 1981), but others indicated a positive correlation to finer sediments (Grippo et al. 2010, van der Wal et al. 2010, Underwood and Kromkamp 1999, McIntire and Amspoker 1986). In contrast to these studies, others have found no relationships to sediment grain size (Cammen 1982, Janousek 2009, Du et al. 2010, Gottschalk et al. 2007). However, the general consensus has been that fine sediments support higher algal biomass (Fielding et al. 1998). Concentrated at or near the surface, the algal biomass is dependent upon the ability of algal cells to actively migrate vertically through the sediment. Algae in sandy, and larger coarse sediments, typically have a lower algal representation, but the cells may be distributed to a deeper depth, with light able to penetrate into these layers. Daily tidal mixing will also enhance the resuspension and subsequent settling of algal cells in the sediment. Van der Wal et al. (2010) noted that microscale disturbances involving these algae are often more pronounced in muddy sediments, where temporal fluctuations are less apparent, compared to the lower nutrient concentrations and higher resuspension rates associated with a sandy substrate.

The substrate type grain size not only influences the accumulation of algal biomass, but different estuarine substrates have been associated with distinct algal assemblages (Amspoker and McIntire 1978, Whiting and McIntire 1978, McIntire and Amspoker 1986, Gottschalk et al. 2007). Brotas and Plante-Cuny (1998) noted the highest microphytobenthic diversity occurred in fine muddy estuarine sediments, whereas

Jesus et al. (2009) reported sediment type controls the presence/absence of specific microphytobenthic groups. They found fine cohesive sediments were dominated almost exclusively by diatoms, and the coarse, sandy sediments contained a more diverse community that included diatoms, cyanobacteria and euglenoids. Several authors have concluded that sandy sediments favor the growth of attached algal cells, not only due to the ample surface area of coarse sand grains, but also the necessity for attachment to exist in these turbulent environments (McIntire and Amspoker 1986, Amspoker and McIntire 1978, Whiting and McIntire 1985). In contrast, muddy surface sediments are dominated by mobile (epipelic) algae, since these habitats are generally sheltered from wind/wave action, and often have reduced tidal turbulence (van der Wal et al. 2010, Yallop et al. 1994, Thornton et al. 2002). In this study, all algal components of the microphytobenthic biomass are included. This approach counters the ambiguity and subjectivity of many early algal studies of the benthos by only considering the diatoms either as epipelic (mobile), or epipsammic (attached) taxa. Such groupings are problematic in that they ignore other functional groups capable of motility and productivity (e.g. cyanobacteria, euglenoids, dinoflagellates, etc.).

While there is evidence describing differences in algal species composition along particle size gradients, these are not always reflected in their biomass or productivity rates, which rely more heavily on other variables, such as irradance and nutrient concentrations. (McIntire and Amspoker 1986). There is also linkage between nutrients, sediment type, and their collective influence on the composition of the microphytobenthic communities. Finer, muddy sediments tend to have higher organic matter content, thereby more bacterial decomposition, leading to higher levels of dissolved nutrients available in

the sediment. In contrast, sandflats tend to be more porous, and oligotrophic in comparison, suggesting the possibility of nutrient limitation in coarse-grained environments. Underwood and Kromkamp (1999) suggest that while nutrients may not directly limit photosynthesis or biomass levels in cohesive sediments, nutrient limitation can occur in coarse, sandy sediments. Nutrient limitation in concert with various physical forces (e.g. sediment composition, irradance), would be a factor in determining species composition across these sediment/habitat types. Despite ample evidence supporting sediment as a major factor in shaping microphytobenthic dynamics, this viewpoint remains controversial, particularly when considering the multitude of factors interacting within these intertidal communities.

Sediment Stability

While it is decidedly apparent that sediment characteristics influence the composition and abundance of microphytobenthic communities, these microalgal populations will also influence the nature of the sediment. One key microphytobenthos/sediment interaction is the ability of diatoms and cyanobacteria to produce large amounts of extracellular polymeric substances (EPS), which increases the stability of the surrounding sediment and supports sediment accretion. These extracellular carbohydrates enhance the attachment of cells to sediment grains, and influence the movement and migration of raphid diatoms (both vertically and horizontally) in the sediment (Blasutto et al. 2005). Cellular biomass alone is not an indicator of EPS production. The mechanisms by which microphytobenthos stabilize sediments are dependent on the algal taxa present. Thornton et al. (2002) stated diatoms produce a

carbohydrate-rich EPS that is extruded from these cells during their movement. Conversely, cyanobacteria form amorphous linkages between non-cohesive sediment grains, as well as accumulating an EPS matrix (Yallop et al. 1994). This sediment stabilizing of the microphytobenthos, will also be influenced by the abundance of predators grazing these algae. However, in cohesive sediments, high algal biomass may be the most critical factor, in contrast to any negating grazer effects (Austen et al. 1999).

Chapman et al. (2010) emphasized that several levels of environmental factors impact the presence and composition of the microphytobenthic community. These conditions may initiate a response directly or indirectly, even at extremely small response levels. Results of small-scale studies should not be extrapolated to represent large scale patterns. However, small-scale variations are often real responses to the habitat at the micro-scale level, and should not be relegated as simply noise (Chapman et al. 2010). There are a number of conditions interacting to influence the estuarine microphytobenthic communities, with perhaps even more complex relationships in intertidal zones. The most important factor(s) may be difficult to decipher, as the strength of each of these variables and their effects may vary from habitat to habitat. Continued investigations of microphytobenthic communities, their diversity, biomass, abundances, and productivity, along with their spatial and temporal dynamics will provide further insight into the environmental variables that drive these populations, and the functional roles they play in coastal wetland habitats.

Objectives

This broad scale analysis regarding the microphytobenthos was focused on expanding the current knowledge and importance of this unique community in the shallow bottom sediment of estuarine habitats, and to provide additional information regarding its role as a primary producer in the Chesapeake Bay ecosystem. Emphasis was placed on the algal constituents within the various estuarine and sediment habitats of Chesapeake Bay. This study emphasized the following objectives: 1) identify and quantify the seasonal microphytobenthic algal species composition, 2) provide information regarding their biomass and community composition, 3) determine seasonal primary productive rates from both this community and the phytoplankton within the water column for comparisons, 4) describe seasonal and spatial trends regarding the benthic micro-algal abundance, biomass, community composition, and primary productivity, and 5) examine the conditions which shape these micro-algal communities.

CHAPTER II

METHODS

Study Sites

Eight study sites were located in the lower Chesapeake Bay estuarine system from the Maryland/Virginia border on the Delmarva Peninsula to the Chesapeake Bay entrance, then extending west from Hampton Roads, north along the western shoreline of the Bay, ending in the Great Wicomico River, south of the Potomac River (Fig. 1). A major impediment to site selection was the limited direct public access to the Bay's shoreline. Thus, several sites located in a tributary or embayment, flowing into, adjacent, or otherwise directly connected to the Chesapeake Bay were included in this study. They were exposed to meso- or polyhaline tidal waters of the lower Bay, including their indigenous pelagic and benthic algal flora. These locations represent a broad and diverse geographic area that includes the dominant and characteristic shoreline habitats in lower Chesapeake Bay along with the associated habitat sites at the mouths of the various creeks and rivers bordering the Bay. For sites not directly along the Bay shoreline, the average distance from Chesapeake Bay proper is 2.7 km, with the Lafayette River site the furthest at 14.5 km upstream. These sites were considered representative of the intertidal benthic habitats within the lower Chesapeake Bay regarding their substrate, accessibility, and adjacent wetlands.

The collection sites will be referred to as: 1) "Saxis" - Saxis Wildlife Management Area, Saxis, VA, 2) "Harborton" - Pungoteague Creek, Harborton, VA, 3) "Cape Charles" - Old Plantation Creek, Cape Charles, VA, 4) "Lynnhaven" - Lynnhaven

Inlet, Virginia Beach, VA, 5) "Lafayette" - Lafayette River, Norfolk, VA, 6) "Hampton" - Back River, Hampton, VA 7) "New Point Comfort" – New Point Comfort Natural Area Preserve, Mathews County, VA, and 8) "Great Wicomico" – Cranes Creek, Northumberland County, VA.

Site descriptions

1). Saxis (37° 54' 19.09" N, 75° 41' 02.23" W) – the northernmost site on the eastern shore is located within the Saxis Wildlife Management Area in Accomack County, VA. Managed by the Virginia Department of Game and Inland Fisheries, this area is comprised of ca. 26 km^2 of predominantly tidal wetland (tidal range 0.7 m), with higher hummocky areas inland. The sample site is along a small tidal gut flowing south into Messongo Creek, with muddy sediments dominated by *Spartina alterniflora*, *S. patens*, and *Juncus roemerianus*.

2). Harborton (37° 39' 58.32" N, 75° 49' 50.23" W) – located within Pungoteague Creek in the town of Harborton, Accomack County, VA. The location is adjacent to the Harborton public boat ramp (tidal range 0.5 m), and is comprised of sandy sediments, with a thin line of vegetation (*S. alterniflora*, *Iva frutescens*) separating the shoreline from a gravel parking lot.

Fig. 1 Sampling sites located in the lower Chesapeake Bay, January 2010 – December 2011. 1) Saxis, 2) Harborton, 3) Cape Charles, 4) Lynnhaven, 5) Lafayette, 6) Hampton, 7) New Point Comfort, and 8) Great Wicomico.

3). Cape Charles (37° 14' 9.79" N, 76° 00' 33.42" W) – the southernmost site on the Delmarva Peninsula, is located on the property of Bay Creek Resort and Club, Cape Charles, Northampton County, VA. This is an un-vegetated muddy sediment (tidal range 0.7 m) on the backside of a sand spit within Old Plantation Creek. While the sampling area is un-vegetated, the immediate area surrounding the site is heavily vegetated with *S. alterniflora*, *S. patens*, *I. frutescens*, and *Baccharis halimifolia* along with a variety of other wetland and upland vegetation.

4). Lynnhaven (36° 54' 28.17" N, 76° 05' 37.08" W) – located directly on the southern shore of Chesapeake Bay, at the mouth of the Lynnhaven Inlet (tidal range 0.7), west of the Lesner Bridge, Virginia Beach, VA. This site is characterized as a high-energy, un-vegetated, coarse, sandy sediment, with heavy human impact, in terms of foot traffic, particularly during the summer months. This habitat is also subject to extreme turbulence from wind driven waves and boat wakes, as well as tidal currents.

5). Lafayette (36° 53' 25.67" N, 76° 17' 55.43" W) – the furthest upstream (14.5 km) of all sites sampled, this area is located within Colley Bay, a heavily developed urban tidal embayment of the Lafayette River, Norfolk, VA. The specific sampling location is between a recently restored tidal wetland (tidal range 0.8 m), and a small channel leading from a storm water culvert to a large mudflat. The area is characterized by both naturally-occurring and planted *S. alterniflora* and *S. patens*, as well as other planted upland vegetation (*I. frutescens*, *Panicum virgatum*). Additionally, a large portion of the shoreline in this area is comprised of concrete and asphalt rip-rap, along with fallen trees as a result of erosion via sheet flow from a landward athletic field. All sampling at this site was conducted outside of, but adjacent to the restored wetland area.

6). Hampton (37° 05' 41.71" N, 76° 17' 37.62" W) – located adjacent to the Dandy Point public boat ramp, Hampton, VA. The sampling site consists of muddy sediment within a heavily vegetated *S. alterniflora* marsh (tidal range 0.7 m) at the bottom of a steep embankment, and subject to runoff from a landward asphalt parking lot. A variety of mixed vegetation separates the shoreline from the parking area, including *I. frutescens*, and *Phragmites australis*.

7). New Point Comfort (37° 19' 12.62" N, 76° 16' 54.77" N) – located on the eastern shore of Mobjack Bay, within the New Point Comfort Natural Area Preserve, Mathews County, VA. This site is a pristine mixed *S. alterniflora*/*S. patens* marsh (tidal range 0.7 m), with a predominantly fine grained sand and clay sediment.

8). Great Wicomico (37° 49' 02.47" N, 76° 19' 39.25" W) – located on private property in Cranes Creek, a tidal creek to the south of the Great Wicomico River, Northumberland County, VA. This site (tidal range 0.4 m) consists of muddy shoreline with fibrous sediments, sheltered from wind and wave action, bordered landward by a thin band of *S. alterniflora*, abruptly transitioning to a regularly mowed lawn.

Benthic fauna frequently observed on, or in the immediate vicinity of most sites included the ribbed mussel (*Geukensia demissa*), Virginia oyster (*Crassostrea virginica*), marsh periwinkle (*Littorina irrorata*), eastern mudsnail (*Ilyanassa 21iatom a*), Atlantic blue crab (*Callinectes sapidus*), Atlantic ghost crab (*Ocypode quadrata*), fiddler crab (*Uca sp.*), hermit crab (*Pagurus sp.*), and barnacle (*Balanus sp.*), along with a variety of other benthic infaunal organisms. Additionally, an assortment of transient and resident shorebirds and wading birds were present at these sites throughout the sampling period,

and on occasion, the northern raccoon *(Procyon lotor)* and white-tailed deer (*Odocoileus virginianus*) tracks were observed, as well as sightings of muskrat (*Ondatra zibethicus*) and nutria (*Myocastor coypus*).

Sampling frequency

During a 2-year period (January 2010 – December 2011), sites were sampled 5 times annually. The 5 sampling periods were separated seasonally as: winter (January – February), spring (March – April), summer (2 collections, June – July, August – September), and autumn (October – December). Seasonal months for collections were based according to their average water temperatures from Murray and Wetzel (1987). All samples were taken during low tide/emersion during daylight hours.

Benthic algae are also known to migrate in response to light stimulus, as well as migration related to diel and tidal cycles (Thornton et al 2002). Sampling any less than 1 cm in coarse sandy sediments would exclude a large portion of the active microphytobenthic community (Skinner et al. 2006). In finer sediments, the photic zone is often limited to depths of 2.5 – 5.0 mm (Rizzo et al 1996). Based on preliminary sampling and that the majority of sites sampled were characterized by finer sands and silts, 0.5 cm cores were taken to collect all algae biomass present, including the migratory fraction.

Field sampling

At each site, 10 replicate cores (3.0 cm i.d.) were collected randomly within a 1 m^2 quadrat placed in the mid-intertidal zone devoid of macrophytes with Tenite™ plastic tubing, then capped at the bottom, and transported in the dark and on ice in a cooler to the campus laboratory. Quadrats were located away from vegetation stands, as seasonal changes in aboveground plant biomass create dynamic light regimes at the marsh surface (Pinckney and Zingmark 1993). Plant detritus on the sample's sediment surface was discarded. Sediment cores were taken to a depth of 0.5 cm after preliminary sampling revealed no indication of microalgal biomass below this depth in most sediments. While a surface scrape may have been sufficient at the stations characterized by fine-grained cohesive sediments, areas with high wave action and sediment scour often displace algal cells to depths several centimeters below the surface. In this study, even at the most turbulent station (Lynnhaven), little or no algal biomass was found below a 0.5 cm depth. In order to avoid any bias regarding benthic microalgal biomass variation along an elevation gradient within the intertidal zone (Austen et al. 1999), all cores were taken in the mid-intertidal, roughly half the distance between the high and low tide lines, based on personal observation. At the time of sediment sampling, 0.5 L whole water surface (< 1.0 m) samples were also collected in polyethylene bottles, sub-tidally in areas adjacent to the sediment sampling sites, (e.g. below mean low water, MLW), and brought to the laboratory on ice in the dark. Light (PAR) measurements at the sediment surface were recorded with a Quantum MQ-200 light meter (Apogee Instruments Inc.) and meteorological conditions were noted on site. Water and sediment temperatures were measured with a long stem hand-held thermometer, while water column and sediment

pore-water salinity were determined with water placed in a hand-held refractometer (Fisher Scientific). Sediment grain size was analyzed for every benthic collection (n = 78) via the same coring method used for taxonomic and productivity analyses. Grain size measurements were carried out using a Malvern Mastersizer laser particle analyzer.

Phytoplankton and Sediment Community Analysis

Water column samples for taxonomic analysis were processed by a modified Utermöhl protocol (Marshall et al. 2006). Upon arrival in the laboratory, replicate water samples (500 ml) were fixed with Lugol's solution, and pooled to create a composite sample, and processed through a series of settling and siphoning steps to produce a 30 – 40 ml concentrated phytoplankton sample. The concentrate was then settled via serial dilution into a settling chamber and examined with an inverted light microscope (Nikon Eclipse TS100) for algal species composition and abundance.

Sediment algal samples were sectioned to a depth of 0.5 cm (core area: 7.065 cm^2), ensuring that the sediment surface was perpendicular to the long axis of the cores to minimize unevenness in the thickness of the surficial 0.5 cm. Two 0.5 cm subsections were pooled together, fixed with Lugol's solution, and diluted to 500 ml with filtered water from each site. From this volume, a known volume was placed in a settling chamber, and examined with an inverted light microscope (Nikon Eclipse TS100) for species composition and abundance.

Microalgae from both the water column and sediment were counted using a minimum-count basis of 200 cells and 10 random fields at 315X to determine dominant

taxa, after which, the entire settling chamber surface was scanned at 125X for net microalgal abundance. Algal taxa were identified to the generic level, and when possible, to species. Microalgal biomass both in the water column and the sediment was calculated based on a carbon content per bio-volume estimate according to Smayda (1978).

Sediment Grain-Size Analysis

A superficial 0.5 cm slice of sediment core from each site was also examined for sediment grain size analysis during each sampling period at every site. Sediment cores for grain size analysis were processed following the protocol of Folk (1980). Initially, sediment core slices were dried at 100°C for 24 hrs to remove all water from the samples. Samples were weighed to obtain dry weight and combusted at 550°C for 6 hrs in a muffle furnace (Jesus et al. 2009). Granulometric analysis was completed via laser analysis in a Malvern Mastersizer 2000 (Malvern Instruments Ltd.). Statistics of grain size distribution were calculated according to Folk (1980). Sediments were categorized according to mean grain size (Wentworth 1922) and placed into the following classes: coarse silt or silts and clays (<63 μm), very fine sands (63 – 125 μm), fine sands (125 – 250 μm), medium sands (250 – 500 μm), and coarse sands (>500 μm).

Primary Productivity

The protocol described below has been the standard method for determination of Chesapeake Bay phytoplankton primary productivity since 1989 (Marshall and Nesius 1996). This protocol involves exposing the organisms of interest (sediment and water column microalgae) to inorganic radio-labeled carbon (^{14}C) which is then taken up by the microalgae during incubation and incorporated in their biomass, which can then be quantified using a scintillation counter (Beckman LS1701).

While there is no current standard method in place for the measurement of microphytobenthic primary production, there are several widely used methods. Two common approaches are the oxygen microelectrode method (Revsbech and Jørgensen 1983) and the ^{14}C uptake method (Strickland and Parsons 1972), with the latter having several variations. The ^{14}C uptake/slurry method chosen for the measurement of microphytobenthic primary productivity in this study was based primarily on logistical constraints. Unlike intact sediment cores, the slurry method allows the radioisotope to evenly reach all layers of sediment and microalgae within those layers (Jonsson 1991, Underwood and Kromkamp 1999, Cibic et al. 2008). Additionally, depending on the consistency of the sediments being sampled, obtaining and maintaining a complete intact sediment core may not be possible. One drawback of the slurry method is that it destroys existing microgradients at the sediment surface, which may affect algal photosynthetic rates, in addition to exposing microalgae from deeper layers to the same light regimes as microalgae at the sediment surface. Therefore, this method measures the rate of potential primary production (Underwood and Kromkamp 1999).

Cores were sectioned to 0.5 cm depth, obtaining a 3 ml volume equivalent, and diluted to 100 ml in filtered seawater from each corresponding site. Each dilution was sub-sampled (2.0 ml) and re-suspended up to 100 ml with filtered seawater from each site following a modified protocol from Cibic et al. (2008). Sediment samples were placed in 250 ml acid-washed milk-dilution bottles inoculated with 50 µl $NaH^{14}CO_3$ and incubated at saturated light conditions for ca. 2 hr.

Similar to the sediment samples, water column samples were inoculated with 50 µl $NaH^{14}CO_3$ and incubated simultaneously with sediment samples, with incubator water temperature maintained at the same temperature as that recorded at the collection site. Light intensity in the incubator was kept constant at 500 µE, which is sufficient for near maximum potential for autotrophy (Rizzo et al. 1996).

For both sediment and water column samples, triplicate light and duplicate dark samples were incubated, along with a time-zero ^{14}C-incorporation control. After incubation, 15 ml subsamples of each sample were filtered through a 0.45 µ Millipore filter. Filtered samples were then fumed over HCl for 24 hr and added to 7 ml scintillation cocktail (Scintisafe). Samples were analyzed on a Beckman LS1701 liquid scintillation counter along with ^{14}C standards to determine reactivity of the isotope added to each sample. Sample alkalinity was measured via standard titration methods (Palmer 1992) to calculate the amount of inorganic carbon present at each sampling site. Carbon fixation rates for the water column were determined according to Strickland and Parsons (1972) using the following formula:

$$\frac{(R_s - R_b) \times A \times F_T \times 1.05}{R \times N}$$

Where:

R_s = counting rate of sample
R_b = counting rate of blank
A = total carbonate alkalinity
F_T = approximated to 0.95; coverts carbonate alkalinity to total carbon dioxide
1.05 = isotope coefficient, since uptake of ^{14}C is 5% lower than the uptake of ^{12}C
R = reactivity of ^{14}C
N = incubation time (hr)

Rates for the sediment community, expressed as a rate per area (mg C m^{-2} hr^{-1}) were calculated following a modified equation from Cibic et al. (2008):

$$\frac{CO_2 \times \left(\frac{15}{100} * 0.001\right) \times DPM_{L-D} \times K1 \times 1.05}{DPM\ (ST) \times T \times 7.065 \times 10^{-4}}$$

Where:

CO_2 = alkalinity of the overlying water used to suspend the sediment
15/100 = the filtered volume from the 100 ml incubated
3.4 = coverts volume of incubation bottle from ml to L
DPM_{L-D} = average disintegrations per minute (3 light minus 2 dark)
K1 = 1416, the dilution factor derived from all dilutions of initial core
1.05 = isotope coefficient, since uptake of ^{14}C is 5% lower than the uptake of ^{12}C
DPM (ST) = activity of the ^{14}C standard solution
T = incubation time (hr)
7.065 = core area in cm^2
10^{-4} = converts cm^2 of the core area into m^2

Statistical Analyses

Variability of productivity rates, both temporally (within stations) and spatially (between stations) was tested using an analysis of variance (ANOVA) series using IBM

SPSS version 20. Variability of community structure, both temporally and spatially was tested using ordination analysis. Ordination analyses were used to determine the effects of multiple environmental factors (temperature, salinity, grain size (sediment samples only) controlling the variability of both primary productivity and community structure. Non-metric multidimensional scaling (NMS) was carried out using PC-ORD version 5.33 on the "slow and thorough" autopilot mode, using a Bray-Curtis distance matrix.

CHAPTER III

RESULTS – COMMUNITY COMPOSITION, ABUNDANCE, AND BIOMASS

This study included a total of 78 collection events, with both the phytoplankton and microphytobenthos sampled during each collection event. Two stations (Cape Charles and Great Wicomico) were not collected during 2010 winter due to adverse weather restrictions. Twice yearly summer collections were averaged to create a composite summer season at each station. Initial analysis of all data collected indicated significant differences between habitats with the phytoplankton and microphytobenthos differing across all attributes. The phytoplankton community had significantly higher species richness ($p = 0.024$) and primary productivity rates ($p = 0.004$), however, total abundance ($p < 0.0001$), biomass ($p = 0.005$), and the Shannon Index of diversity ($p < 0.0001$) were significantly higher in the benthos. As such, further analyses treated each habitat as separate data sets. In instances where significant differences were found within each habitat, Tukey post-hoc tests were performed to identify significant differences among stations. Among all phytoplankton collections, no significant differences were observed for any of the measured parameters (Table 1). Conversely, among the microphytobenthos, significant differences were recorded for all parameters except species richness (Table 2). In several instances, primary productivity measurements were discarded, as control experiments revealed abnormally low reactivity of stock solutions, and considering the sensitivity of the method, these rates were deemed inaccurate.

Table 1 Summary of analysis of variance tests of phytoplankton parameters across all stations.

	Df	f	P
Abundance	7	1.505	0.186
Biomass	7	1.056	0.404
Productivity	7	1.371	0.243
Species Richness	7	2.014	0.070
Shannon Index	7	0.552	0.791

Table 2 Summary of analysis of variance tests of microphytobenthic parameters across all stations. * indicates significance at the $p < 0.05$ level.

	Df	f	p
Abundance	7	3.151	0.007*
Biomass	7	2.434	0.030*
Productivity	7	5.411	0.000*
Species Richness	7	1.996	0.072
Shannon Index	7	6.578	0.000*
Phi value	7	15.802	0.000*

Community Composition

Over the 2-year study, a total of 142 taxa were identified (Table 3). These included 124 taxa in the phytoplankton, with 64 diatoms representing 52% of the taxa, dinoflagellates 17%, chlorophytes 11%, and cyanobacteria 10%. Other taxa present included charophytes, cryptophytes, chrysophytes, euglenophytes, haptophytes, and ochrophytes. The microphytobenthic communities were represented by 95 taxa and were similarly dominated by diatoms (61%), followed by cyanobacteria (18%), and chlorophytes (8%), with other groups less common and rarely present.

Species richness was significantly higher in the phytoplankton than in the benthos ($p = 0.024$) throughout the duration of the study (Fig. 2), with a broad range of species present across both habitats (Tables 4 and 5). The phytoplankton species richness averaged 33 and ranged from a high of 47 (Lynnhaven, winter 2011), to a low of 20 (Great Wicomico spring 2011). Among the microphytobenthos, species richness averaged 22 and ranged from 41 (Harborton, winter 2010) to its lowest of 7 (New Point Comfort, winter 2011). Conversely, the Shannon Index of diversity (H′) (Fig. 3) was significantly higher in the benthos than in the phytoplankton ($p = 0.000$). Shannon indices in the phytoplankton (avg. 1.67) ranged from a high of 2.29 (Lynnhaven, spring 2010) to a low of 0.36 (Great Wicomico, fall 2011). In the benthos, H′ (avg. 2.39) ranged from 3.57 (Lafayette, winter 2010) to 0.64 (Lynnhaven, winter 2011), and differed significantly across all stations sampled ($p < 0.0001$).

Table 3 Species inventory of taxa identified in the phytoplankton and benthos.

	Phytoplankton	**Benthos**
Bacillariophyta		
Amphiprora sp.	X	X
Amphora sp.	X	X
Asterionella formosa		X
Asterionellopsis glacialis	X	X
Aulacoseira granulata	X	X
Aulacoseira sp.	X	X
Bacillaria paxillifer	X	X
Cerataulina pelagica	X	X
Chaetoceros neogracilis	X	
Chaetoceros pendulus	X	
Chaetoceros sp.	X	X
Chaetoceros subtilis	X	X
Cocconeis sp.	X	X
Corethron sp.	X	X
Coscinodiscus sp.	X	X
Cyclotella spp.	X	X
Cyclotella striata	X	X
Cylindrotheca closterium	X	X
Cymbella sp.	X	X
Dactyliosolen fragilissimus	X	X
Delphineis surirella		X
33iatom asp.	X	X
Diploneis sp.	X	X
Ditylum brightwellii	X	X
Eucampia zodiacus	X	
Eunotia sp.	X	X
Fragilaria sp.	X	X
Gomphonema sp.		X
Grammatophora sp.	X	X
Guinardia delicatula	X	X
Guinardia flaccida	X	
Gyrosigma balticum	X	X
Gyrosigma fasciola	X	X
Gyrosigma sp.	X	X
Hemiaulus hauckii	X	X
Hemiaulus sp.	X	X
Leptocylindrus danicus	X	
Leptocylindrus minimus	X	
Licmophora sp.	X	X
Melosira moniliformis	X	X
Melosira varians		X
Navicula sp.	X	X
Nitzschia sp.	X	X
Odontella mobiliensis	X	
Odontella rhombus f. trigona	X	

Table 3 Continued

	Phytoplankton	Benthos
Bacillariophyta		
Odontella sinensis	X	X
Odontella sp.	X	X
Paralia sulcata	X	X
Pinnularia sp.	X	X
Plagiogramma sp.	X	X
Pleurosigma angulatum		X
Pleurosigma sp.	X	X
Proboscla alata	X	X
Pseudo-nitzschia pungens	X	
Pseudo-nitzschia seriata	X	X
Rhaphoneis amphiceros	X	X
Rhaphoneis sp.	X	X
Rhizosolenia imbricata		X
Rhizosolenia setigera	X	X
Rhizosolenia sp.		X
Rhizosolenia styliformis	X	
Skeletonema costatum	X	X
Skeletonema potamos	X	
Stephanopyxis palmeriana	X	
Striatella sp.	X	X
Surirella sp.	X	X
Synedra sp.	X	X
Tabellaria sp.		X
Thalassionema nitzschioides	X	X
Thalassiorsira leptopus	X	
Thalassiosira sp.	X	
Triceratium sp.	X	X
Charophyta		
Cosmarium sp.	X	
Desmidium sp.		X
Spirogyra sp.	X	X
Staurastrum sp.	X	
Chlorophyta		
Ankistrodesmus falcatus	X	X
Ankistrodesmus falcatus var. mirabilis		X
Chlamydomonas sp.	X	
Crucigenia irregularis		X
Crucigenia sp.	X	
Crucigenia tetrapedia	X	
Dictyosphaerium sp.		X
Dimorphococcus lunatus	X	
Oocystis sp.	X	
Pandorina sp.		X

Table 3 Continued

	Phytoplankton	Benthos
Chlorophyta		
Pediastrum duplex	X	
Pediastrum duplex gracilimum	X	
Pyramimonas sp.	X	X
Scenedesmus acuminatus	X	
Scenedesmus dimorphus	X	
Scenedesmus quadricauda	X	X
Tetraedron sp.	X	
Ulothrix sp.	X	X
Cryptophyta		
Cryptomonas erosa	X	X
Cryptomonas sp.	X	X
Chrysophyta		
Ebria tripartita	X	X
Cyanobacteria		
Anabaena sp.	X	X
Aphanocapsa sp.		X
Aphanothece gelatinosa	X	
Aphanothece sp.		X
Chroococcus dispersus		X
Chroococcus sp.	X	X
Chroococcus turgidus	X	
Dactylococcopsis raphidioides	X	X
Dactylococcopsis sp.		X
Lyngbya aestuarii	X	X
Lyngbya sp.	X	
Merismopedia elegans	X	X
Merismopedia tenuissima	X	X
Microcystis incerta	X	X
Phormidium sp.	X	X
Pseudanabaena sp.	X	X
Spirulina sp.	X	X
Dinophyta		
Amphidinium sp.	X	
Ceratium furca	X	
Ceratium fusus	X	
Ceratium schroeteri	X	
Cochlodinium heterolobatum	X	
Dinophysis sp.	X	
Diplopsalis lenticula	X	
Gonyaulax sp.	X	
Gymnodinium sp.	X	X
Gyrodinium aureolum	X	

Table 3 Continued

	Phytoplankton	Benthos
Dinophyta		
Gyrodinium sp.	X	X
Heterocapsa triquetra	X	
Katodinium rotundatum	X	
Polykrikos kofoidii	X	
Prorocentrum gracile	X	
Prorocentrum micans	X	X
Prorocentrum minimum	X	X
Prorocentrum triestinum	X	
Protoperidinium mite	X	
Protoperidinium sp.	X	
Scrippsiella trochoidea	X	X
Euglenophyta		
Euglena acus		X
Euglena elastic	X	X
Euglena proxima	X	
Euglena sp.	X	X
Haptophyta		
Rhabdosphaera hispida	X	
Ochrophyta		
Dictyocha fibula	X	X
Synura uvella	X	X

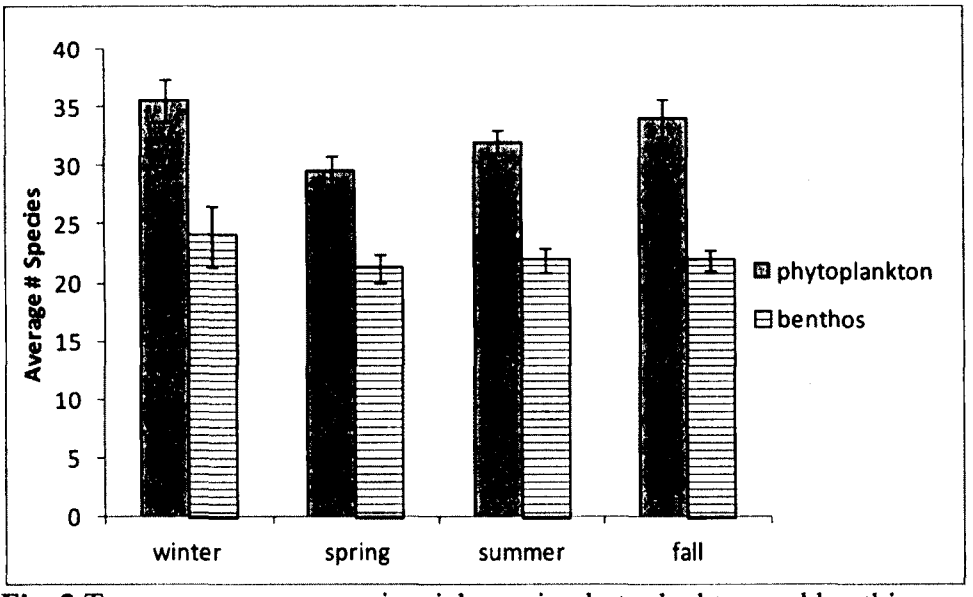

Fig. 2 Two-year average species richness in phytoplankton and benthic samples.

Table 4 Phytoplankton diversity indices for each year and season of study. SR = species richness, H′ = Shannon Index, NC = not collected. Stations denoted as: SXS = Saxis, HARB = Harborton, CC = Cape Charles, LYNN = Lynnhaven, LAF = Lafayette, HAMP = Hampton, NPC = New Point Comfort, GWR = Great Wicomico.

	2010				2011			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
SXS	42; 0.41	34; 1.64	35; 1.58	40; 2.03	33; 1.44	31; 1.90	30; 1.62	30; 1.86
HARB	33; 0.79	38; 2.12	33; 1.63	30; 2.05	38; 1.91	26; 1.88	27; 1.41	35; 2.19
CC	NC	27; 2.14	37; 1.88	46; 1.64	29; 1.69	31; 1.58	37; 1.88	42; 2.25
LYNN	37; 1.30	37; 2.29	41; 1.81	43; 1.71	47; 1.87	34; 1.21	33; 1.23	37; 2.09
LAF	33; 0.60	27; 1.93	29; 1.93	30; 1.82	30; 0.85	30; 1.85	23; 1.59	27; 1.74
HAMP	41; 1.79	28; 2.13	33; 1.30	31; 1.75	46; 1.94	25;1.17	28; 1.39	31; 1.96
NPC	37; 1.42	25; 1.72	36; 1.98	36; 2.12	23; 1.60	35; 1.50	33; 1.67	33; 2.02
GWR	NC	25; 2.00	32; 1.95	32; 1.96	29; 2.06	20; 1.17	32; 1.23	21; 0.36

Table 5 Microphytobenthos diversity indices for each year and season of study. SR = species richness, H′ = Shannon Index, NC = not collected. Stations denoted as: SXS = Saxis, HARB = Harborton, CC = Cape Charles, LYNN = Lynnhaven, LAF = Lafayette, HAMP = Hampton, NPC = New Point Comfort, GWR = Great Wicomico.

	2010				2011			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
SXS	30; 2.98	22; 2.83	21; 1.75	25; 3.26	21; 2.53	19; 2.13	18; 2.30	22; 2.53
HARB	41; 2.74	22; 1.95	29; 2.34	23; 0.77	22; 1.74	19; 0.81	23; 1.05	22; 1.50
CC	NC	25; 2.45	23; 2.85	24; 1.38	23; 2.68	26; 2.64	22; 2.50	25; 2.96
LYNN	23; 2.43	25; 2.86	18; 2.16	19; 2.60	15; 0.64	16; 1.59	16; 2.08	19; 0.90
LAF	33; 3.57	25; 3.17	24; 2.46	21; 2.31	29; 3.32	16; 2.47	19; 2.53	24; 3.02
HAMP	35; 3.55	29; 2.92	28; 3.11	22; 2.72	18; 2.54	23; 2.32	21; 2.73	23; 2.63
NPC	11; 1.84	25; 2.60	22; 2.57	18; 2.45	7; 1.60	13; 1.56	19; 1.74	13; 1.44
GWR	NC	21; 3.27	31; 3.43	25; 2.56	27; 3.49	14; 2.41	20; 2.80	25; 3.16

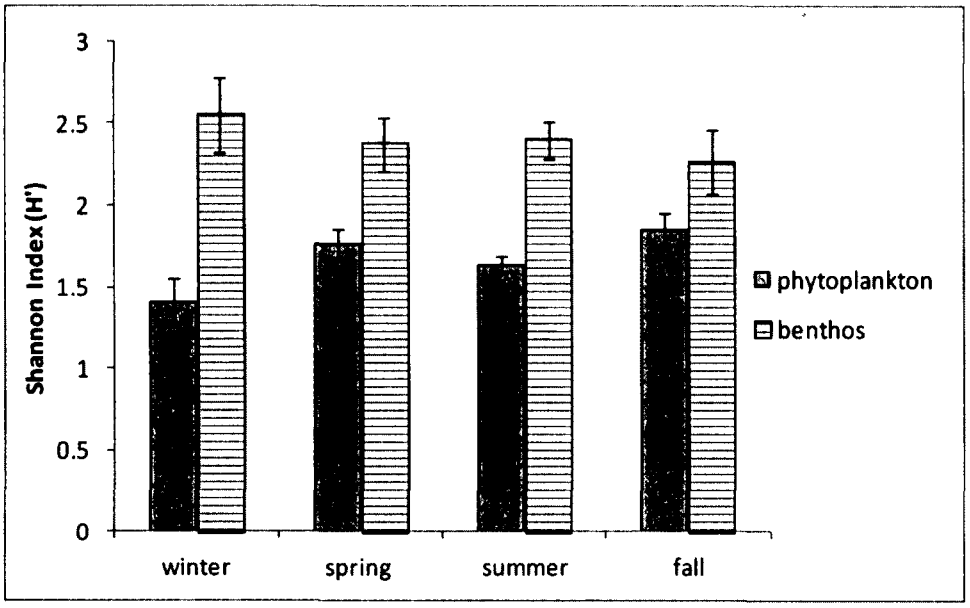

Fig. 3 Two-year average of Shannon Index of biodiversity in phytoplankton and benthic samples.

Seasonal trends in composition and biomass were apparent throughout the study in both habitats. The phytoplankton community was dominated by diatoms in winter and early spring, with dinoflagellates co-dominating with diatoms from late spring throughout summer and early fall, before returning to a winter, diatom-rich community (Figs. 4, 5). The micophytobenthos followed a similar pattern of seasonality, with these habitats comprised of diatoms throughout winter and spring, with a gradual shift to a mixed community of diatoms, cyanobacteria, and chlorophytes during late spring and early summer, before returning to mainly a fall/winter diatom population (Figs. 6, 7). These trends were apparent in both cell abundance and biomass for both phytoplankton and microphytobenthic communities.

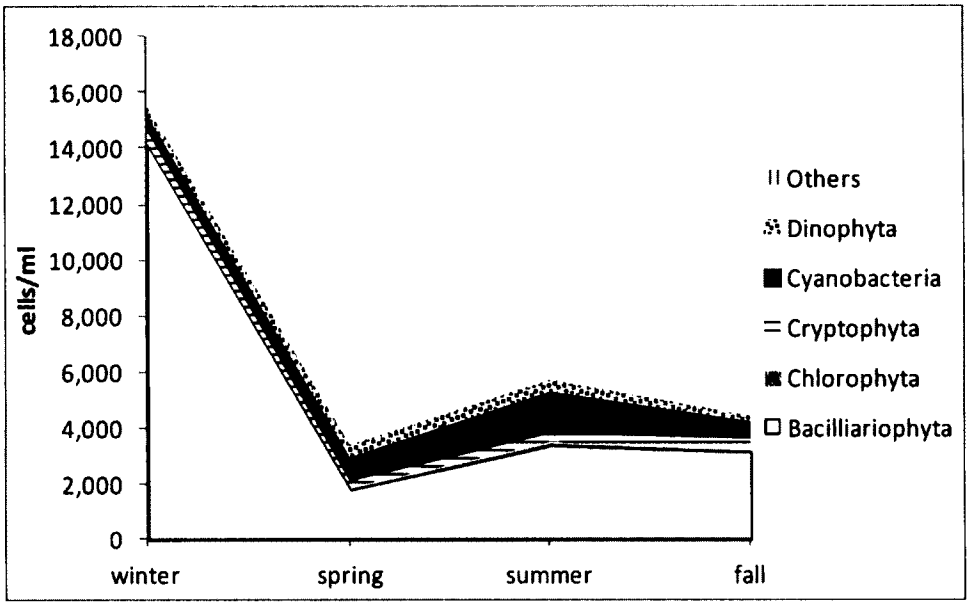

Fig. 4 Two-year average phytoplankton abundance (cells/ml) across all stations.

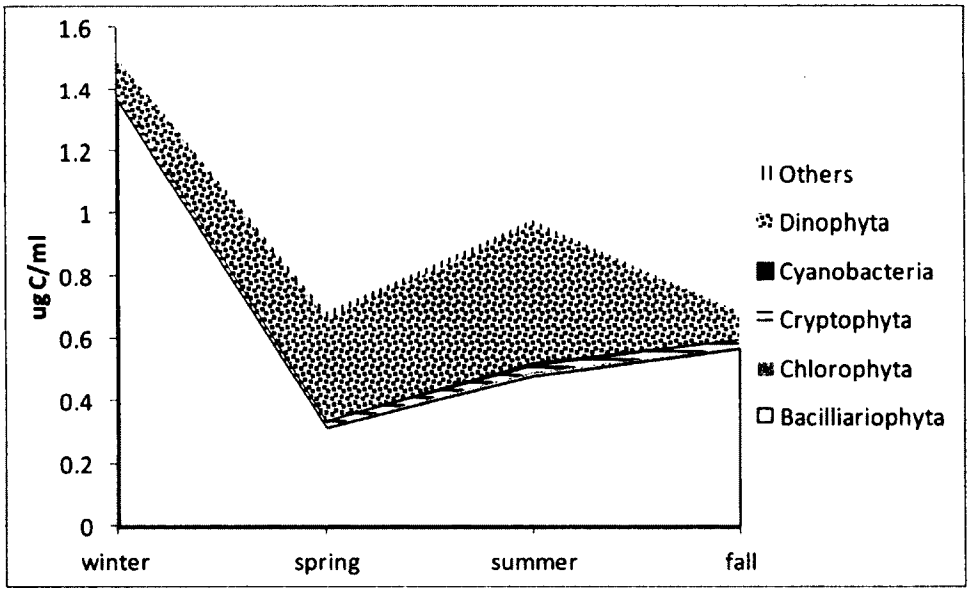

Fig. 5 Two-year average phytoplankton biomass (ug C/ ml) across all stations.

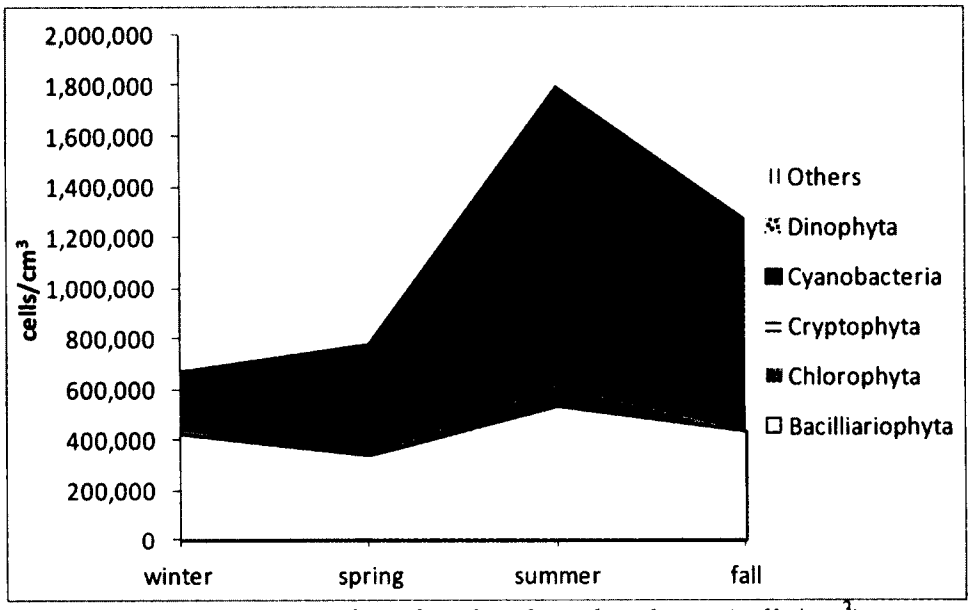

Fig. 6 Two-year average microphytobenthos abundance (cells/cm^3) across all stations.

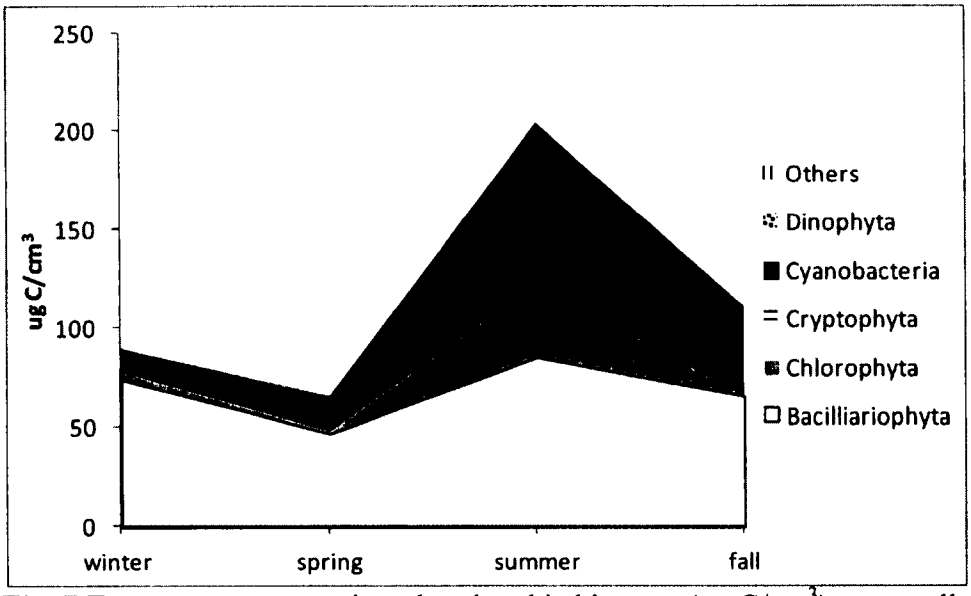

Fig. 7 Two-year average microphytobenthic biomass (ug C/cm^3) across all stations.

Phytoplankton Abundance

Phytoplankton Abundance - 2010

Total phytoplankton cell abundance was highest during the 2010 winter (Fig. 8), with cell densities at all stations > 10^4 cells/ml, with a peak density (> 7.0 X 10^4 cells/ml) at the Saxis station, which was mainly composed of dense concentrations of the centric diatom *Skeletonema costatum* (> 6.5 X 10^4 cells/ml). Diatoms dominated cell abundances at all stations during 2010. Densities dropped in the 2010 spring (Fig. 9), with all concentrations < 7.0 X 10^3 cells/ml at each station, and were again highest at the Saxis station (> 6.0 X 10^3 cells/ml). The cyanobacteria and dinoflagellates were present at all stations. Cell abundances increased during the 2010 summer (Fig. 10), but did not attain densities noted in winter. Diatoms, along with filamentous cyanobacteria composed the majority of algal taxa. Fall densities mirrored those in the spring (10^3 – 4.0 X 10^3 cells/ml), with an assemblage of diatoms, cyanobacteria, and cryptophytes representing the dominant algae present (Fig. 11). Prominent algal taxa throughout the 2010 sampling period included the diatoms *S. costatum*, *Cerataulina pelagica*, *Cylindrotheca closterium*, and *Chaetoceros sp.*, plus the dinoflagellate *Gonyaulax sp.*, cryptomonad *Cryptomonas sp.*, and cyanobacteria *Pseudanabaena sp.*

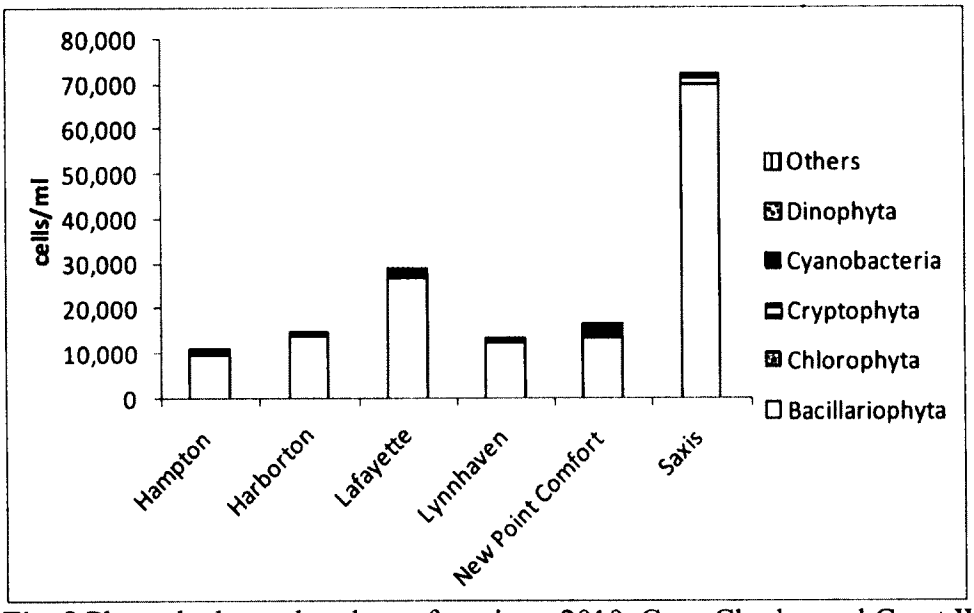

Fig. 8 Phytoplankton abundance for winter 2010. Cape Charles and Great Wicomico not collected due to weather.

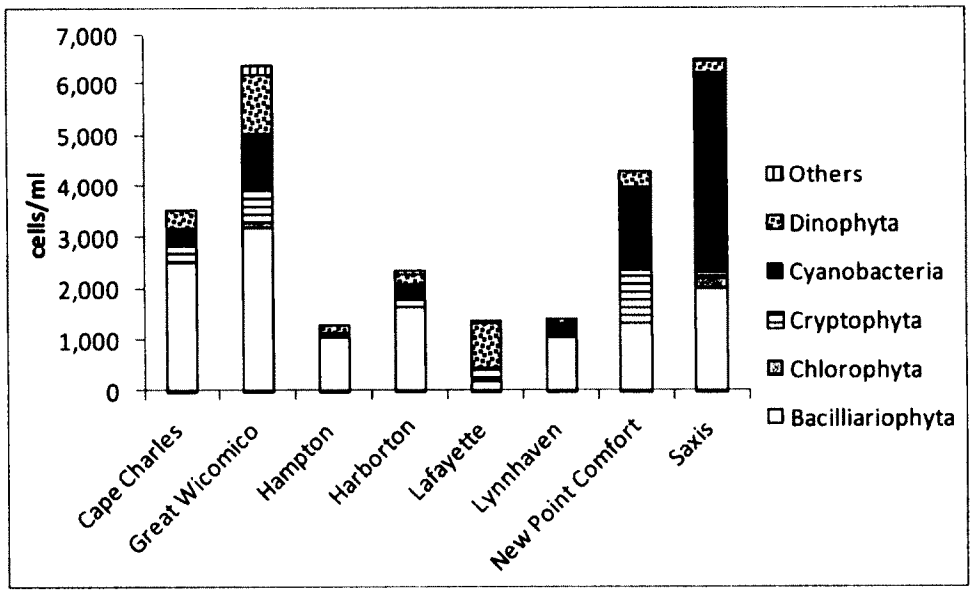

Fig. 9 Phytoplankton abundance for spring 2010.

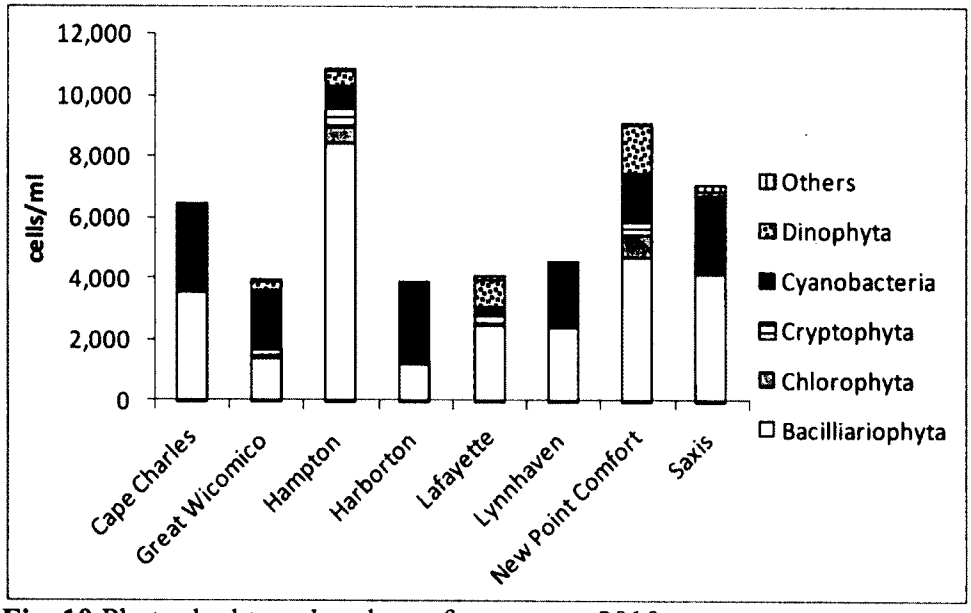

Fig. 10 Phytoplankton abundance for summer 2010.

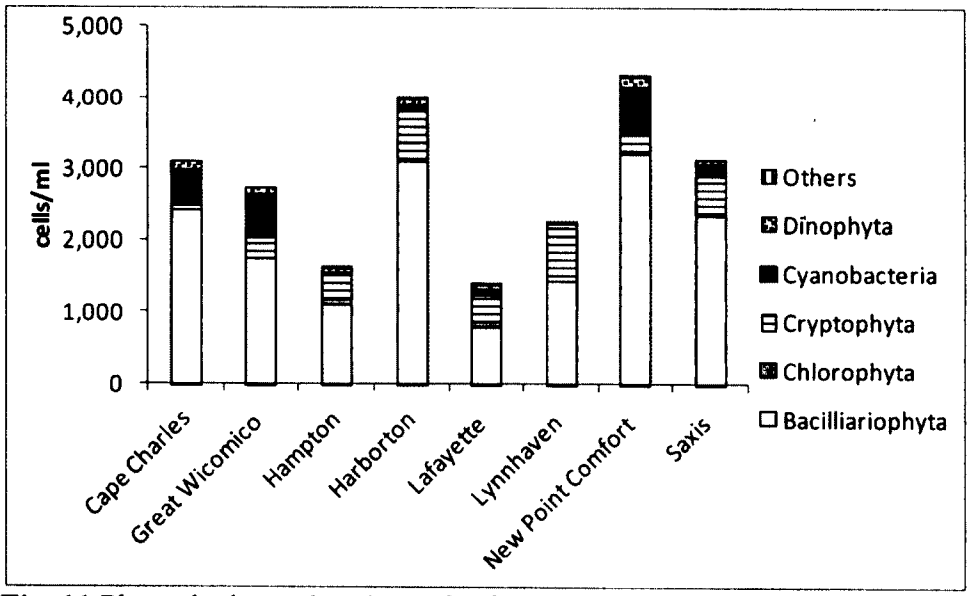

Fig. 11 Phytoplankton abundance for fall 2010.

Phytoplankton Abundance – 2011

Microalgal abundances in 2011 followed similar trends as those the previous year. In winter, cell densities ranged from $1.0 \times 10^3 - 1.4 \times 10^4$ cells/ml (Fig. 12), with the diatom *S. costatum* again dominant. Spring densities regressed, with all but one station (Saxis) having cell abundances $< 4.0 \times 10^3$ cells/ml (Fig. 13). Taxonomic composition was generally split between diatoms and cyanobacteria during spring, with the diatoms *S.costatum* and *C. closterium*, and cyanobacteria *Pseudanabaena sp.* and *Merismopedia elegans* being dominant. In the 2011 summer there was an increase of phytoplankton cell densities, though no station had densities > than 1.0×10^4 cells/ml (Fig. 14). The diatom *C. closterium* was in high densities at every station during the 2011summer, with the highest density at the Hampton site ($> 7.0 \times 10^3$ cells/ml). In general, diatoms and filamentous cyanobacteria dominated cell abundances at every station during the summer. Fall cell densities exhibited a similar pattern in 2011 (as those in 2010), with abundances between 10^3 and 5.0×10^3 cell/ml (Fig. 15), except for high numbers at Great Wicomico ($> 1.3 \times 10^4$ cells/ml) and Saxis ($> 1.8 \times 10^4$ cells/ml), that were driven by high densities of *C. closterium* and several pennate diatoms, respectively.

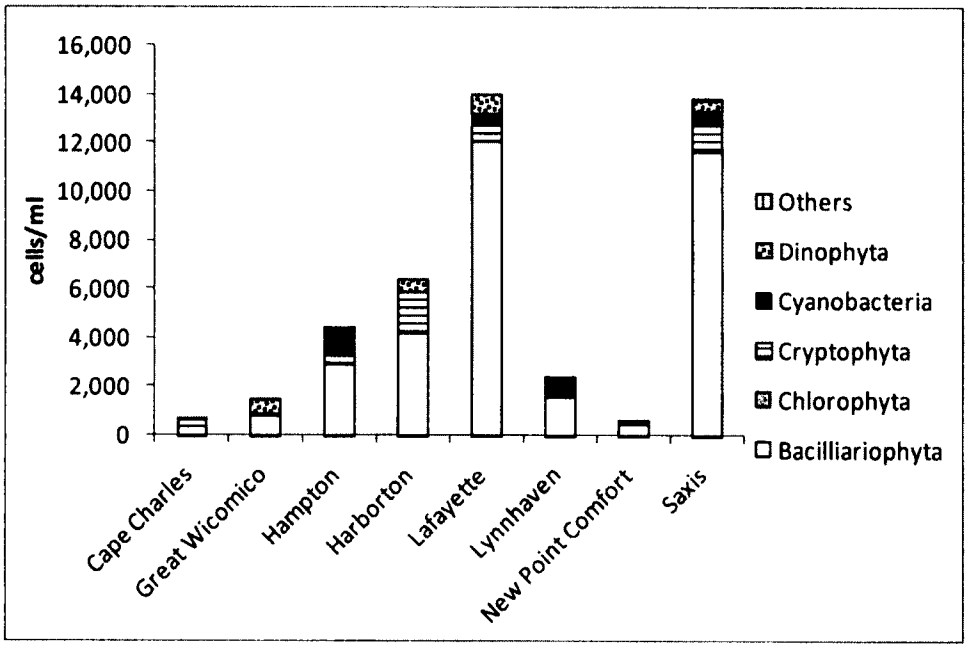

Fig. 12 Phytoplankton abundance for winter 2011.

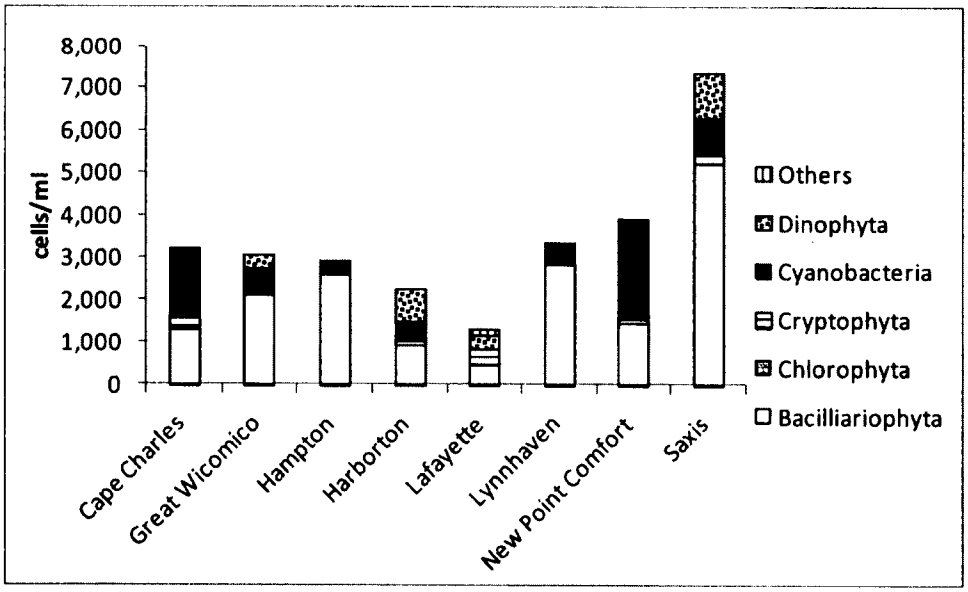

Fig. 13 Phytoplankton abundance for spring 2011.

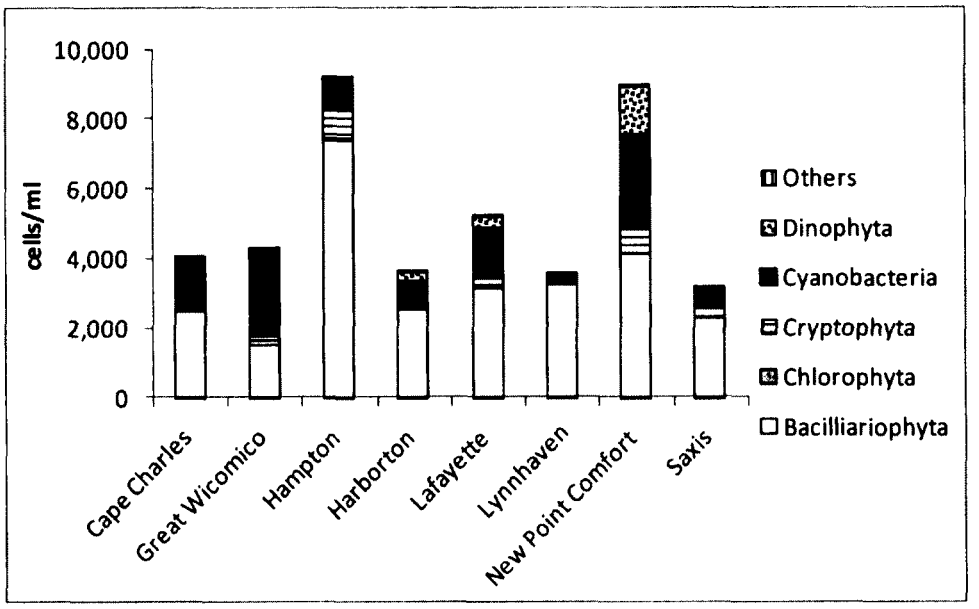

Fig. 14 Phytoplankton abundance for summer 2011.

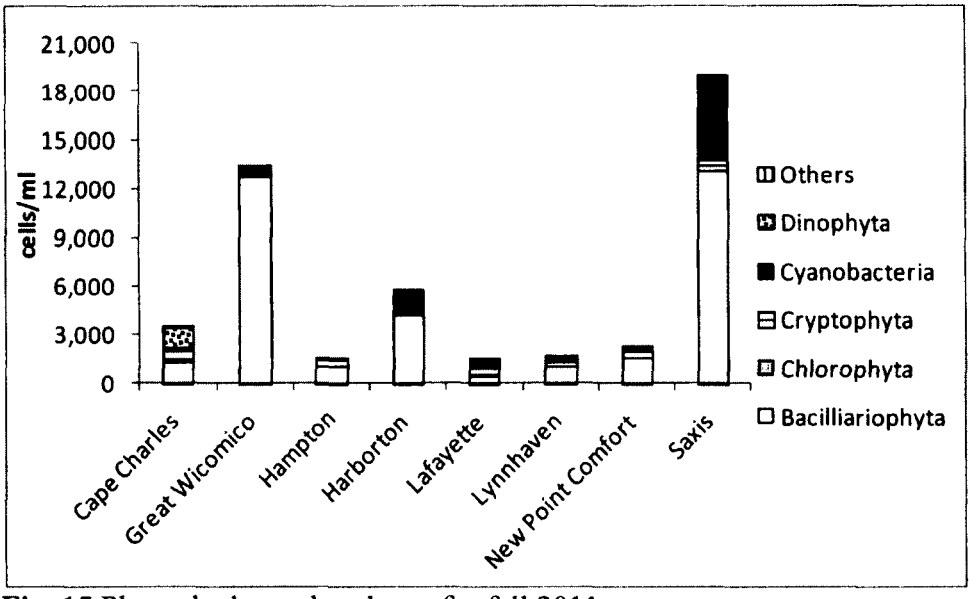

Fig. 15 Phytoplankton abundance for fall 2011.

Phytoplankton Biomass

Phytoplankton Biomass - 2010

The 2010 phytoplankton biomass values for winter ranged from 0.6 – 3.3 ug C/ml, and consisted mainly of diatoms, which were the dominant flora during this sampling period (Fig. 16). In spring there was a shift in biomass, produced by a diatom-dominated flora, to that of dinoflagellates, with these taxa almost doubling the biomass of diatoms across all stations (Fig. 17). The dinoflagellate biomass was highest in the Lafayette (2.08 ug C/ml), where *Gymnodinium sp.* and *Gonyaulax sp.* were the dominant taxa, and in the Great Wicomico site (1.12 ug C/ml), where high *Gyrodinium sp.*, *Gymnodinium sp.*, and *Scrippsiella trochoidea* were present. The summer of 2010 had similar distributions of diatom and dinoflagellate biomass across all stations (Fig. 18). New Point Comfort contained the highest dinoflagellate biomass (2.10 ug C/ml) during this sampling period, with the Lafayette having values (1.21 ug C/ml) also high, and likely the result of a *Cochlodinium polykrikoides* bloom in August of that year. The fall had similar patterns of algal biomass with the winter (Fig. 19) dominated by diatoms, but these values were lower at most stations < 0.5 ug C/ml).

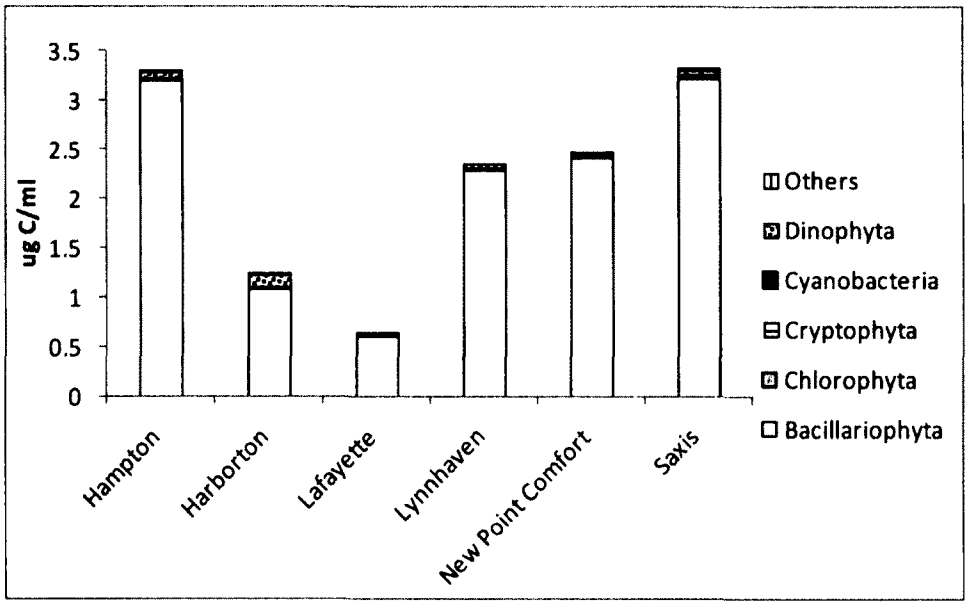

Fig. 16 Phytoplankton biomass for winter 2010. Cape Charles and Great Wicomico not collected due to weather.

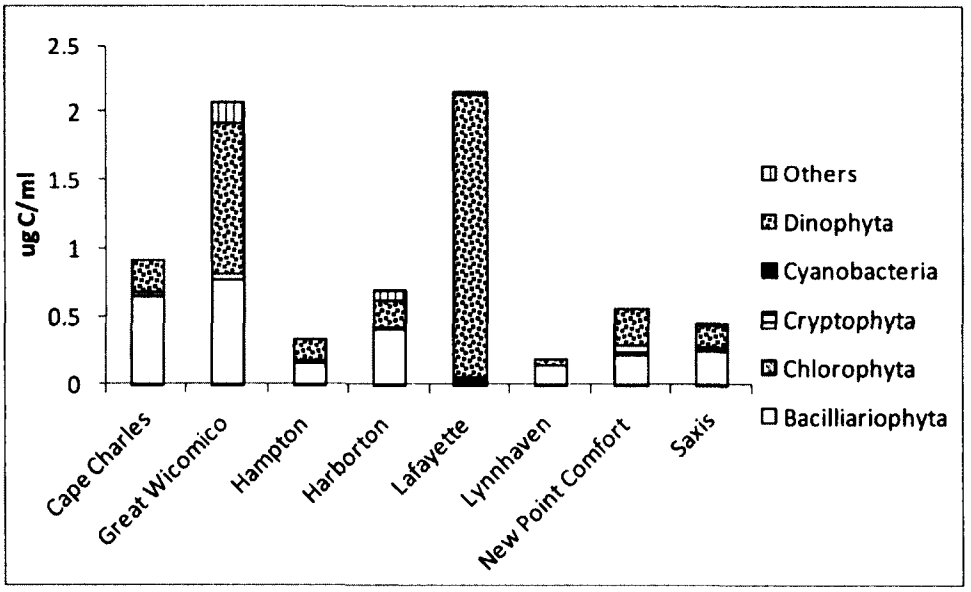

Fig. 17 Phytoplankton biomass for spring 2010.

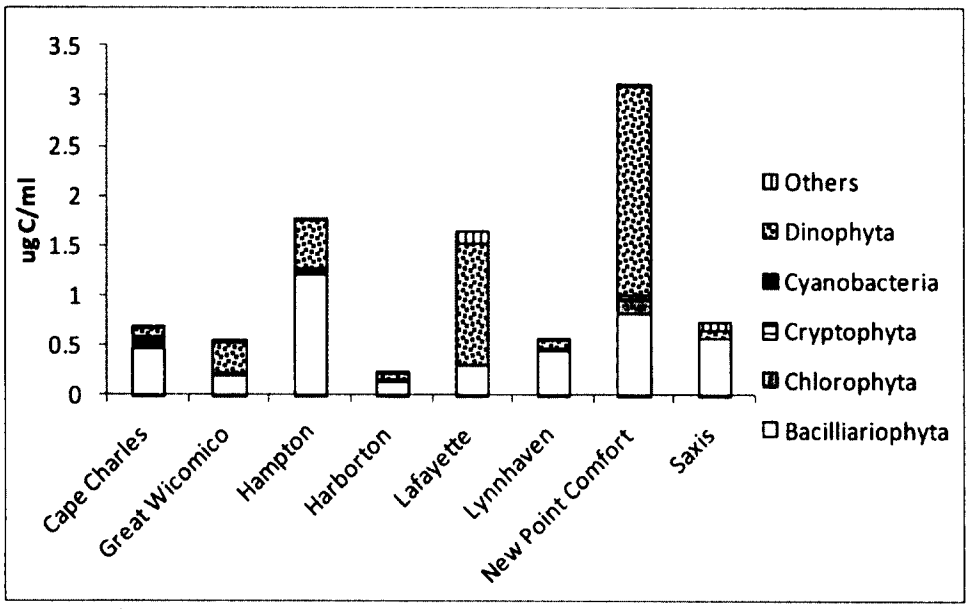

Fig. 18 Phytoplankton biomass for summer 2010.

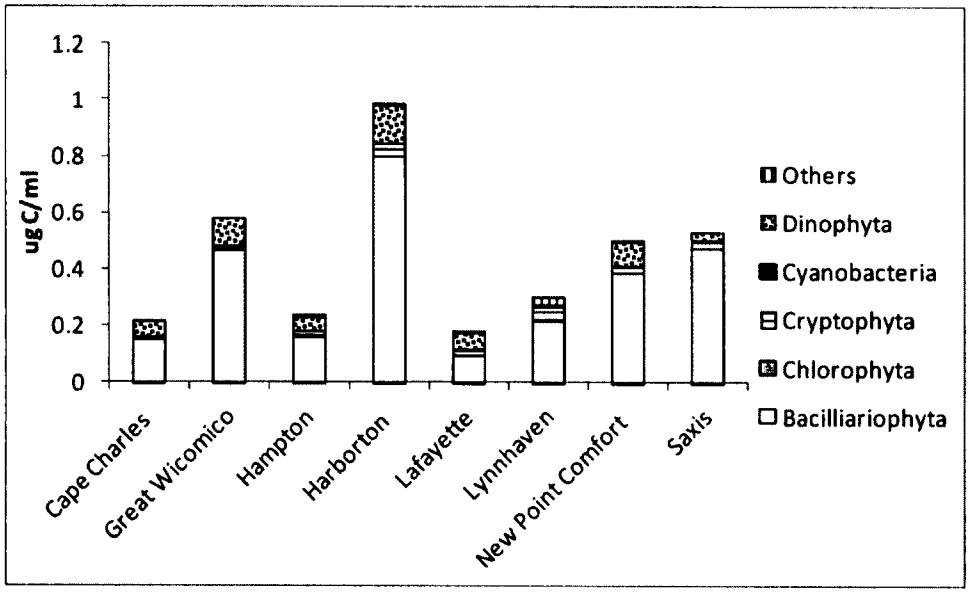

Fig. 19 Phytoplankton biomass for fall 2010.

Phytoplankton Biomass – 2011

High microalgal diatom biomass during the 2011 winter was similar to the previous year, except for two stations (Lafayette and Great Wicomico) that had high dinoflagellate biomass of 0.48 ug C/ml and 0.39 ug C/ml respectively (Fig. 20). These high dinoflagellate values came from the same taxa present during the winter and spring of 2010. These were *Gymnodinium sp.*, and *S. trochoidea*, plus *Gyrodinium aureolum.* The spring biomass values were below 0.5 ug C/ml at most stations (Fig. 21) that were dominated by diatom biomass, except for high concentrations of the dinoflagellates *Gymnodinium sp.* and *Heterocapsa rotundatum* at the Lafayette site. The 2011 summer had a slight increase in overall biomass, though most stations had values below 1.0 ug C/ml including several stations < 0.5 ug C/ml (Fig. 22). Diatoms continued to constitute the majority of the biomass at all stations, except for New Point Comfort, which had elevated dinoflagellate biomass (1.85 ug C/ml) due to the increased *Gonyaulax sp.* concentrations. Fall 2011 exhibited a broad range of biomass values, from 0.1 ug C/ml in the Lafayette, to 2.6 ug C/ml at Saxis (Fig. 23). Diatoms again composed the majority of the biomass at all stations except Cape Charles, which had increased densities and biomass of the dinoflagellates *Gymnodinium sp.*, *Prorocentrum minimum*, and *Heterocapsa triquetra.*

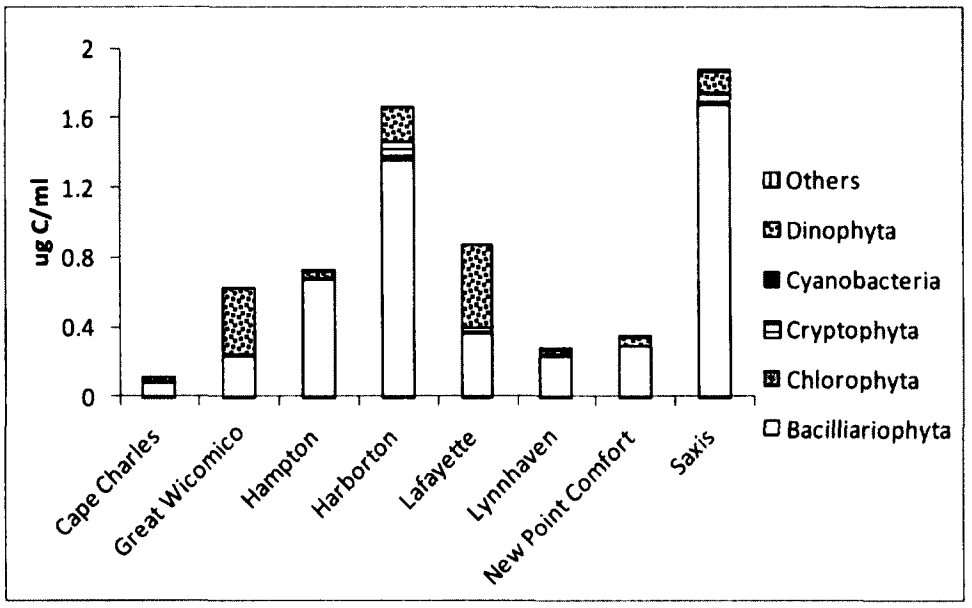

Fig. 20 Phytoplankton biomass for winter 2011.

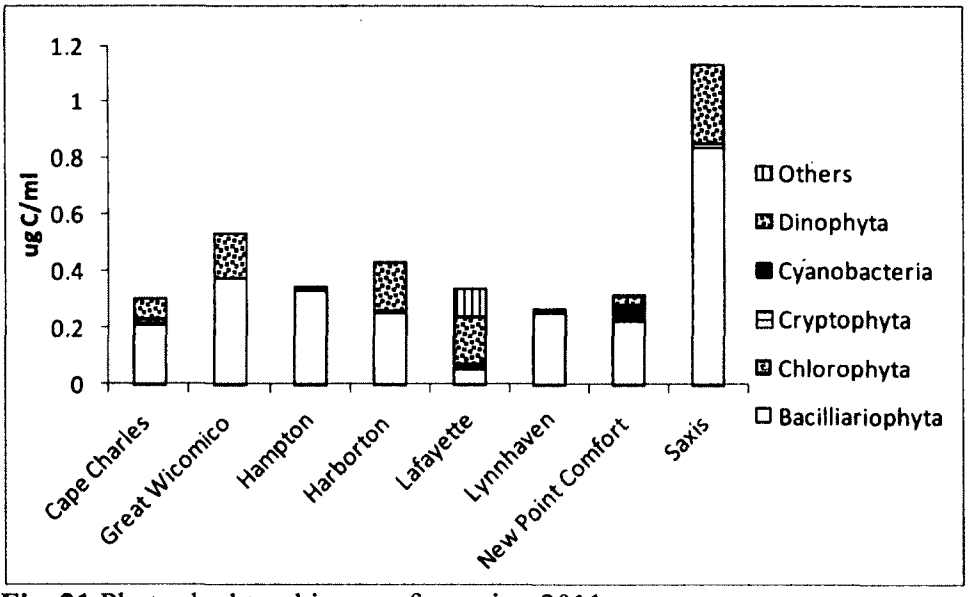

Fig. 21 Phytoplankton biomass for spring 2011.

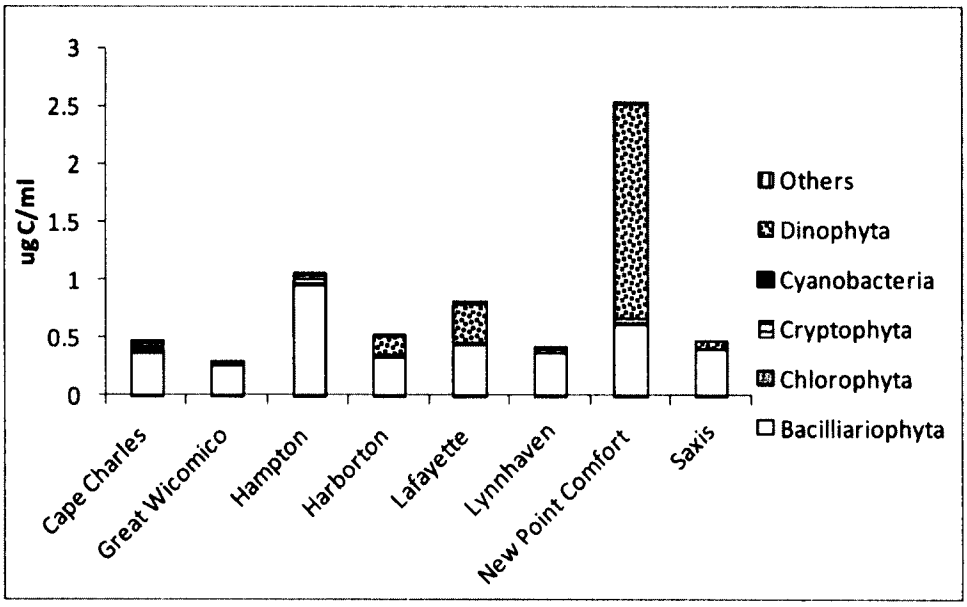

Fig. 22 Phytoplankton biomass for summer 2011.

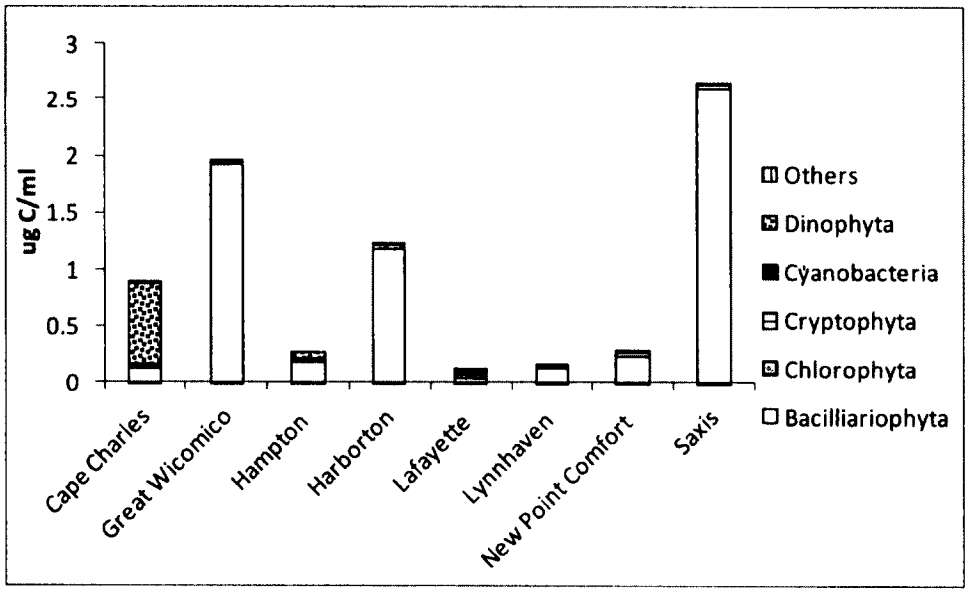

Fig. 23 Phytoplankton biomass for fall 2011.

Microphytobenthic Abundance

Microphytobenthic Abundance - 2010

Across all stations during both sampling years, the benthic microalgal abundance was significantly higher ($p < 0.0001$) than the pelagic phytoplankton abundance. The cell densities were generally in the 1.0×10^5 cells/cm^3 range and frequently eclipsing 10^6 cells/cm^3, whereas phytoplankton densities were generally below 5.0×10^3 cells/ml. In the winter of 2010, the benthic cell abundance was mainly comprised of diatoms except at one station (Harborton) where cell densities > 10^6 cells/cm^3 of the cyanobacteria *Phormidium sp.* were present (Fig. 24). In spring, the benthos remained dominated by diatoms (Fig. 25), though increasing numbers of cyanobacteria were present, namely *Anabaena sp.*, *Aphanocapsa sp.*, and *Lyngbya aestuarii*. The diatoms *Fragilaria sp.*, *Gyrosigma sp.*, *Navicula sp.*, and *Melosira moniliformis* were most abundant at all stations during spring 2010. During the 2010 summer, algal densities increased (Fig. 26) with all but two stations having counts over 10^6 cells/cm^3. These algae were dominated by cyanobacteria at nearly every station, with *L. aestuarii*, *Merismopedia elegans*, *Chroococcus sp.*, and *Anabaena sp.* the most abundant taxa. Cyanobacteria continued to dominate into the fall of 2010 at all stations (Fig. 27). During summer the total cell abundance declined at the Saxis, Lynnhaven, and Hampton sites, while increasing in the other locations, with most remaining above 10^6 cells/cm^3. Much like the previous sampling season, *L. aestuarii*, and *M. elegans* were the dominant taxa.

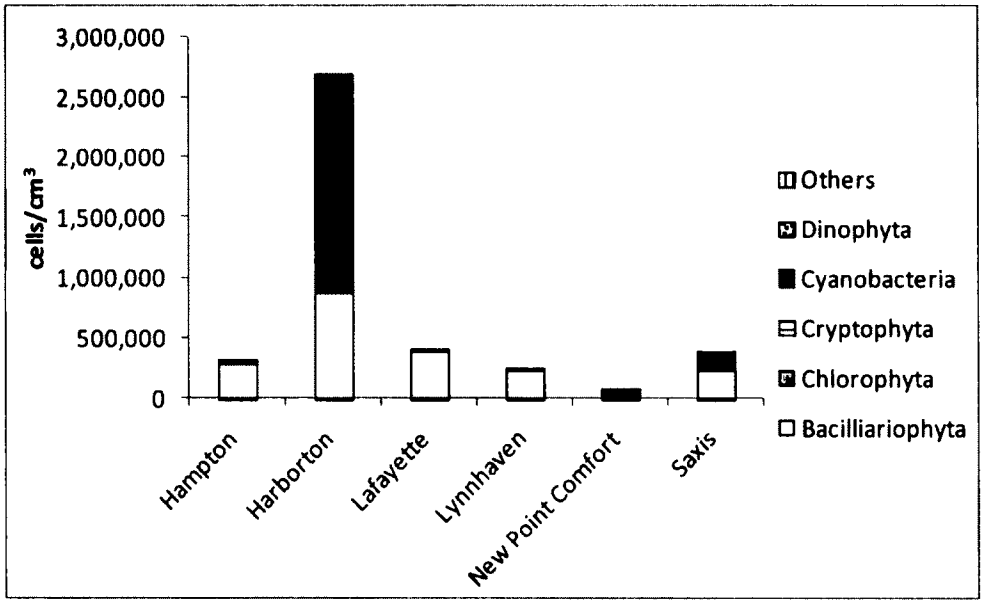

Fig. 24 Microphytobenthic abundance for winter 2010. Cape Charles and Great Wicomico not collected due to weather.

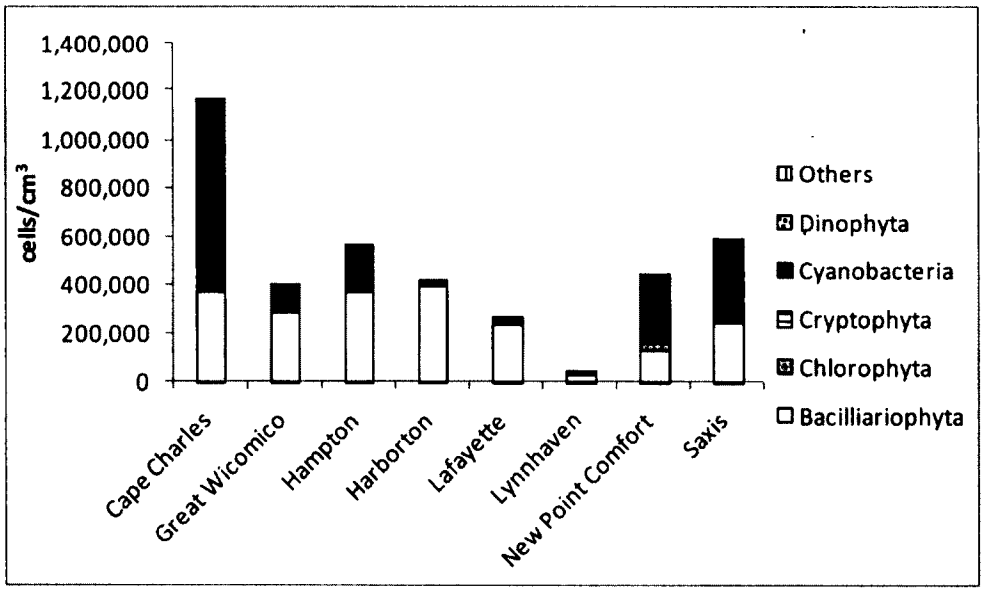

Fig. 25 Microphytobenthic abundance for spring 2010.

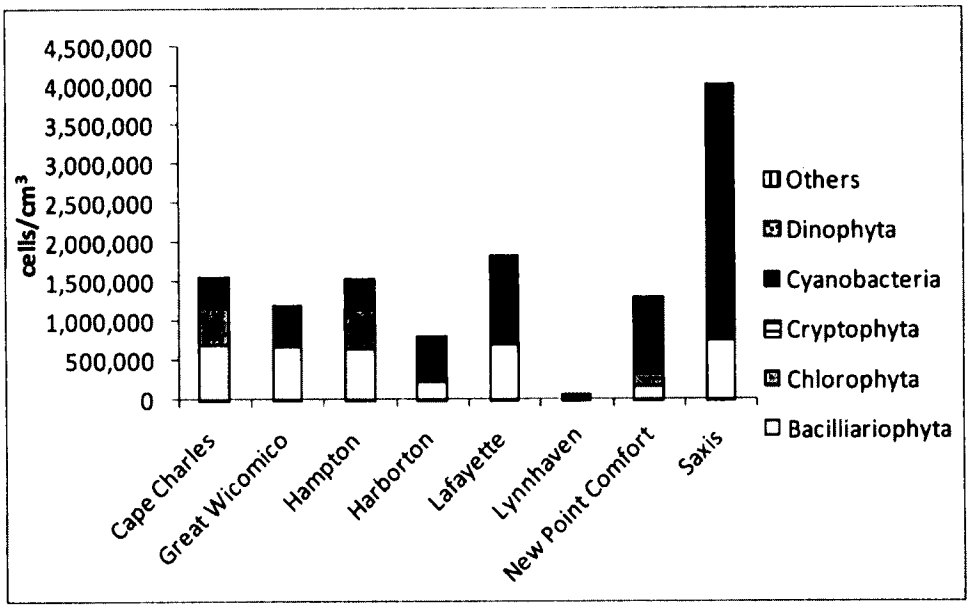

Fig. 26 Microphytobenthic abundance for summer 2010.

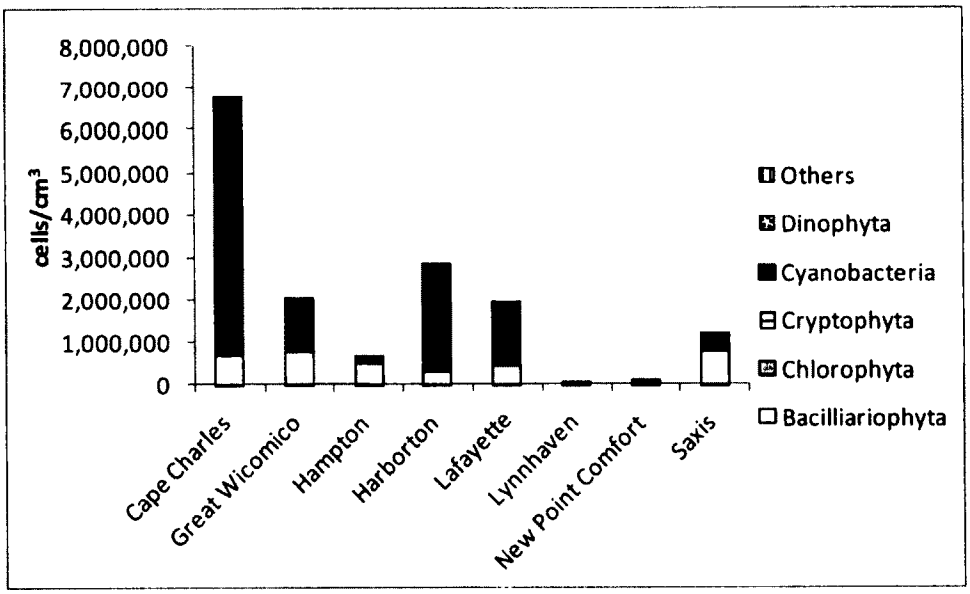

Fig. 27 Microphytobenthic abundance for fall 2010.

Microphytobenthic Abundance – 2011

Similar to 2010, diatoms were most abundant in the benthos during the 2011 winter sampling (Fig. 28). Overall cell densities were < 1.0 X 10^6 cells/cm^3 at all but two stations (Lynnhaven, New Point Comfort). Dominant taxa were *Bacillaria paxillifer*, *Thalassionema nitzschioides*, *Gyrosigma sp.*, and *Navicula sp.*, which had high densities at all stations. The spring 2011 benthic communities shifted to cyanobacteria, with densities within the 5.0 X 10^5 – 10^6 cells/cm^3 range (Fig. 29). The cyanobacteria *L. aestuarii*, *Anabaena sp.*, and *M. elegans* were dense during this season, particularly at the Harborton site, where *M. elegans* densities exceeded 3.0 X 10^6 cells/cm^3. Cell densities in 2011 summer increased compared to the previous season, with almost all stations having abundances > 10^6 cells/cm^3 (Fig. 30), and all but one station (Lynnhaven) dominated by cyanobacteria (e.g. *Anabaena sp.*, *M. elegans*, and *L. aestuarii*). Microphytobenthic abundance in the fall of 2011 reverted back to winter conditions, with most stations falling below the 1.0 X 10^6 cells/cm^3 level, with diatoms the dominant microalgal group (Fig. 31).

Analysis of variance tests showed significant differences in microphytobenthic average abundance across stations over the span of this study. Tukey post-hoc tests revealed both Cape Charles ($p = 0.018$) and Harborton ($p = 0.013$) had significantly higher cell abundances than the Lynnhaven station.

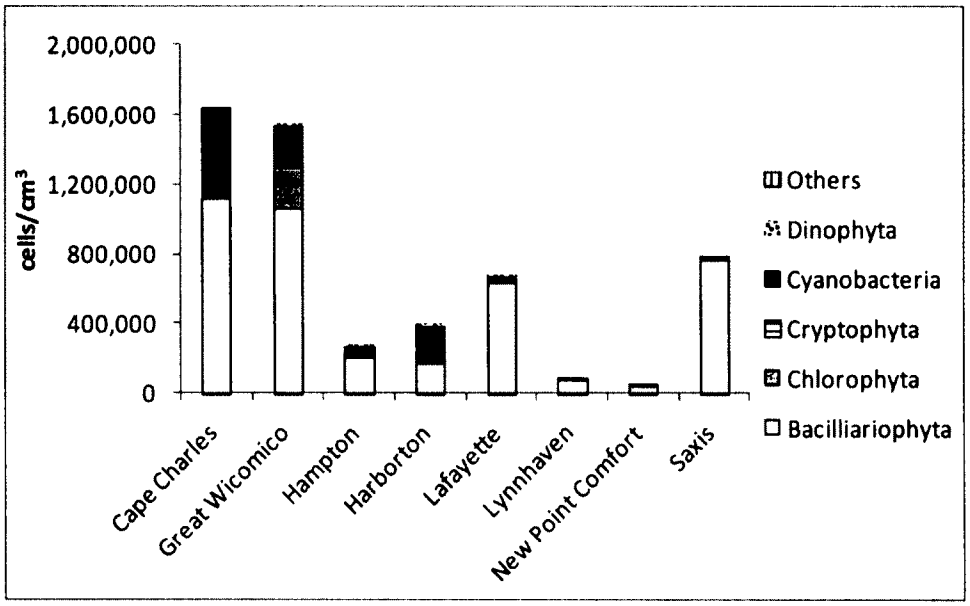

Fig. 28 Microphytobenthic abundance for winter 2011.

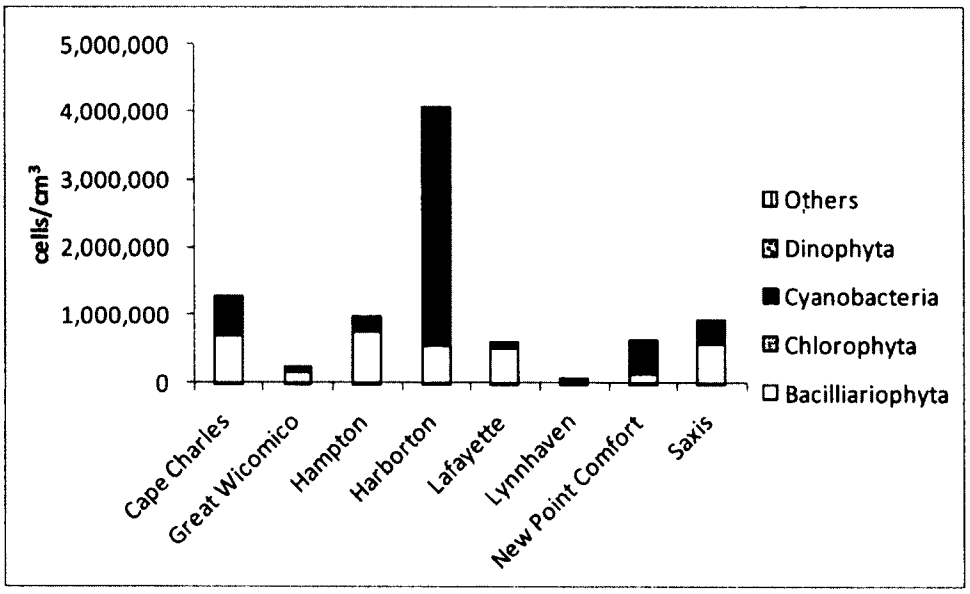

Fig. 29 Microphytobenthic abundance for spring 2011.

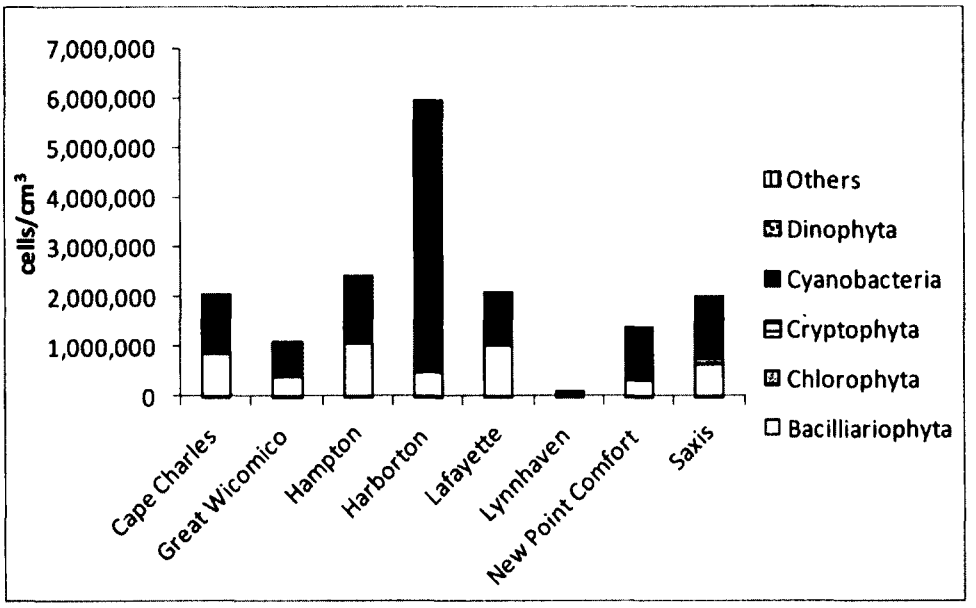

Fig. 30 Microphytobenthic abundance for summer 2011.

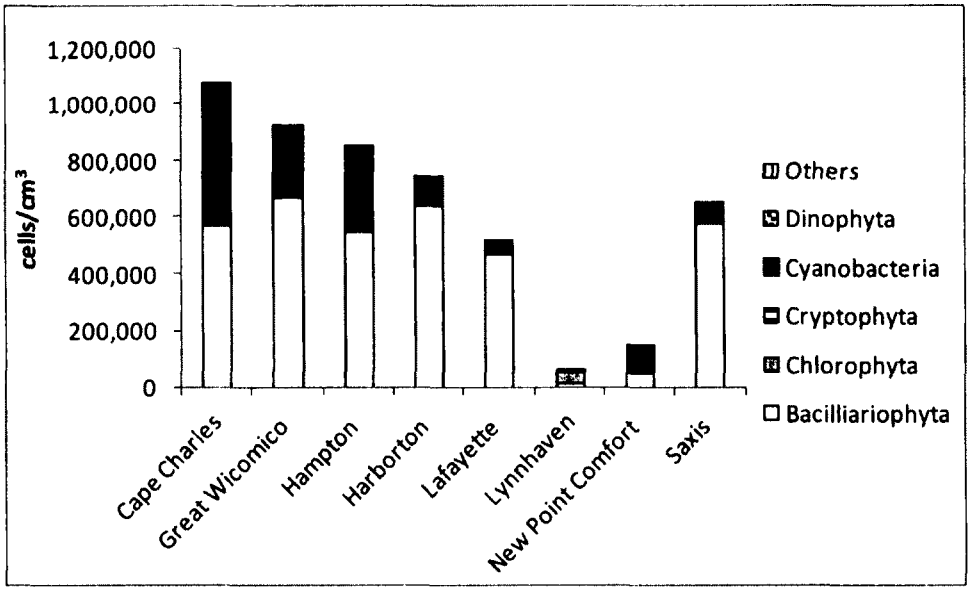

Fig. 31 Microphytobenthic abundance for fall 2011.

Microphytobenthic Biomass

Microphytobenthic Biomass - 2010

The microphytobenthic biomass had a similar pattern as their abundance, with values significantly higher ($p < 0.0001$) than phytoplankton biomass over the course of the sampling period. Within the benthos, only Cape Charles and Lynnhaven were had significantly different biomass values ($p = 0.042$). Biomass during the 2010 winter ranged from 11 – 280 ug C/cm^3, with the majority from the diatoms (Fig. 32). Algal biomass increased at nearly every station in the 2010 spring, again dominated by diatoms at most stations, as well as having an increased overall cyanobacteria biomass (Fig. 33). Algal biomass increased at every sampling station during the 2010 summer, with a high of 529 ug C/cm^3 at the Saxis site, with all but one station over 110 ug C/cm^3 (Fig. 34). The fall biomass was split evenly between diatoms and cyanobacteria (Fig. 35), and in general, the biomass decreased from summer values.

Microphytobenthic Biomass – 2011

The 2011 microalgal biomass of the benthos followed the same trends as in 2010, with the majority of algal biomass consisting of diatoms, that included a wide range of values across sites (Fig. 36). Spring sampling produced slightly lower overall biomass values in the benthos (Fig. 37), with increasing cyanobacteria biomass occurring at most stations. A pronounced cyanobacteria increase was at the Harborton site due to the colonial cyanobacteria *M. elegans* having a biomass value of 93.48 ug C/cm^3. Similar to 2010, the 2011 summer had increased overall biomass (Fig. 38) along with generally an

even distribution of diatom and cyanobacteria biomass across all stations. The fall microphytobenthic biomass returned to trends noted the previous winter, with overall biomass lower than in summer and diatoms dominating at every station (Fig. 39).

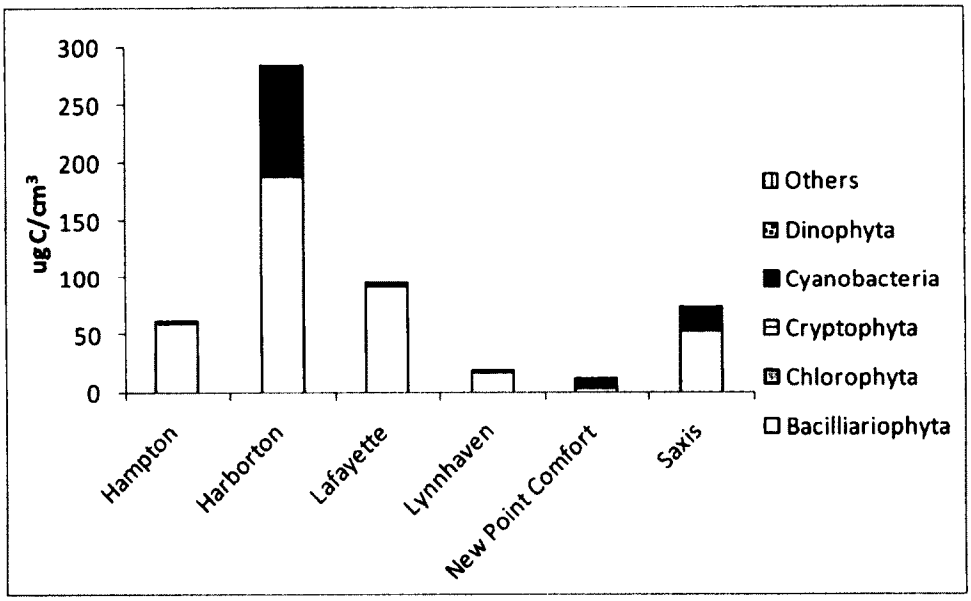

Fig. 32 Microphytobenthic biomass for winter 2010. Cape Charles and Great Wicomico not collected due to weather.

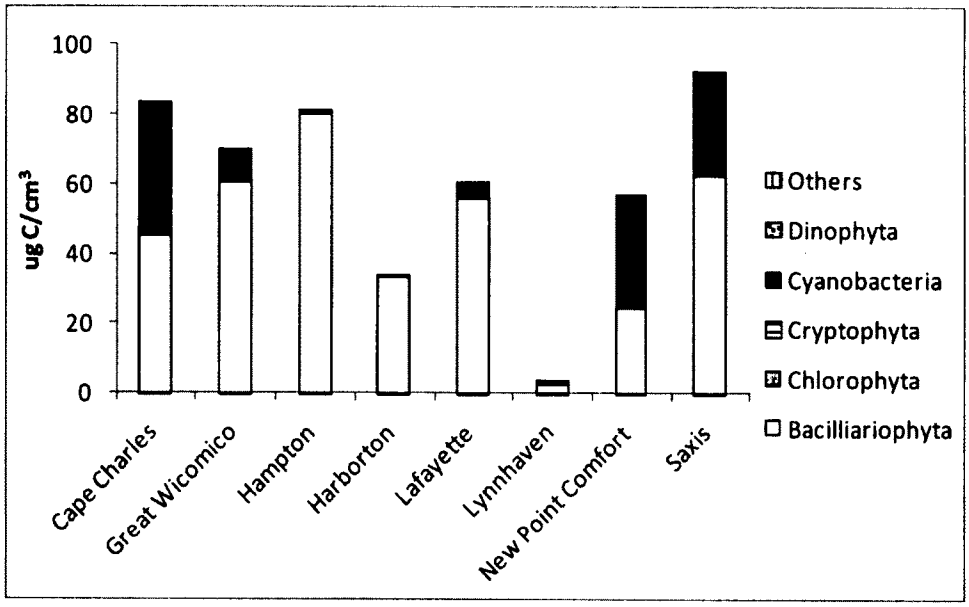

Fig. 33 Microphytobenthic biomass for spring 2010.

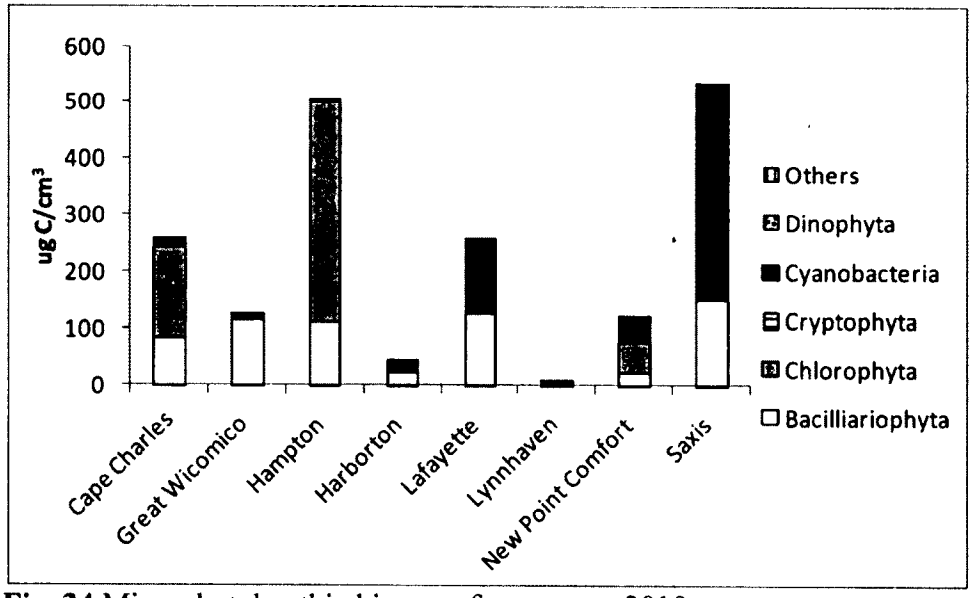

Fig. 34 Microphytobenthic biomass for summer 2010.

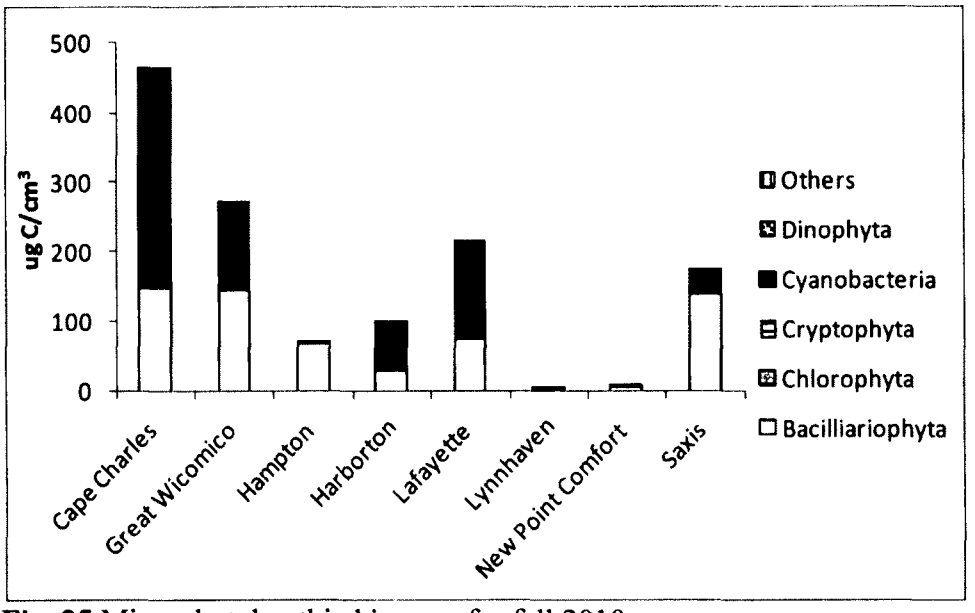

Fig. 35 Microphytobenthic biomass for fall 2010.

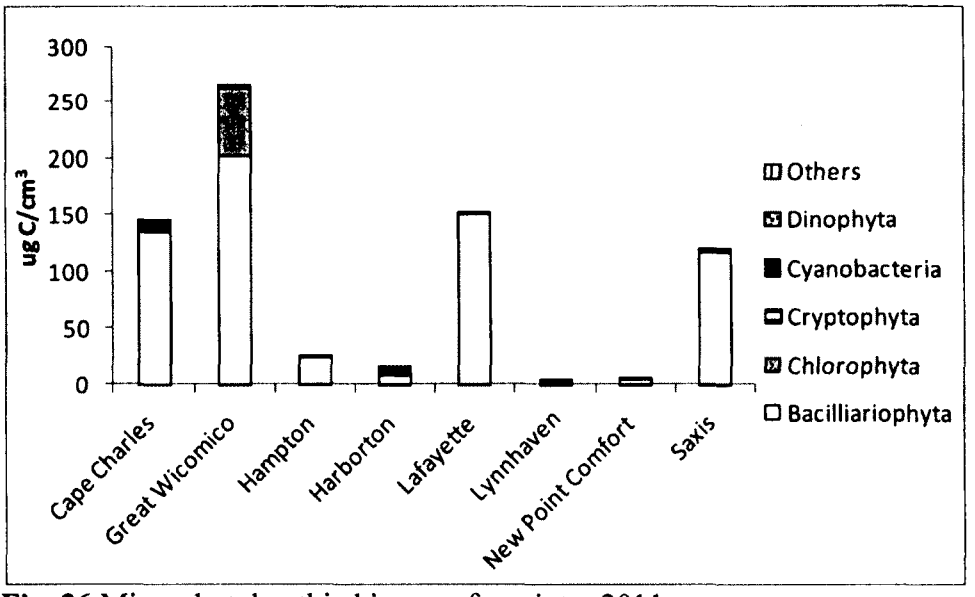

Fig. 36 Microphytobenthic biomass for winter 2011.

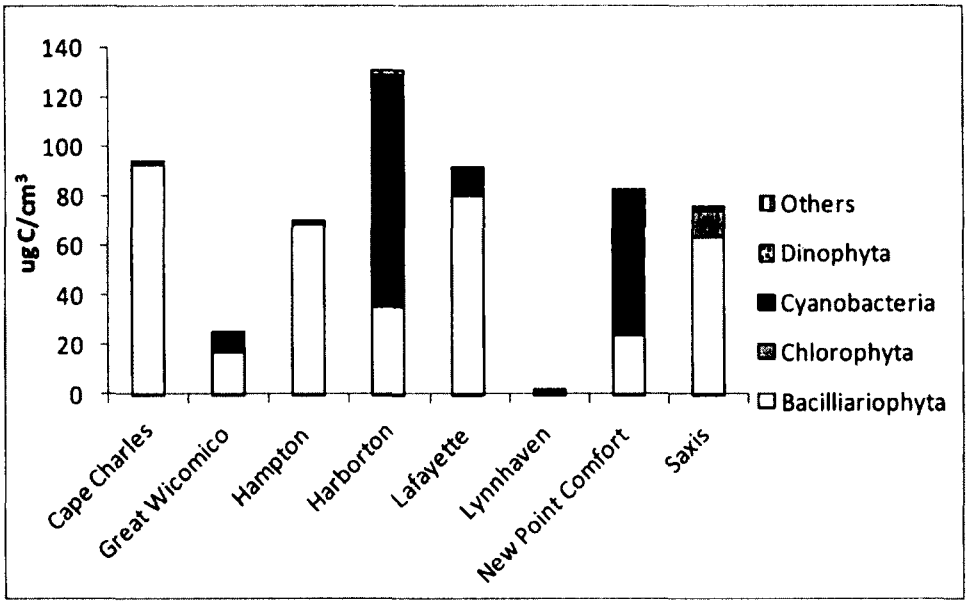

Fig. 37 Microphytobenthic biomass for spring 2011.

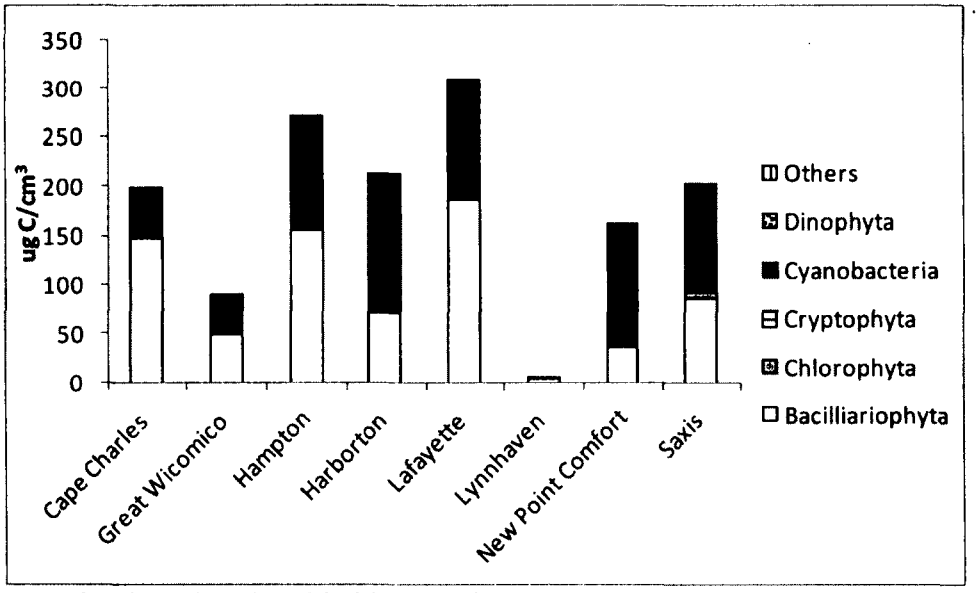

Fig. 38 Microphytobenthic biomass for summer 2011.

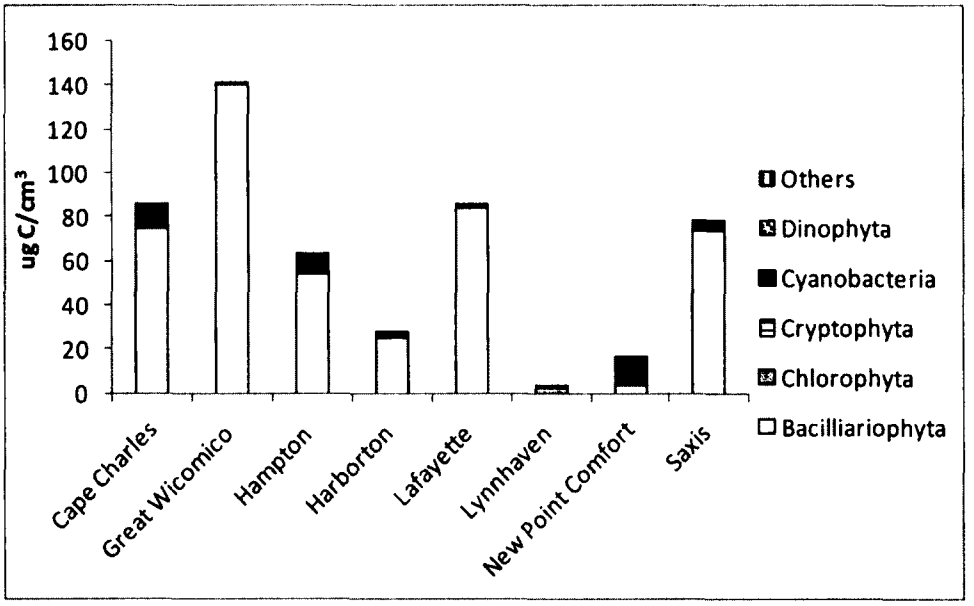

Fig. 39 Microphytobenthic biomass for fall 2011.

CHAPTER IV

RESULTS - PRIMARY PRODUCTIVITY

Phytoplankton

Two-year average phytoplankton primary productivity rates ranged from a high of 755 mg C/m^3/hr at the Lafayette station, to a low of 141 mg/C/m^3/hr at the New Point Comfort station (Fig. 40). Overall, productivity rates in the phytoplankton were variable across all stations, showing no apparent seasonal trends, however these differences in rates were not significant ($p = 0.243$). The 2010 winter saw a high of 1270 mg C/m^3/hr at the Lafayette station, and a low at Hampton, with a rate of 89 mg C/m^3/hr (Fig. 41). Spring productivity increased overall, though the highest rate decreased from the winter, with 734 mg C/m^3/hr at Harborton and New Point Comfort again showing the lowest rate at 90 mg C/m^3/hr (Fig. 42). Summer and fall rates continued to be variable, with New Point Comfort again having the lowest rate, and Harborton the highest, with a station-wide average of 277 mg C/m^3/hr in the spring (Fig. 43, while rates averaged 130 mg C/m^3/hr in the fall (Fig. 44). Productivity rates in 2011 winter decreased from 2010, with an average of 139 mg C/m^3/hr (Fig. 45). From 2011 winter through the spring and summer, the Lafayette station continued to have the highest phytoplankton productivity rates (Figs. 46, 47), and average rates increased through fall to a two-year high of 728 mg C/m^3/hr (Fig. 48).

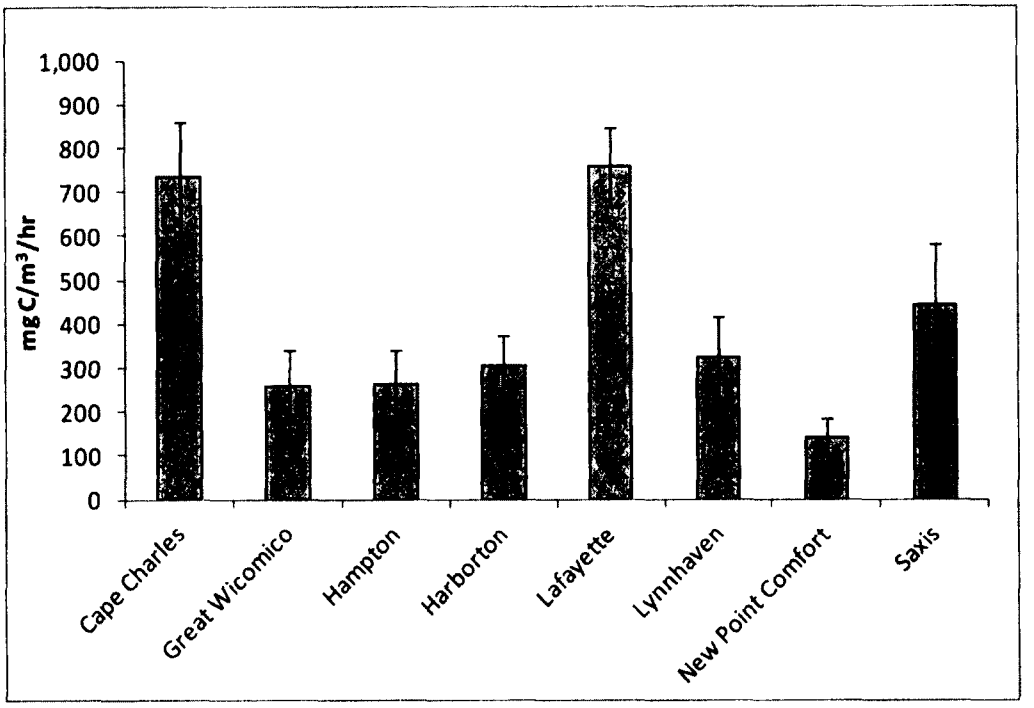

Fig. 40 Two-year average phytoplankton primary productivity rates. Error bars = s.e.

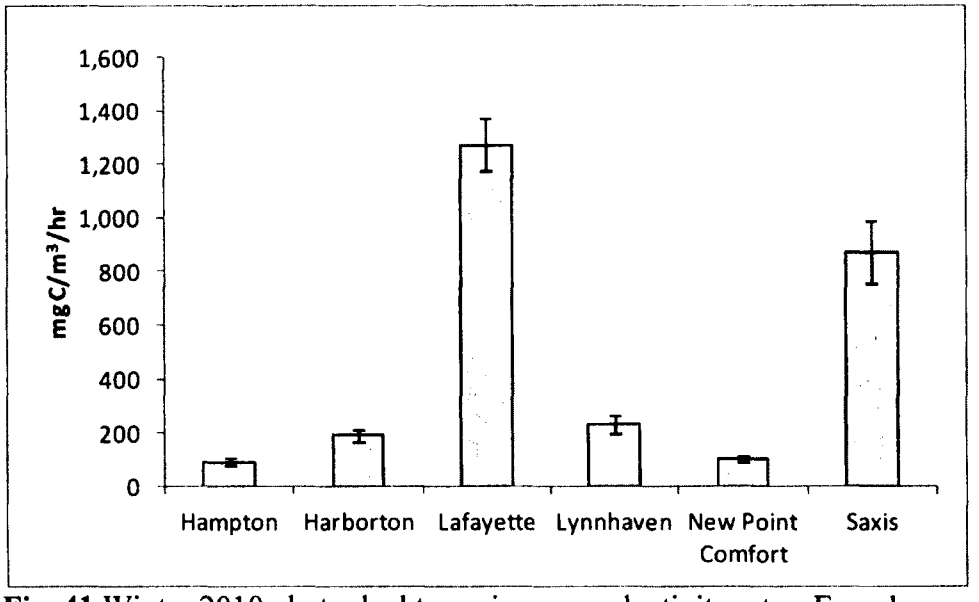

Fig. 41 Winter 2010 phytoplankton primary productivity rates. Error bars = s.e.

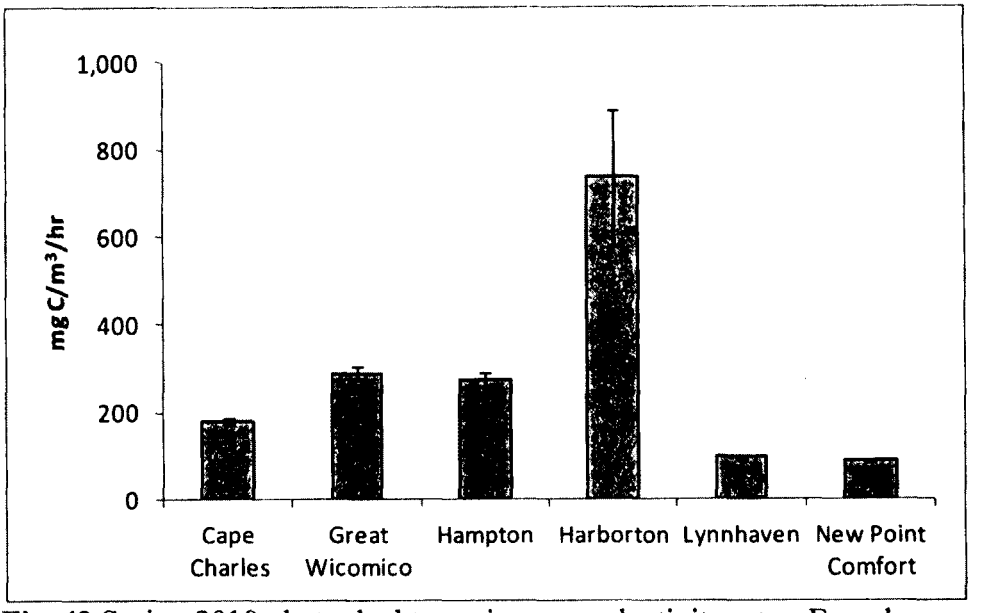

Fig. 42 Spring 2010 phytoplankton primary productivity rates. Error bars = s.e.

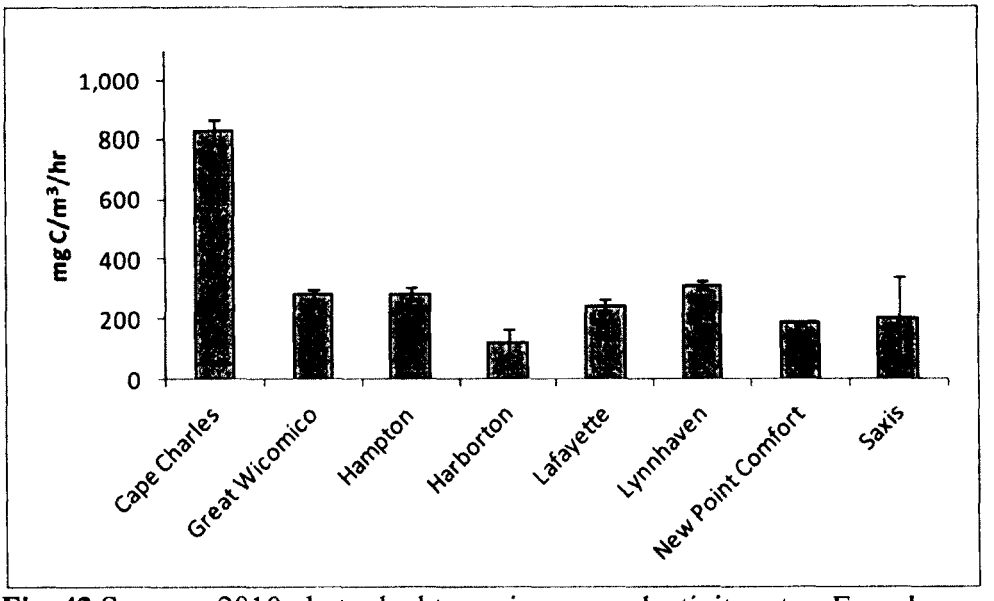

Fig. 43 Summer 2010 phytoplankton primary productivity rates. Error bars = s.e.

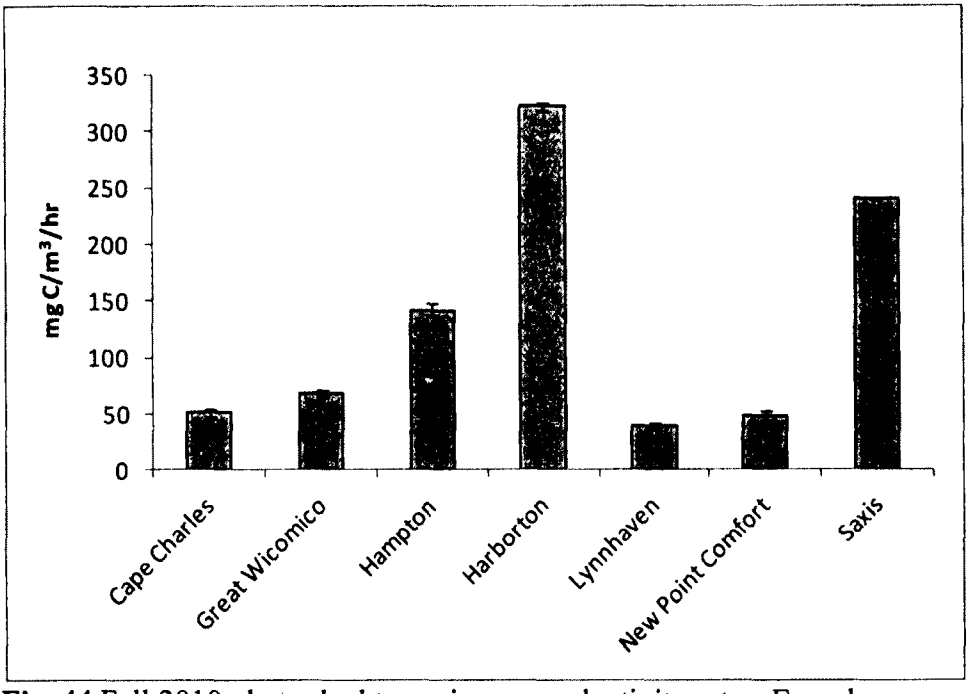

Fig. 44 Fall 2010 phytoplankton primary productivity rates. Error bars = s.e.

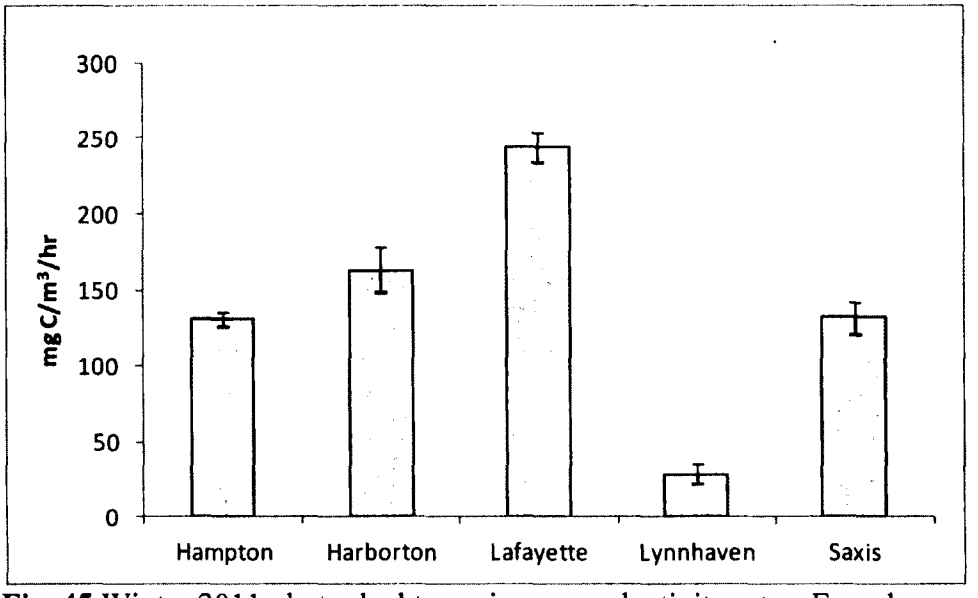

Fig. 45 Winter 2011 phytoplankton primary productivity rates. Error bars = s.e.

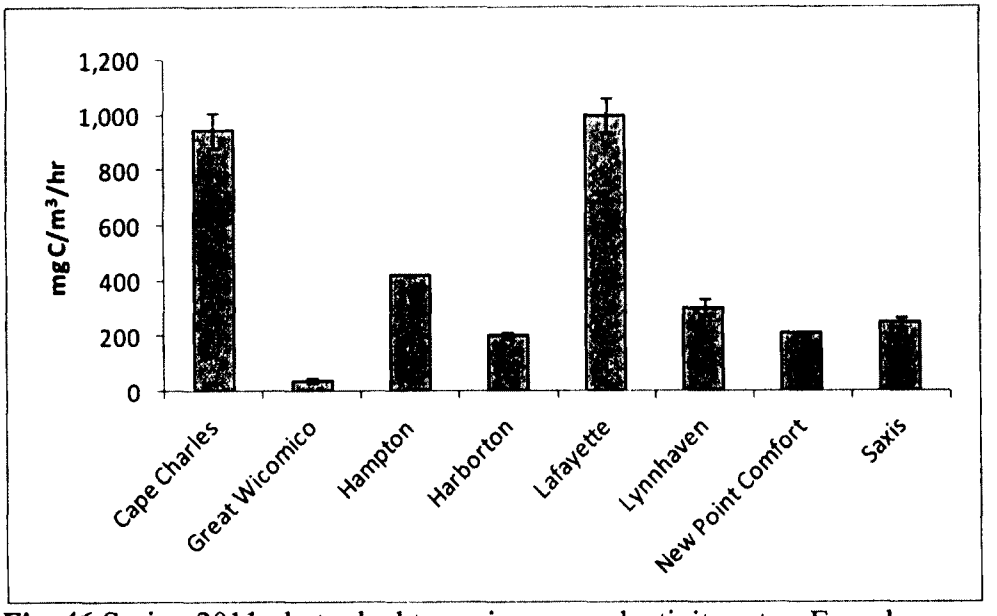

Fig. 46 Spring 2011 phytoplankton primary productivity rates. Error bars = s.e.

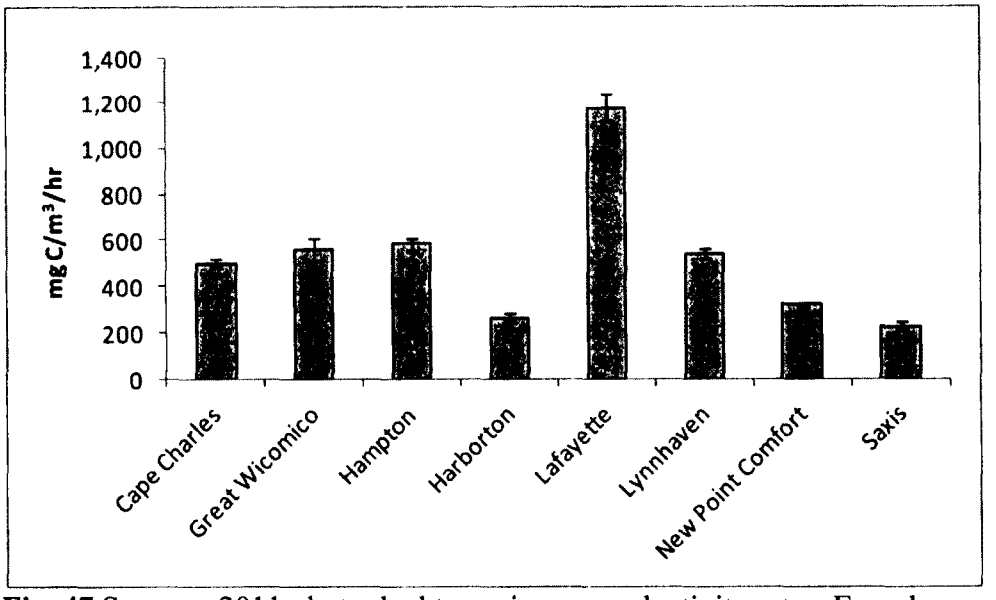

Fig. 47 Summer 2011 phytoplankton primary productivity rates. Error bars = s.e.

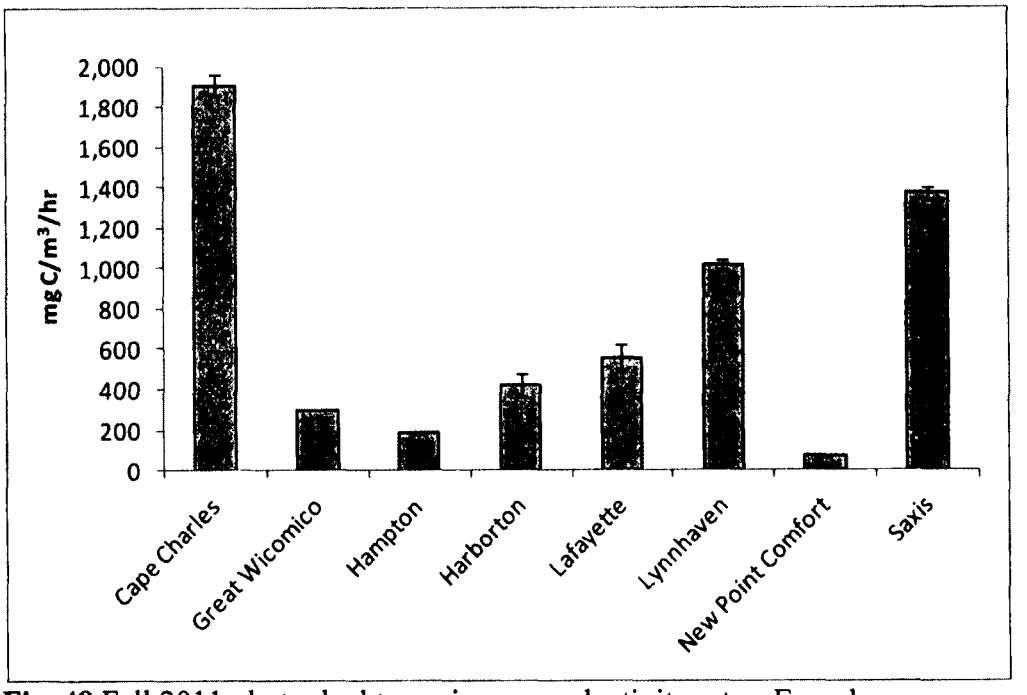

Fig. 48 Fall 2011 phytoplankton primary productivity rates. Error bars = s.e.

Microphytobenthos

Microphytobenthic primary productivity rates had similar variability as those in the phytoplankton, with fluctuating values throughout the sampling period. The Cape Charles station had higher productivity rates over the course of the study, and overall significantly higher than Great Wicomico ($p = 0.004$), Hampton ($p = 0.001$), Harborton ($p = 0.001$), Lynnhaven ($p < 0.0001$), New Point Comfort ($p < 0.0001$), and Saxis ($p = 0.018$). The two year average rate was 2.75 mg C/m^3/hr, with a high of 20 mg C/m^3/hr at Cape Charles in 2011 spring. Cape Charles also recorded the highest overall average productivity rate at 10.33 mg C/m^3/hr during the study (Fig. 49). In 2010 winter, rates ranged from 0.95 mg C/m^3/hr at New Point Comfort to 5.92 mg C/m^3/hr at the Lafayette station (Fig. 50). Rates decreased slightly in the 2010 spring to an average of 1.95 mg C/m^3/hr (Fig. 51), down from 2.02 mg C/m^3/hr in 2010 winter. The Cape Charles and Saxis stations showed large increases of rates in the 2010 summer, with overall rates averaging 4.78 mg C/m^3/hr (Fig. 52), while average fall rates dropped to 1.49 mg C/m^3/hr (Fig. 53). Winter microphytobenthic productivity rates dropped to a two-year low average of 0.81 mg C/m^3/hr (Fig. 54), then an increase in 2011 spring, with Cape Charles showing a high of 20.7 mg C/m^3/hr (Fig. 55). Average summer productivity rates dropped to 1.75 mg C/m^3/hr (Fig. 56), before reaching an average seasonal high of 4.55 mg C/m^3/hr in 2011 fall (Fig. 57).

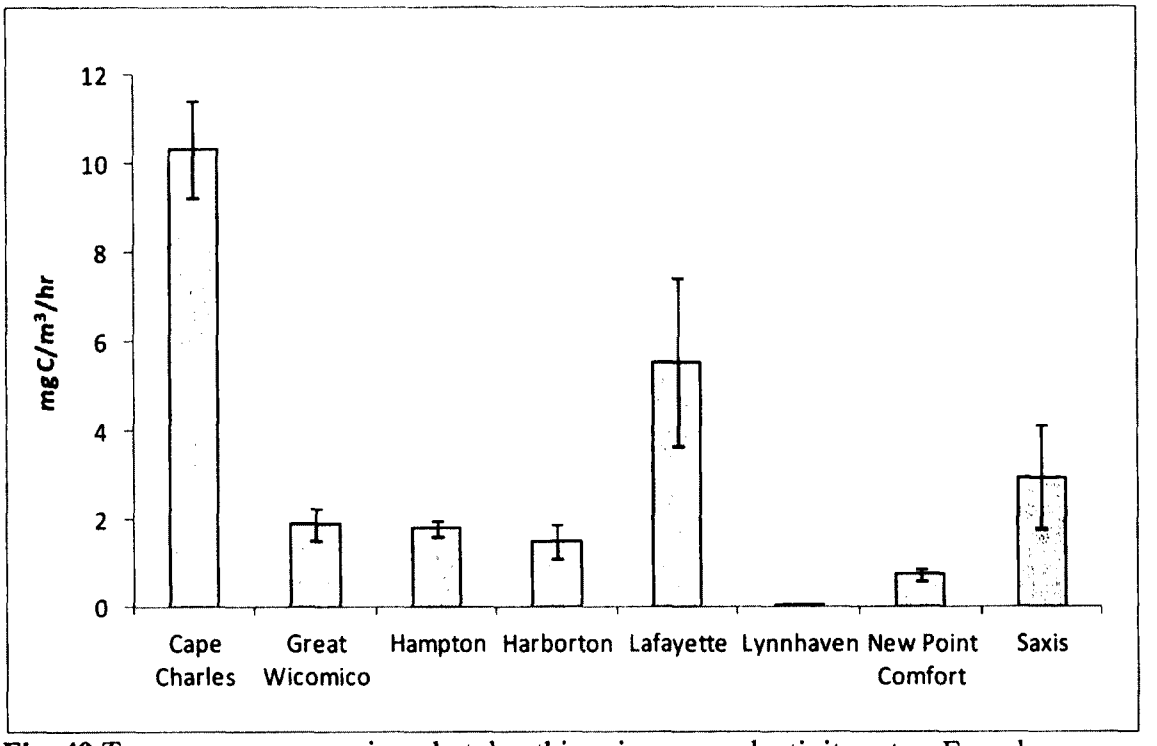

Fig. 49 Two-year average microphytobenthic primary productivity rates. Error bars = s.e.

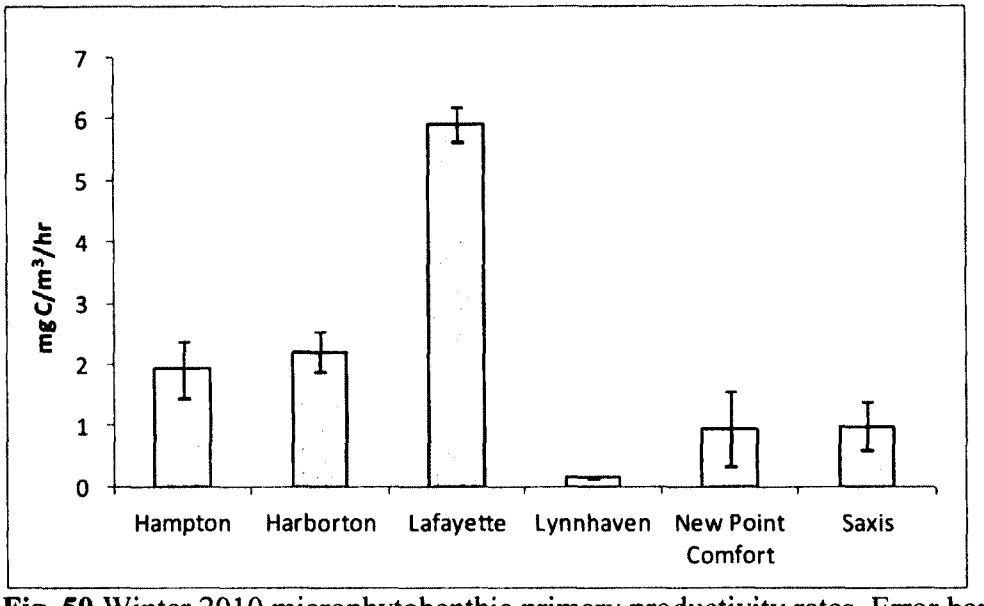

Fig. 50 Winter 2010 microphytobenthic primary productivity rates. Error bars = s.e.

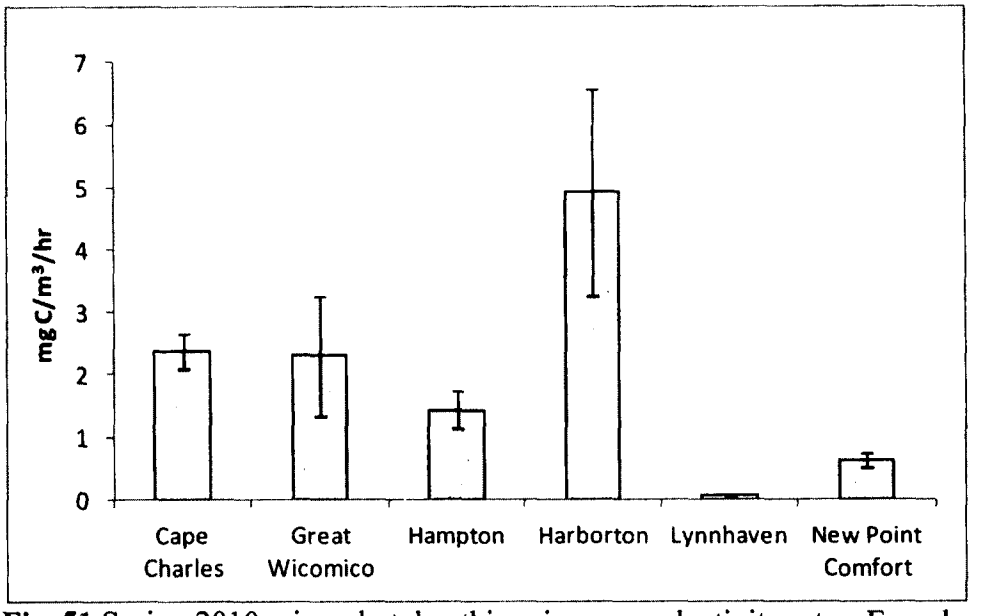

Fig. 51 Spring 2010 microphytobenthic primary productivity rates. Error bars = s.e.

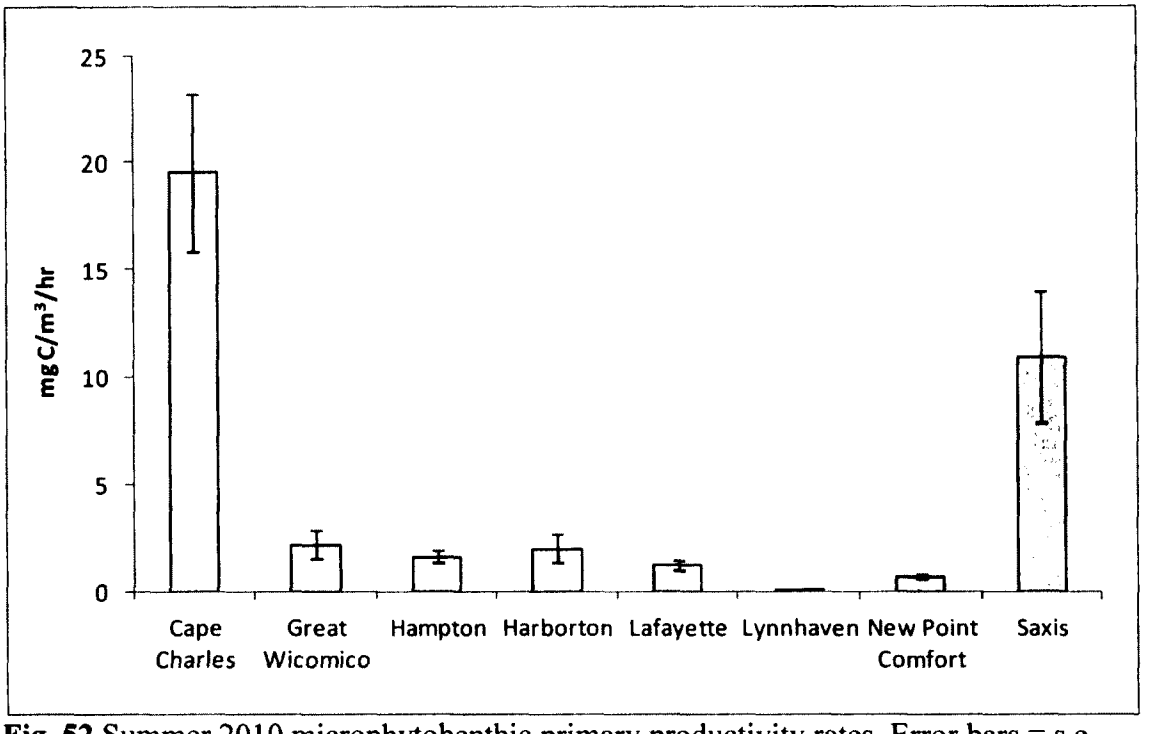

Fig. 52 Summer 2010 microphytobenthic primary productivity rates. Error bars = s.e.

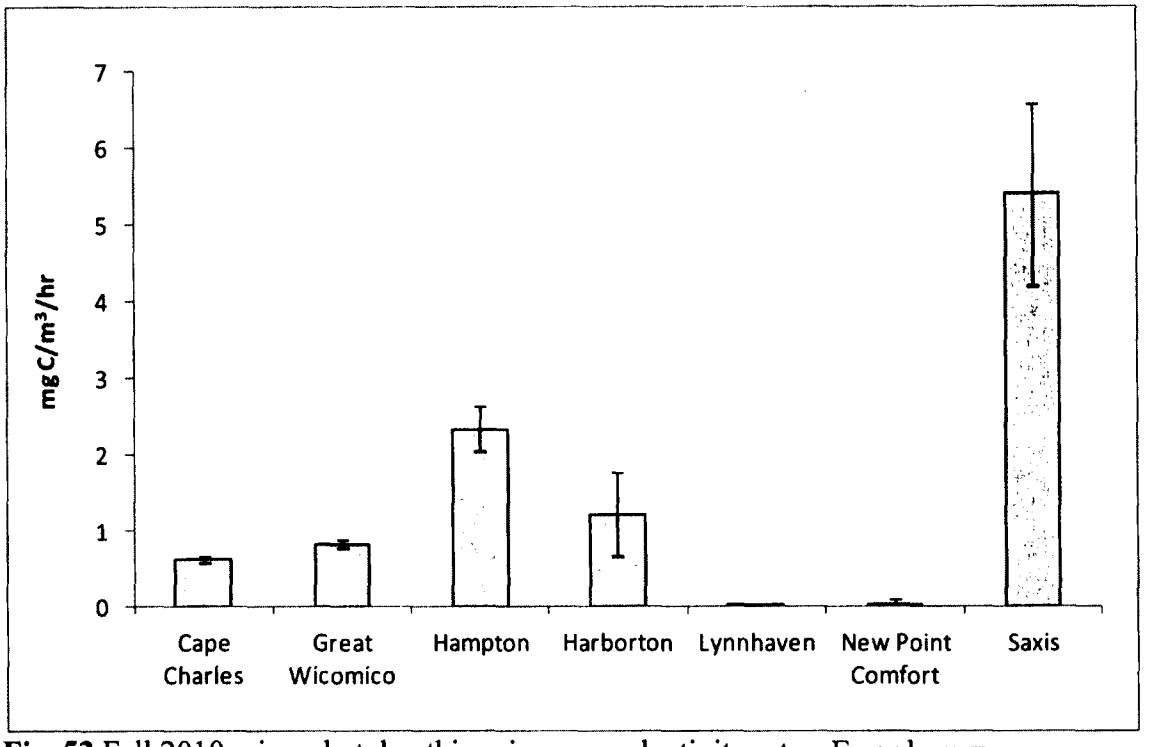

Fig. 53 Fall 2010 microphytobenthic primary productivity rates. Error bars = s.e.

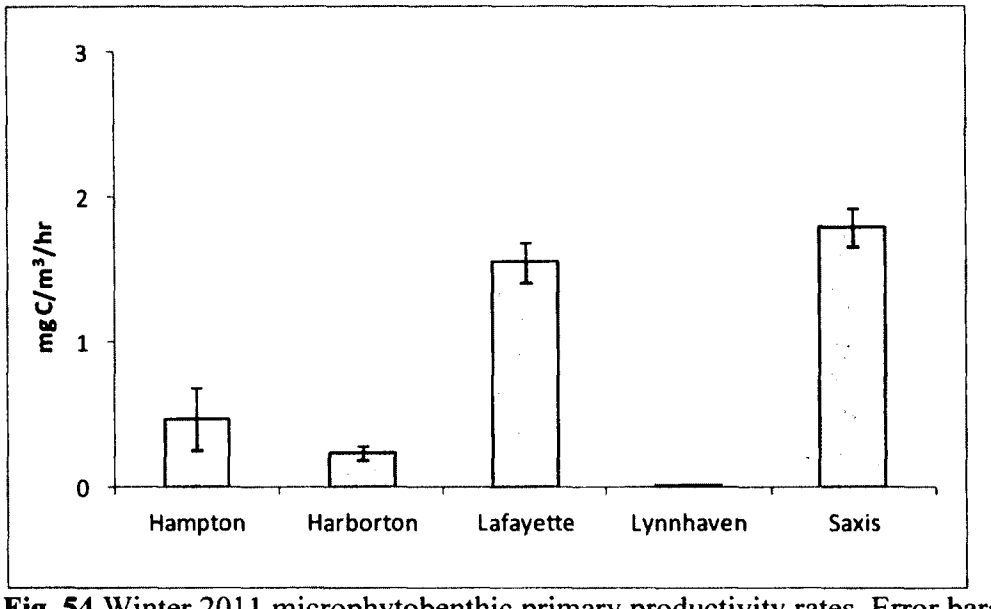

Fig. 54 Winter 2011 microphytobenthic primary productivity rates. Error bars = s.e.

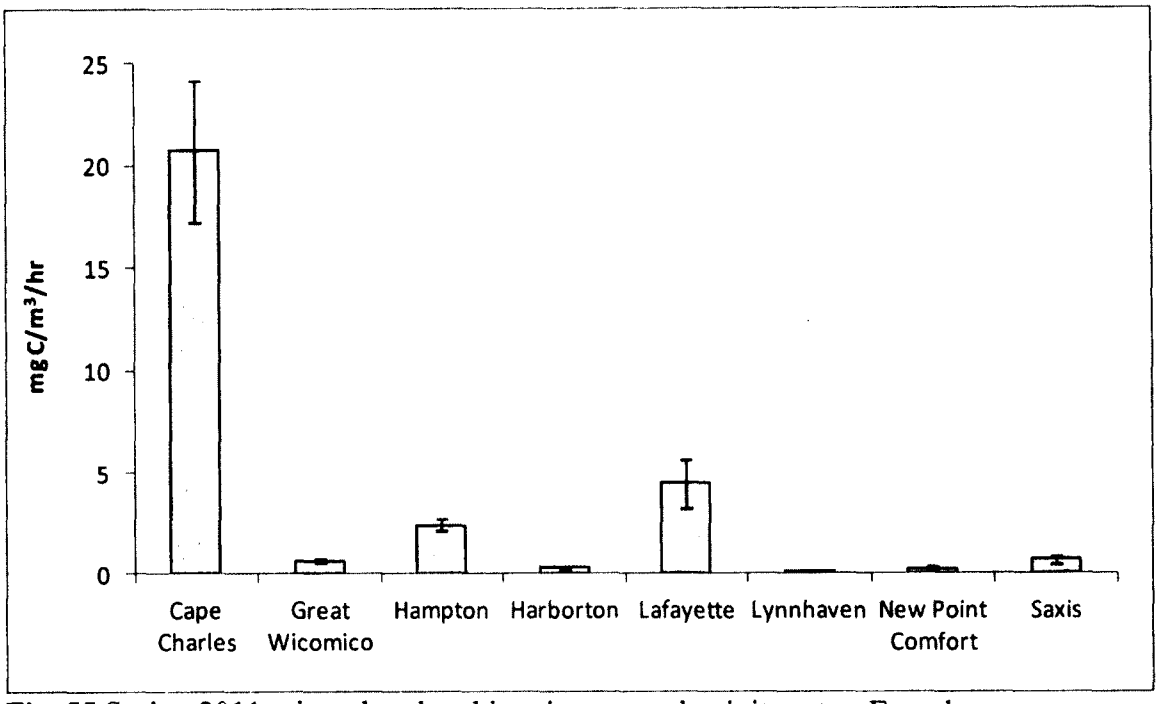

Fig. 55 Spring 2011 microphytobenthic primary productivity rates. Error bars = s.e.

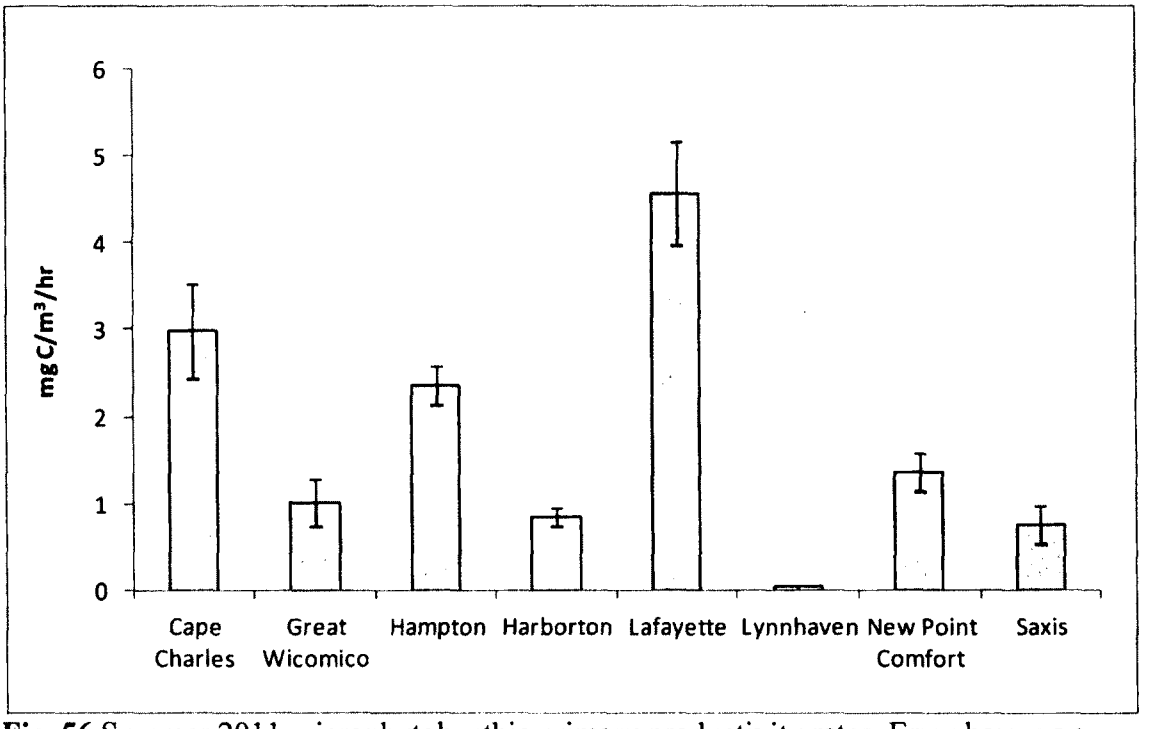

Fig. 56 Summer 2011 microphytobenthic primary productivity rates. Error bars = s.e.

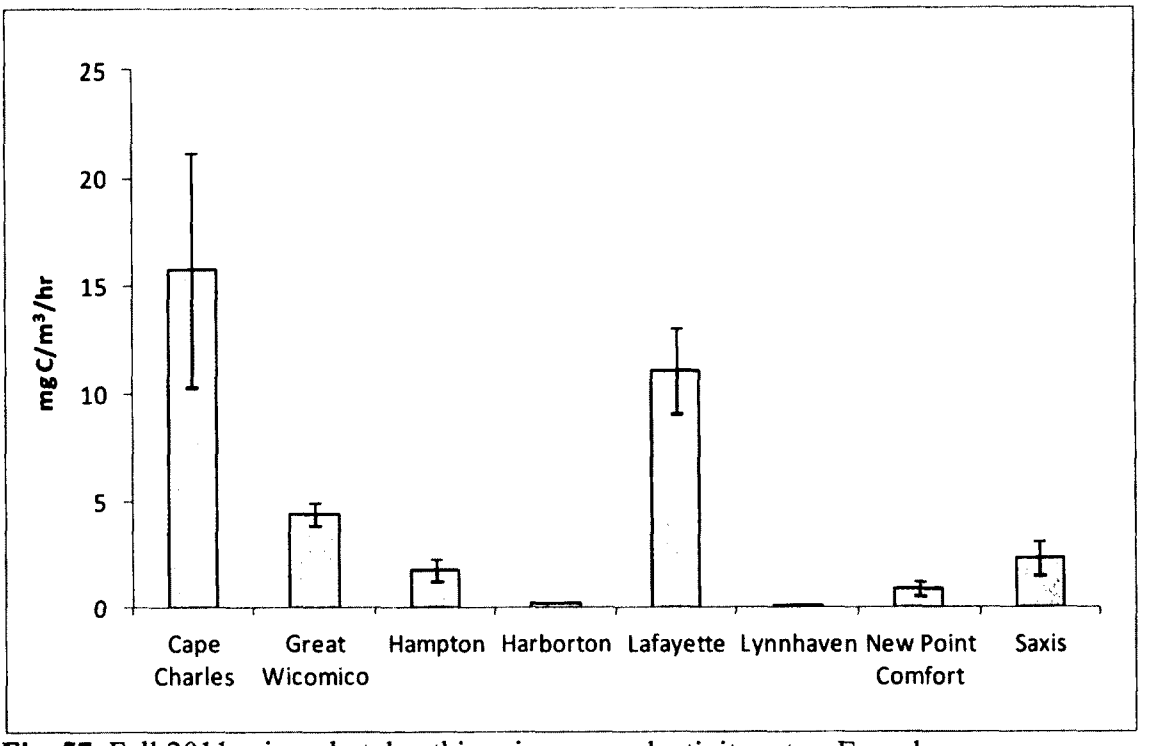

Fig. 57 Fall 2011 microphytobenthic primary productivity rates. Error bars = s.e.

CHAPTER V

RESULTS - SEDIMENT GRAIN-SIZE ANALYSIS

Grain size distribution for each site was averaged over the course of the 2-year study (Figs. 58-65), assigning a Wentworth size class to each station. A range of sediment classes were observed, the coarsest being Lynnhaven, with a mean grain size of 442 μm, followed by Harborton (427 μm), Great Wicomico (302 μm), New Point Comfort (198 μm), Lafayette (153 μm), Cape Charles (126 μm), Hampton (97 μm), and Saxis (63 μm). Sediment properties are summarized in Table 6. These include phi units (ϕ), a logarithmic transformation of millimeters into whole integers, Wentworth size class, mean grain size, sorting ϕ, and sorting class, which describes the grain-size variation of a sample by encompassing the largest parts of the size distribution as measured from a cumulative curve (Folk 1980). Significant differences in sediment grain size were found between stations, ($p < 0.0001$), with stations categorized into the following size classes: medium sand (Great Wicomico, Harborton, Lynnhaven), fine sand (Lafayette, New Point Comfort), very fine sand (Cape Charles, Hampton) and coarse silt (Saxis).

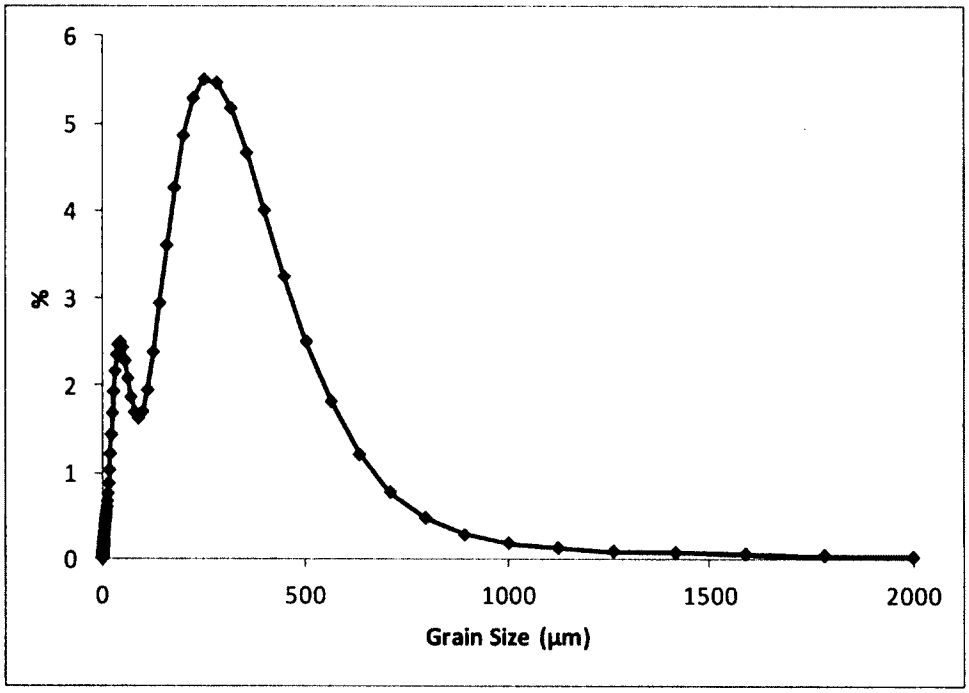

Fig. 58 Two-year average of sediment grain size (μm) distribution at Cape Charles.

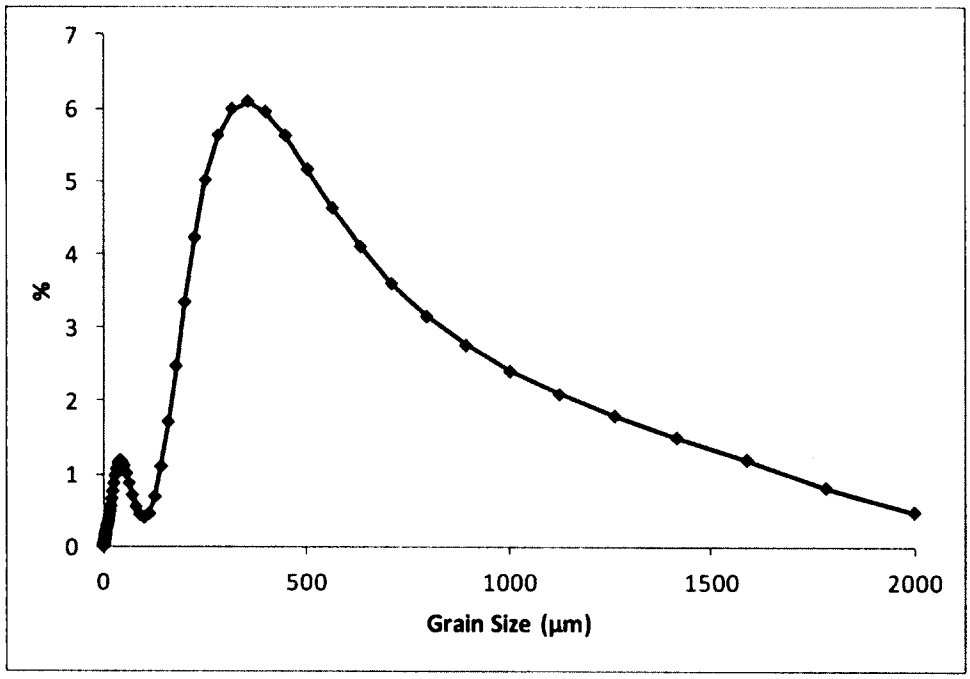

Fig. 59 Two-year average of sediment grain size (μm) distribution at Great Wicomico.

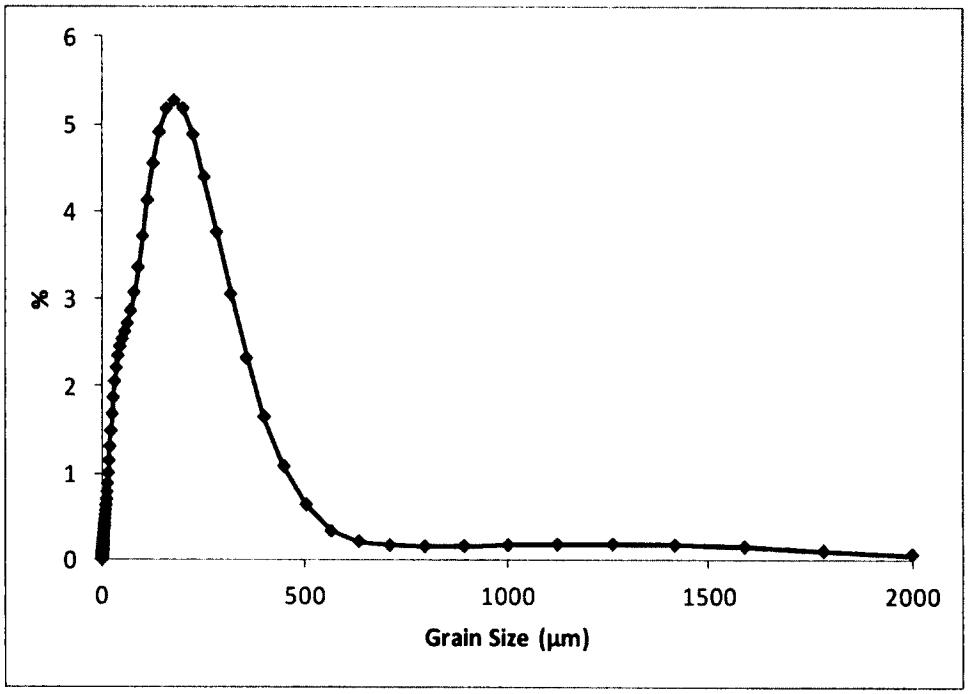

Fig. 60 Two-year average of sediment grain size (μm) distribution at Hampton.

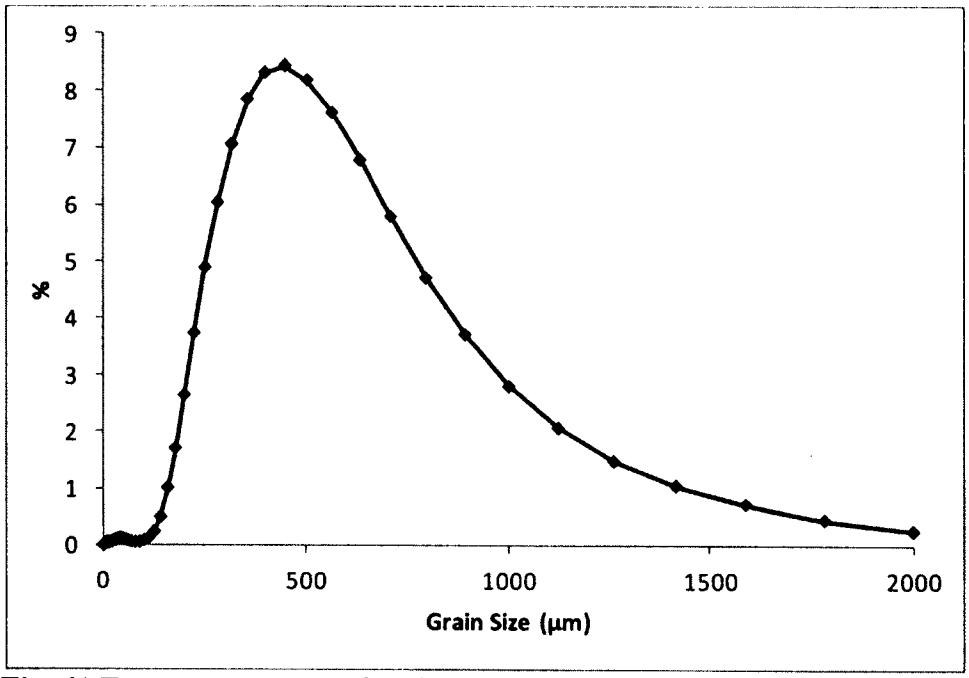

Fig. 61 Two-year average of sediment grain size (μm) distribution at Harborton.

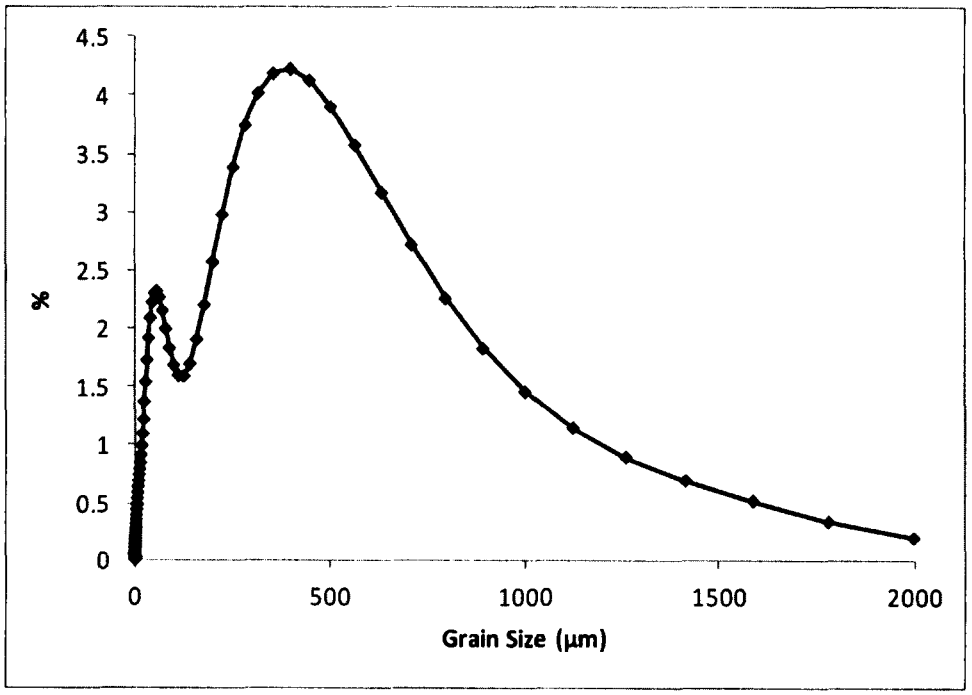

Fig. 62 Two-year average of sediment grain size (μm) distribution at Lafayette.

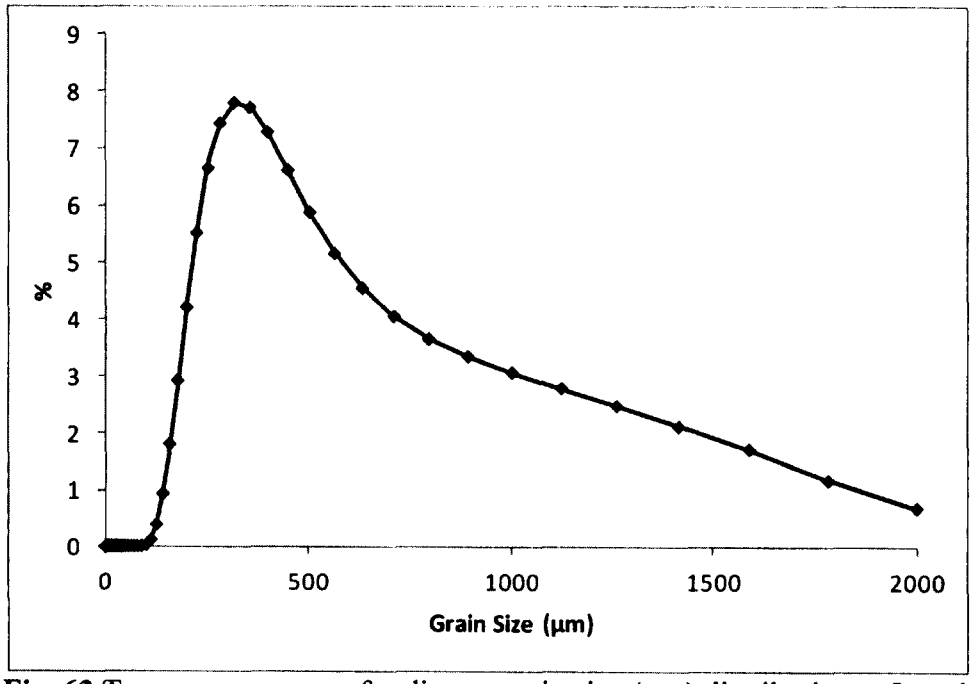

Fig. 63 Two-year average of sediment grain size (μm) distribution at Lynnhaven.

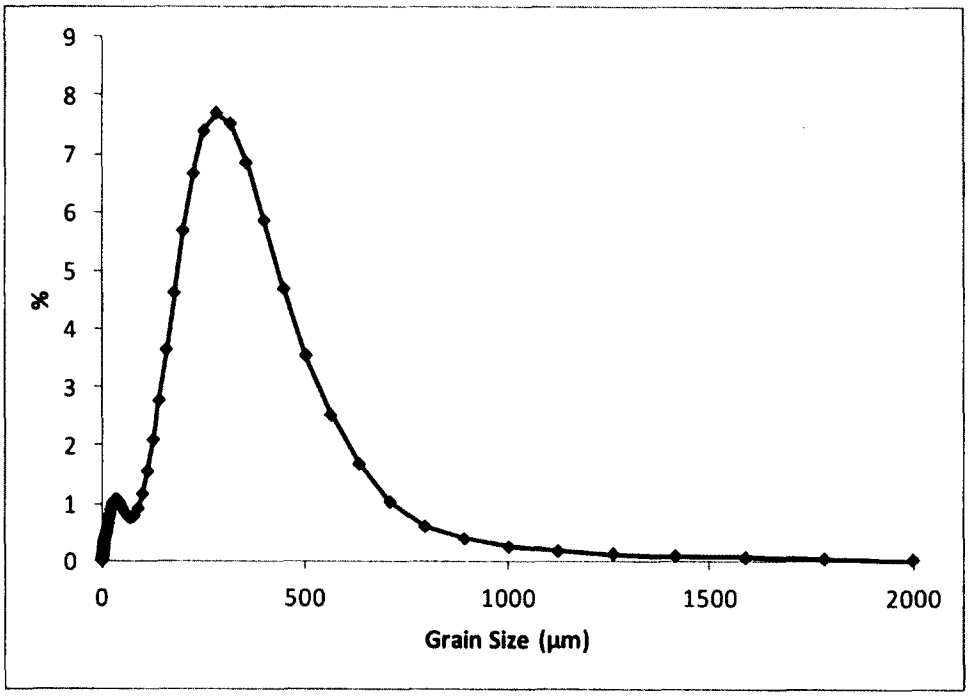

Fig. 64 Two-year average of sediment grain size (µm) distribution at New Point Comfort.

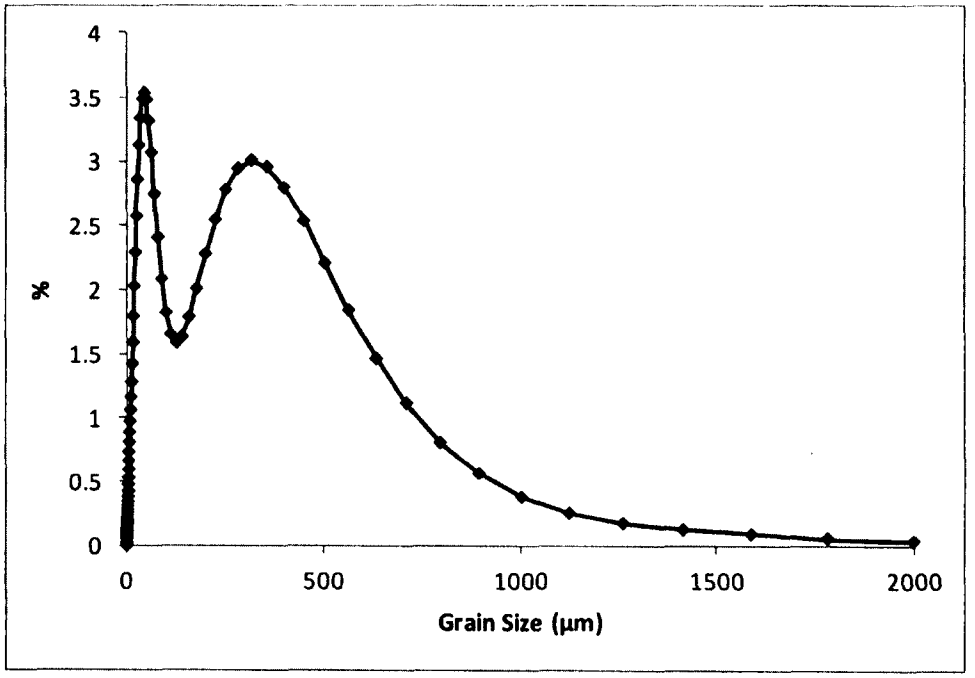

Fig. 65 Two-year average of sediment grain size (µm) distribution at Saxis.

Table 6 Two-year average of sediment properties across all stations.

Sediment Properties					
Station	ϕ	Wentworth class	Sorting ϕ	Sorting	Mean grain size (μm)
Cape Charles	3.13	fine sand	1.64	poorly	126
Great Wicomico	1.90	medium sand	1.51	poorly	302
Hampton	3.50	very fine sand	1.49	poorly	97
Harborton	1.26	medium sand	0.78	moderately	427
Lafayette	2.83	fine sand	2.04	very poorly	153
Lynnhaven	1.26	medium sand	0.73	moderately	442
New Point Comfort	2.63	fine sand	1.29	poorly	198
Saxis	4.00	coarse silt	2.12	very poorly	63

CHAPTER VI

RESULTS - MICROALGAL COMMUNITY RELATIONSHIPS

Pearson correlation analysis was performed to determine the effects of measured parameters and environmental variables on microalgal abundance, biomass, and productivity. In the phytoplankton, salinity proved to be a strong environmental variable, significantly correlating with abundance, biomass, species richness and the Shannon index of diversity (Table 7). Biomass-salinity correlation (Fig. 66) had a significant negative relationship (r = -0.286, p = 0.024), while both species richness (Fig. 67) and Shannon diversity (Fig. 68), gave positive correlations with salinity (r = 0.450, p < 0.0001; r = 0.349, p = 0.005). While salinity factored significantly in shaping phytoplankton communities, it did not have an effect on the microphytobenthos. However, multiple significant correlations were within this dataset (Table 8). Among environmental variables, phi value proved to be a significant factor, positively correlating with species richness (Fig. 69), biomass (Fig. 70) and Shannon diversity (Fig.71).

Table 7 Pearson correlation coefficients (*r*) for multiple correlations of phytoplankton abundance, biomass, productivity rates, species richness (SR), Shannon index (H′), salinity (‰), and temperature (T). N = 62 in all cases except productivity correlations (N = 56). * $p < 0.05$, ** $p < 0.01$.

	Biomass	Productivity	SR	H′	‰	T
Abundance	0.534**	0.247	0.034	-0.164	-0.408**	-0.254*
Biomass	1	0.016	0.109	-0.130	-0.286*	-0.046
Productivity		1	-0.011	0.143	-0.103	0.146
SR			1	0.207	0.450**	0.217
H′				1	0.349**	0.023
‰					1	0.058

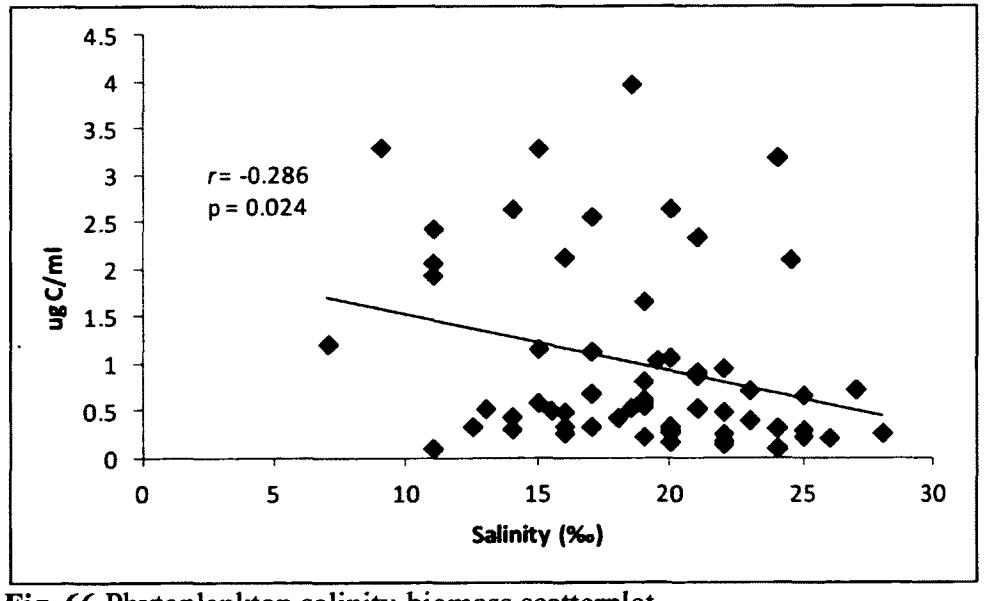

Fig. 66 Phytoplankton salinity-biomass scatterplot.

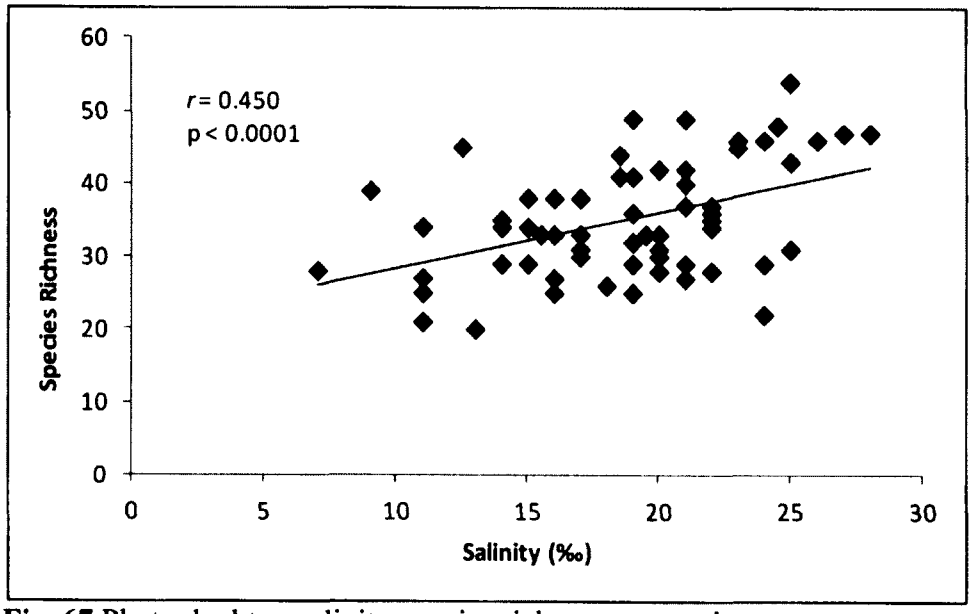

Fig. 67 Phytoplankton salinity-species richness scatterplot.

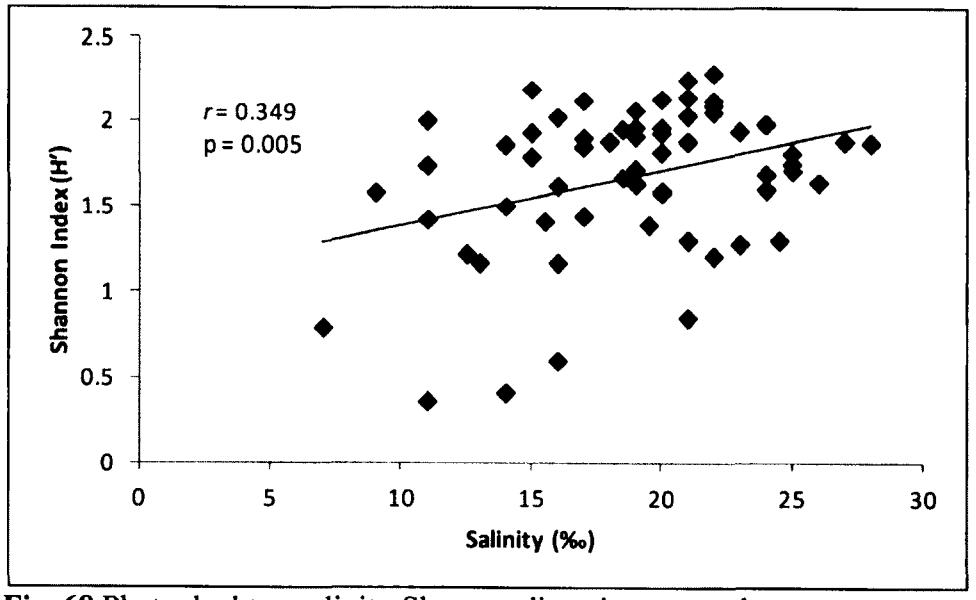

Fig. 68 Phytoplankton salinity-Shannon diversity scatterplot.

Table 8 Pearson correlation coefficients (r) for multiple correlations of microphytobenthic abundance, biomass, productivity rates, species richness (SR), Shannon index (H′), salinity (‰), temperature (T) and phi value (ϕ). N = 62 in all cases except productivity correlations (N = 56). * $p < 0.05$, ** $p < 0.01$.

	Biomass	Productivity	SR	H′	‰	T	ϕ
Abundance	0.736**	0.094	0.282*	-0.294*	0.062	0.046	0.061
Biomass	1	0.243	0.433**	0.104	0.080	0.175	0.334**
Productivity		1	0.138	0.279*	0.043	0.235	0.183
SR			1	0.488**	-0.081	0.257*	0.012
H′				1	-0.213	0.092	0.280*
‰					1	0.058	-0.153
T						1	0.069

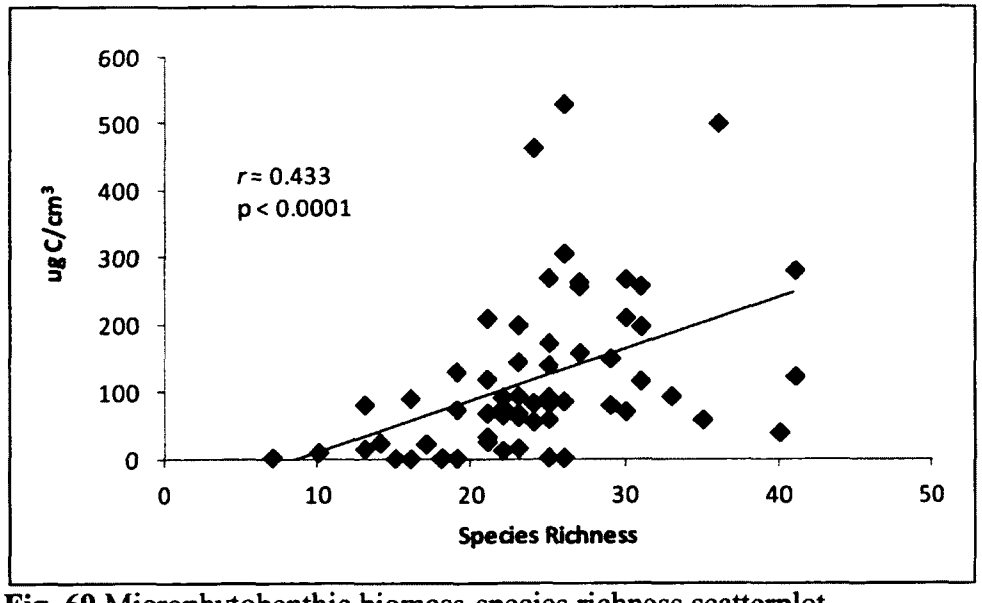

Fig. 69 Microphytobenthic biomass-species richness scatterplot.

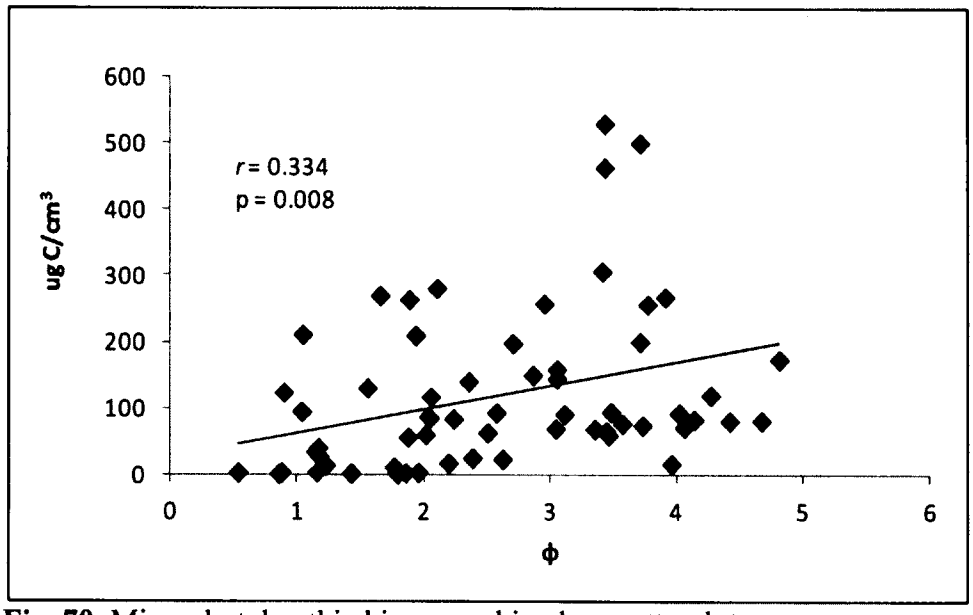

Fig. 70 Microphytobenthic biomass-phi value scatterplot.

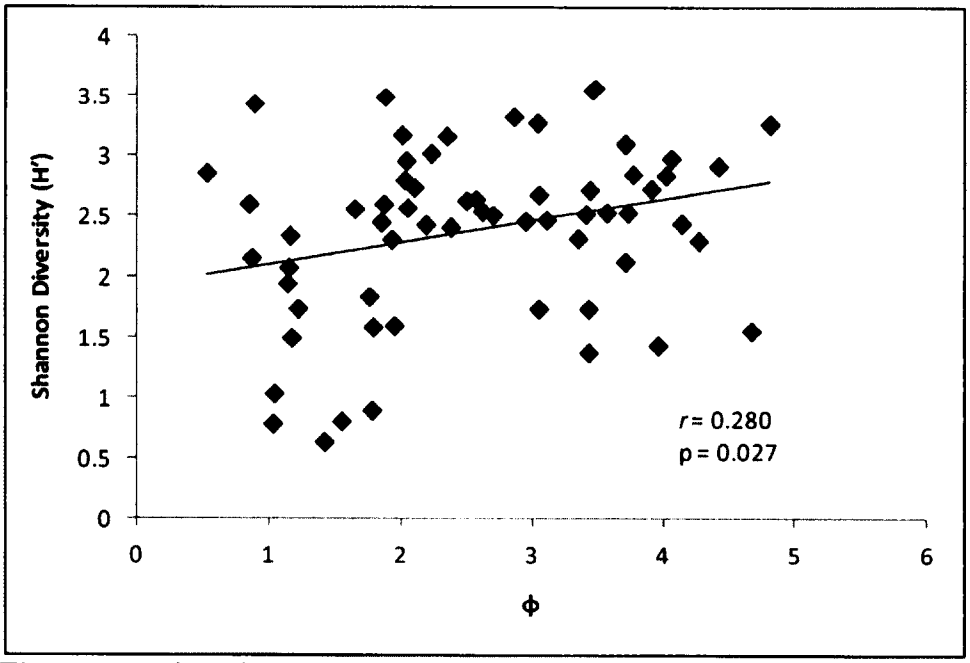

Figure 71. Microphytobenthic Shannon diversity-phi value scatterplot.

Ordination of microalgal communities was performed on abundance data of both algal groups examined (phytoplankton and microphytobenthos) using non-metric multidimensional scaling (NMS). Initial analysis revealed a distinct separation of both microalgal groups, with the relative distance between points indicating relative similarity (closer together) or dissimilarity (farther apart), and each point representing species abundance of individual collections (Fig. 72). As a result of the differences in species composition between habitats (water column vs. benthos), further ordination analyses were conducted separately on each algal group to assess patterns corresponding to spatial (stations), or temporal (seasonal) factors. Among the phytoplankton, while some stations appear closer to each other than others, no strong spatial relationships are apparent (Fig. 73). A clearer relationship is seen when seasons are examined, with winter and summer abundance data opposite each other in the ordination plot, while spring and summer collections are between the two (Fig. 74).

Ordination among the microphytobenthos had stronger spatial relationships than those in the phytoplankton, with several within-station clusters and among-station groups (Fig. 75). Five stations displayed a strong similarity between each other, with Cape Charles, Great Wicomico, Hampton, Lafayette, and Saxis forming a cluster, while the remaining stations (Harborton, Lynnhaven, New Point Comfort) were not only separated (dissimilar) from each other, but also indicated within-station dissimilarity. Microphytobenthic ordination analyses indicated less seasonal patterns than in the phytoplankton, with no temporal patterns present (Fig. 76). Sediment type or grain size was also examined as a predictor of microphytobenthic community structure. Ordination presented a pattern of increasing similarity as sediment grain size decreased from the

coarsest sediment type (medium sand) to the finest (coarse silt), where the station with the finest sediment characteristics (Saxis) formed a tight grouping (Fig. 77). Additionally, the same ordination was performed defining stations characterized as either sand, or mud. Distinction was made between sand and mud, where a station was classified as sand if < 20% of the sediment sample particles were < 63 μm, and classified as mud if > 20% of the sediment particles were < 63 μm. Stations having a greater proportion of larger sediment particles (sand) tended to be more dissimilar than those classified as mud, which had greater similarity (Fig. 78).

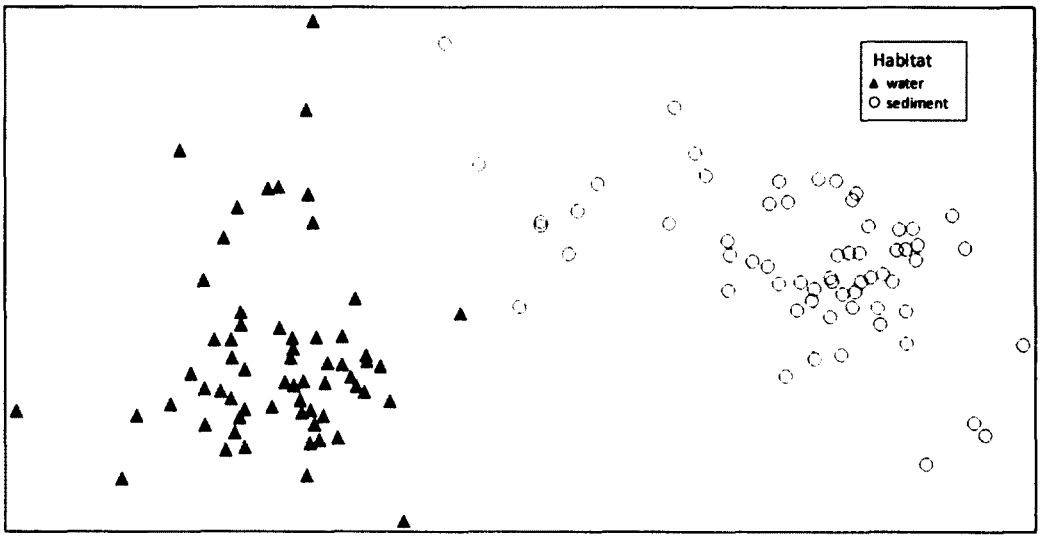

Fig. 72 Ordination of microalgal community composition among the phytoplankton and microphtyobenthos using abundance data. Distances between points are proportional to differences in composition.

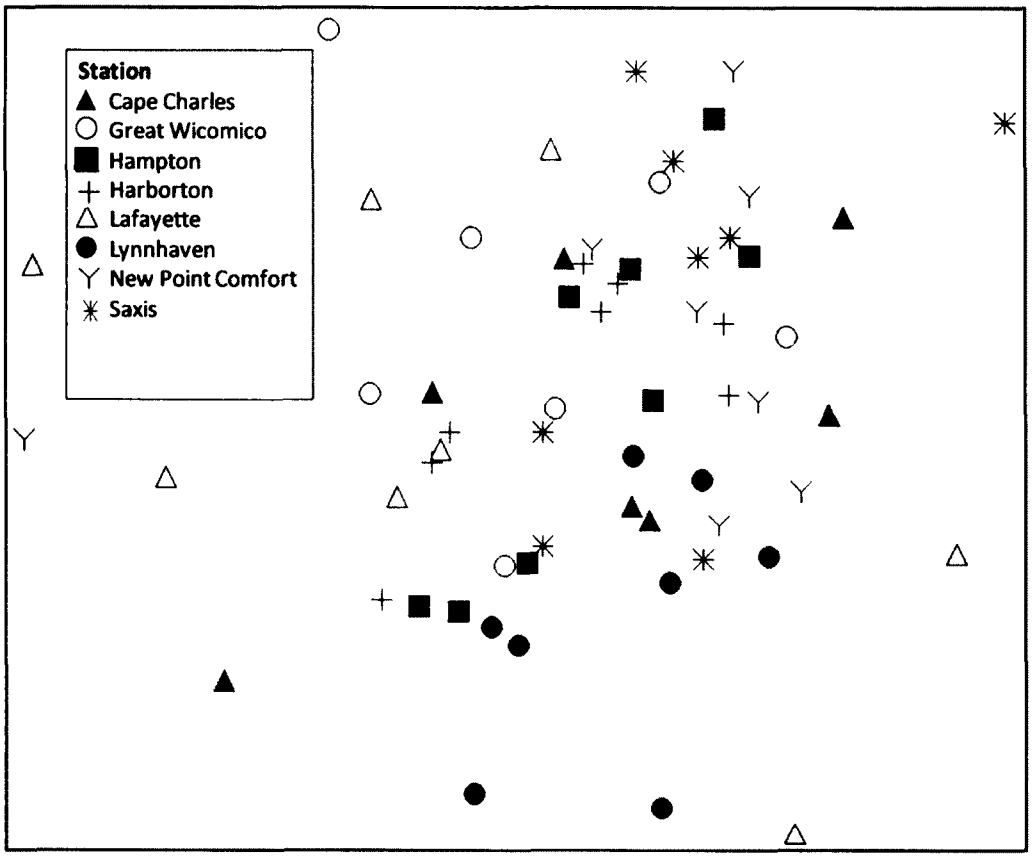

Fig. 73 Ordination of phytoplankton community composition among stations.

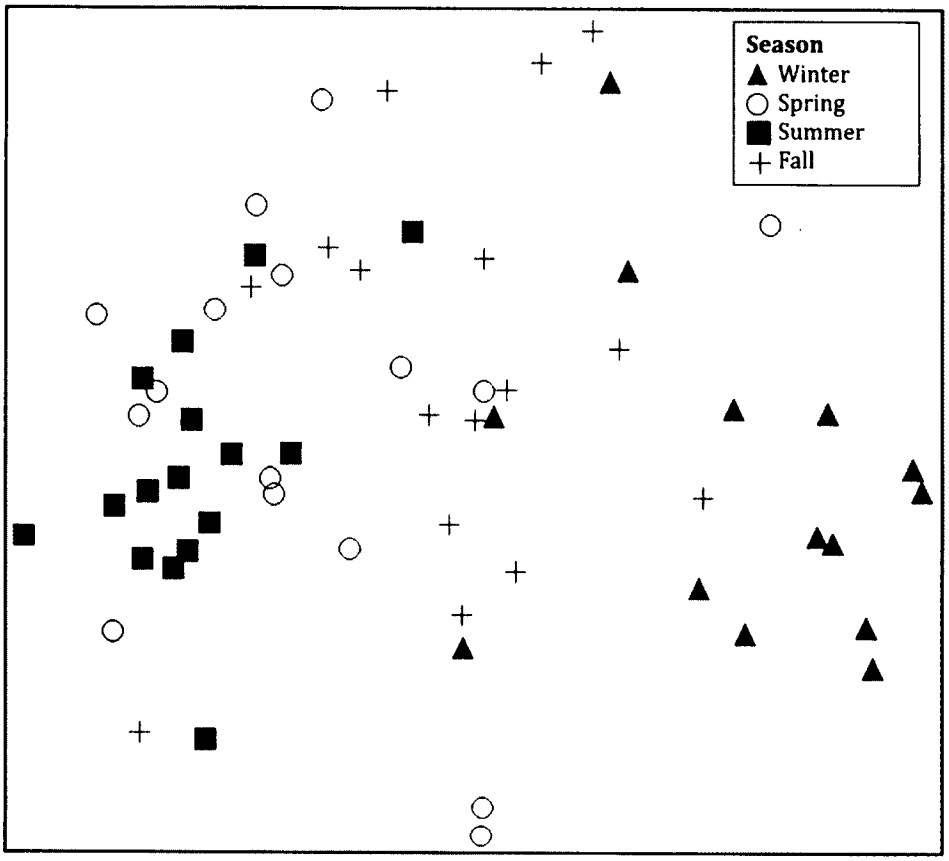

Fig. 74 Ordination of phytoplankton community composition among seasons.

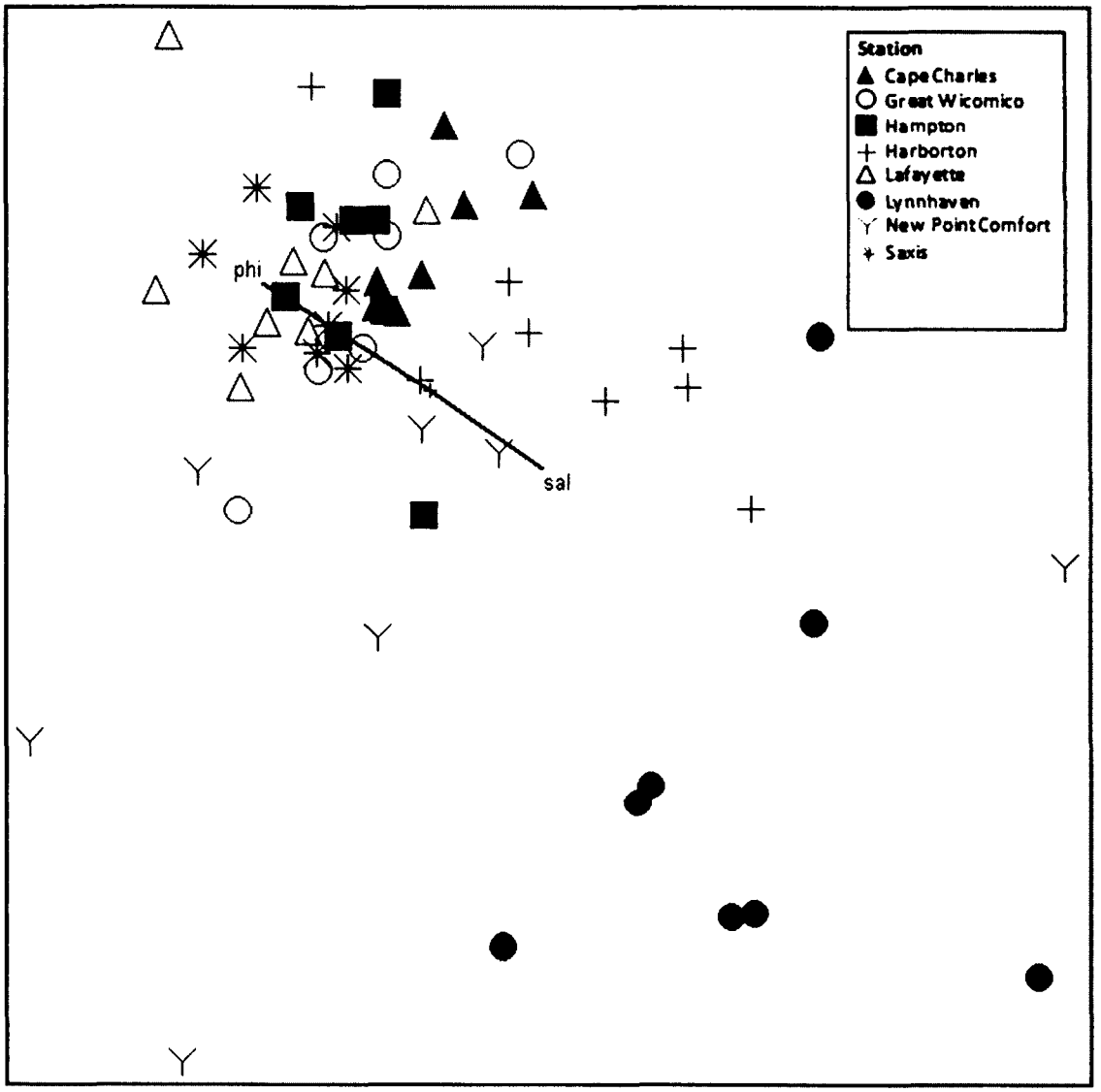

Fig. 75 Ordination of microphytobenthic community composition among stations.

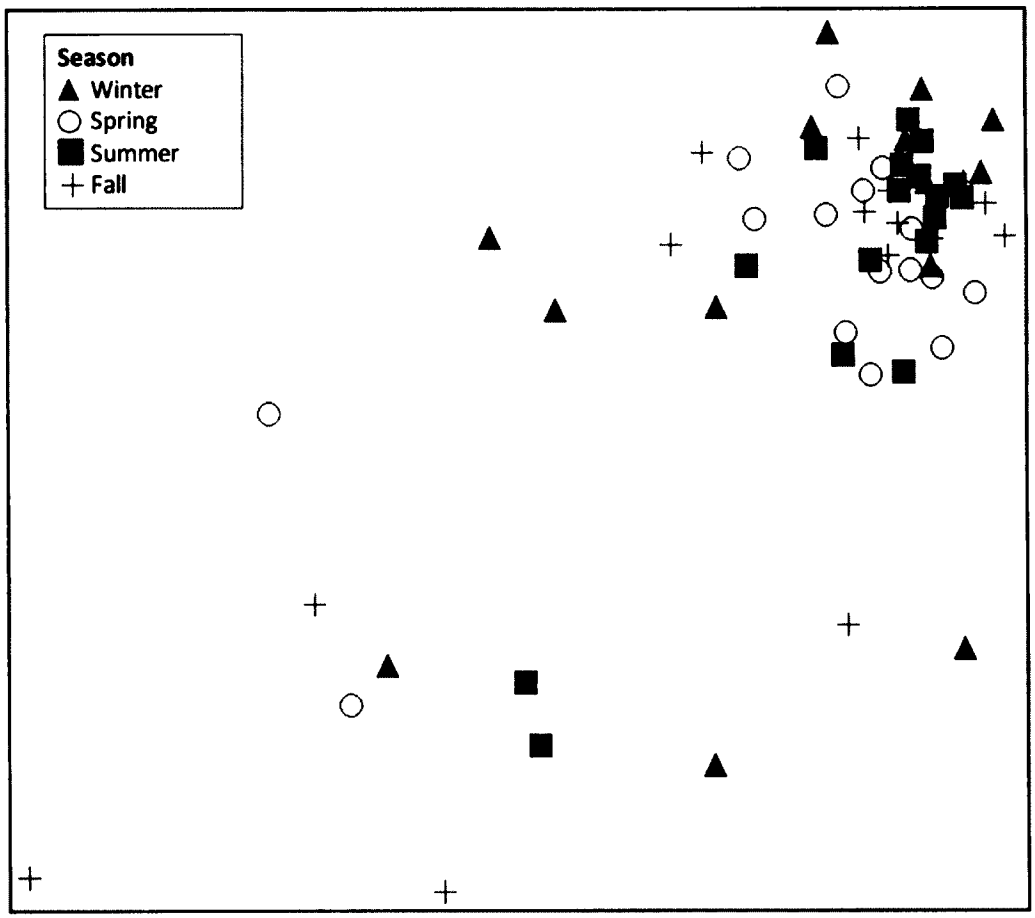

Fig. 76 Ordination of microphytobenthic community composition among seasons.

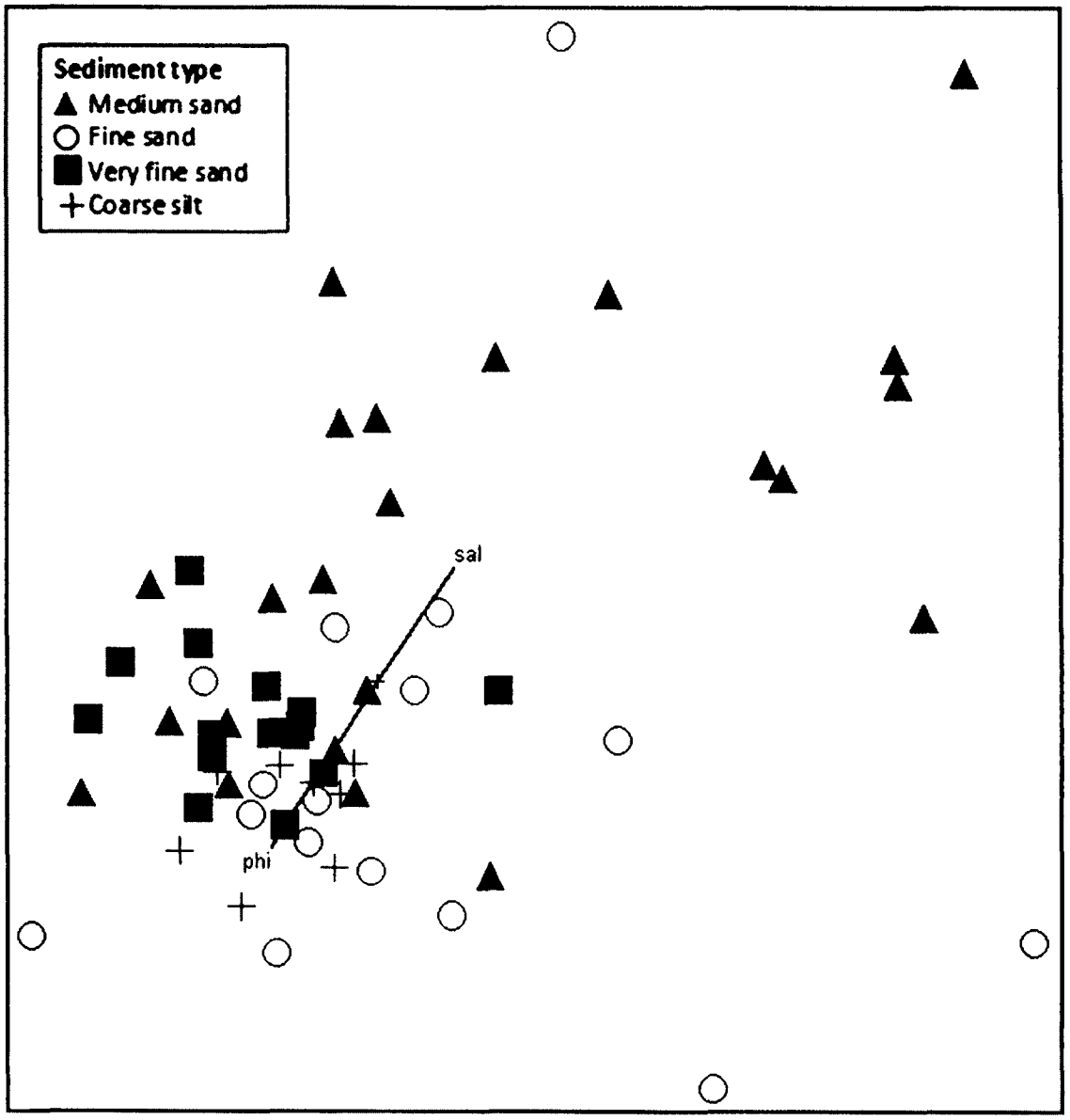

Fig. 77 Ordination of microphytobenthic community analysis with collection events classified into Wentworth sediment class.

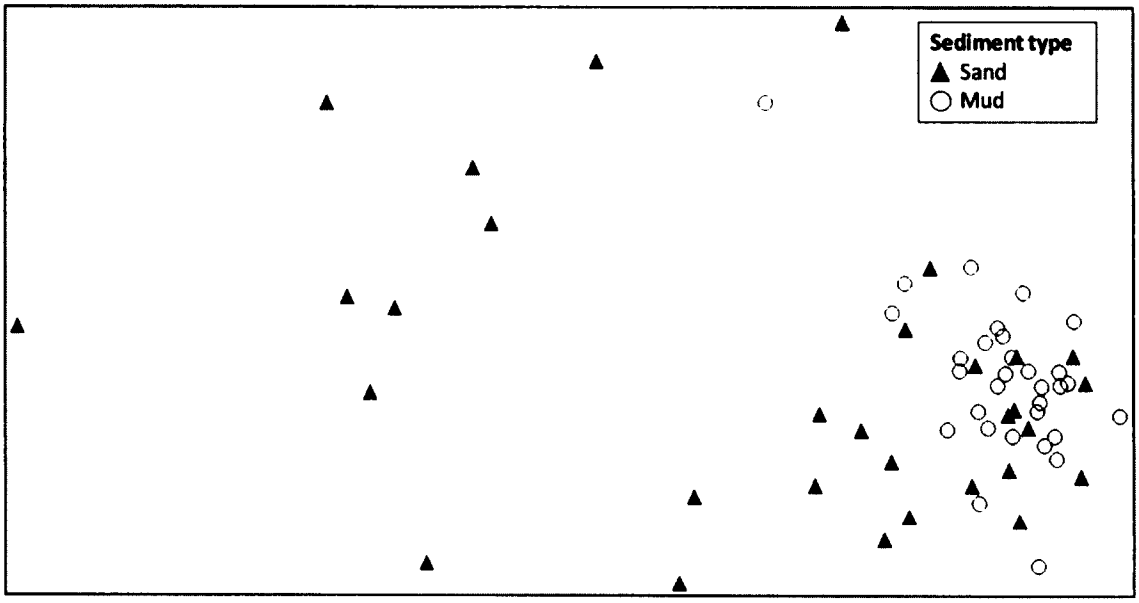

Fig. 78 Ordination of microphytobenthic community composition with collections categorized according to substrate type (sand vs. mud).

CHAPTER VII

DISCUSSION

These results constitute the most comprehensive survey regarding the composition of benthic microalgae in the Chesapeake Bay to date. Data analysis has indicated significant differences were present between the water column phytoplankton and the microphytobenthos regarding every parameter measured, and further testing revealed significant differences among the benthic stations, suggesting a highly variable benthic microalgal community, in contrast to a somewhat homogeneous pelagic phytoplankton environment. Previous Chesapeake Bay microphytobenthic studies are generally focused on a single parameter, or function. The scope of this project reports microphytobenthic densities, biomass, and primary productivity rates over a broad geographic area along with detailed taxonomic information, community structure and trends, plus providing baseline data of the benthic algal communities in lower Chesapeake Bay.

Community Composition, Abundance, and Biomass

The phytoplankton and benthic microalgal communities in this study were considerably different. Ordination analysis of taxonomic data displayed a clear separation of the phytoplankton and benthic microalgal communities. Further investigation into each habitat yielded significant differences throughout the dataset. The phytoplankton was significantly more diverse than the benthos, with all stations having species richness

values > 20 at every sampling, and values consistently > 30. In contrast, the benthic habitat had significantly higher Shannon indices of biodiversity (H'), indicating a more even distribution of algal taxa. Both habitats were dominated by diatoms in terms of species richness, though overall taxomonic makeup of these populations varied between habitats and stations. In the phytoplankton, the centric diatom *Skeletonema costatum* was the most abundant species and diatoms in general were the most abundant microalgal group throughout the study. Aside from the prominence of diatoms, community composition at each phytoplankton station displayed no apparent patterns. NMS ordination analysis did not completely resolve the high variability among phytoplankton community composition, with no apparent similarities within stations. Ordination indicated a somewhat weak seasonal composition relationship, with winter and spring grouping together (e.g. taxonomic similarity). This seasonal similarity may have been driven by the increased densities of cyanobacteria and dinoflagellates present during the spring and summer of both years. High dinoflagellate biomass occurred at several stations during spring and summer seasons, particularly in the 2010 spring/summer, when high values were at the Lafayette, Great Wicomico, and New Point Comfort stations. Relatively large-sized dinoflagellates were in the Lafayette, where *C. polykrikoides* and *P. micans* were in high numbers. Winter/fall relationships were more ambiguous, possibly due to dominance of diatoms and varying combinations of lesser algal groups during these months.

Supporting seasonality as a potential driver of phytoplankton communities was a significant negative correlation between temperature and abundance. While this evidence presents a strong case for temperature as a major driver of these microalgal communities,

phytoplankton data from this study was most influenced by salinity. Significant negative correlations were found between salinity and abundance as well as salinity and biomass (Fig. 65). Conversely, salinity positively correlated with both species richness (Fig. 66) and the Shannon diversity index (Fig 67).

In the benthos, and contrary to available taxonomic data, cyanobacteria were the most prominent group throughout much of the sampling period. In the few publications available that report benthic microalgal taxonomy, diatoms are in most cases described as the dominant microalgal group, and in some instances, although present, no phyla other than diatoms were considered. In this case, although pennate diatoms dominated taxon counts (species richness), cyanobacteria were the most abundant in terms of overall numbers. Though other taxonomic groups were present throughout the year, diatoms and cyanobacteria persisted as the most common and abundant algae in both cell densities and biomass at nearly every station in every sampling season. Diatoms maintained stable cell densities and biomass values throughout the entire sampling period, while cyanobacteria experienced seasonal fluctuations, with particularly high densities during the warmer summer months. High densities of the colonial cyanobacteria *M. elegans* and the filamentous *L. aestuarii* were present during spring and summer seasons, predominantly at the eastern shore stations (Cape Charles, Harborton, and Saxis). While other stations consistently had greater abundance and biomass values (Cape Charles, Saxis), in general, among-station microphytobenthic density and biomass fluctuated erratically throughout the study. Divergent from earlier data, salinity and temperature had little effect on the microphytobenthic communities observed here. Though microphytobenthic community dynamics appeared to be correlated with temperature

based on seasonal increases of algal abundance and biomass during the warm summer months, these relationships were not statistically significant, with only species richness significantly affected by temperature based on Pearson correlation analysis.

NMS ordination analysis indicated weak seasonal effects on community structure, with the majority of spring and summer collections grouping near each other, and fall/winter collections more widely spread, indicating dissimilarity, though these seasonal associations are speculative at best. Spatial relationships in community structure were more apparent however, with several stations clustering near each other (Cape Charles, Hampton, Lafayette, Saxis). Considering the microphytobenthic ordination results in terms of sediment grain size/Wentworth size class at each site, a much clearer picture emerges. As presented in Figure 76, collections in the larger size range (Wentworth 1922) tend to be more taxonomically dissimilar, with stations classified as medium sand and fine sand spread throughout the NMS plot. As size class decreases, stations become clustered together, with the finest-grained sediment type (in this case, coarse silt), being the tightest grouping. The Wentworth size classes are based on phi value (which correspond to mean grain size), with larger phi values corresponding to smaller sediment grain size. In this case, it appears that sediment grain size effects community composition, particularly in sediments with smaller grain sizes. Further supporting sediment grain size effect on microphytopbenthic communities, Pearson correlation analysis gave significantly positive correlations of grain size to both biomass and Shannon diversity. Biomass data from stations with smaller grain sizes (larger phi values) consistently have similar values from season to season, regardless of seasonal variations. It has been suggested that temporal fluctuations of microphytobenthic communities are

less prevalent in fine, muddy sediments compared to less stable, low nutrient sandy sediments (Van der Wal et al. 2010). Microphytobenthic biomass data presented here provides a similar pattern, with only small variations in biomass at sites characterized by fine-grained sediments, while coarse-grained sites were exhibiting larger fluctuations throughout the sample period.

Algal biomass is not the only parameter affected by sediment grain size. As noted elsewhere (McIntire and Amspoker 1986, Gottschalk et al. 2007) and in the current data, grain size is capable of producing taxonomic distinctness among algal assemblages. Typically, sheltered habitats with fine, muddy substrates are taxonomically more diverse than those with larger sediment grains and exposed to more turbulent conditions. Taxonomic data illustrated here concurs with those findings, as stations with fine-grained sediments were consistently more diverse in species richness and Shannon diversity, than stations characterized by coarse sediments. The significant correlation between phi value and Shannon diversity reinforces the results of microphytobenthic community NMS analysis, in that sediment grain size has significant effects on microalgal community composition within the sediment. While the type and strength of sediment grain size effects related to microphytobenthic communities will continue to be debated, this study confirms that sediment type plays a critical role.

However, sediment type alone is not the sole driver of microphytobenthic community dynamics, as a tight linkage exists among both biotic and abotic factors in these environments. Benthic habitats with finer grains tend to be in areas with heavy vegetation and high organic matter, allowing for higher rates of nutrient cycling within the sediment. Cohesive sediments are less porous than coarse sandy sediments, thereby reducing the

rate of nutrient delivery to the water column. The cohesive nature of these sediments, particularly in areas with extensive benthic microalgal development would bind nutrients via sediment stabilization, reducing sediment resupension, and acting as a barrier of sediment-water column nutrient exchange while still being available to sediment surface biofilms. This would negate any effects of nutrient limitation and allowing for growth of a diverse benthic flora. Conversely, habitats with coarse sediment profiles may have low pore water content unable to retain nutrients, thus retarding continued growth of the algal biomass. For example, the Lynnhaven station had the lowest biodiversity, abundance and microalgal biomass throughout the study, as well as the largest mean sediment grain size. The low algal biomass and productivity rates in the coarse-sediment stations of this study may be the product of nutrient limitation, which, while generally a non-factor in fine sediments, is not uncommon in sandy, porous sediments (Underwood and Kromkamp 1999).

Primary Productivity

The range of phytoplankton productivity rates measured here (28 – 1,907 mg $C/m^3/hr$) were higher than historical Chesapeake Bay productivity rates (0.3 – 400 mg $C/m^3/hr$), though still within published ranges (Marshall and Nesius 1996). A plausible cause for elevated rates may have been the close proximity of sampling locations to a variety of nutrient sources. While historical Chesapeake Bay productivity measurements are based on pelagic mainstem Bay stations where nutrients are derived from large scale downstream transport (Marshall and Nesius 1996), stations in this study were along the shoreline, and located within several meters of the low tide line. Therefore, nutrients

derived from terrestrial runoff would generally be at higher concentrations in these near-land areas than those in pelagic waters, and readily available for algal uptake. Additionally, water temperatures in these shallow sub-tidal areas are often considerably elevated during seasonal periods of increased algal development compared with those in deeper waters, and when combined with terrestrially-derived nutrient concentrations, yield higher productivity rates. In general, phytoplankton productivity rates at these sites increased with rising temperatures, though this trend was not significant. The highest average phytoplankton productivity rate (2-year avg. = 755 mg $C/m^3/hr$) was recorded at the Lafayette station, which is located in a heavily urbanized embayment of the tidal Lafayette River. This waterway has undergone extensive eutrophication, and is subject to frequent algal blooms, particularly after prolonged periods of precipitation and increased nutrient entry occurring during late summer and early fall. Furthermore, the Cape Charles station had elevated productivity rates (2-year avg. = 734 mg $C/m^3/hr$) similar to the Lafayette, even though situated in a more rural setting. This station is located adjacent to a golf course, in a semi-enclosed portion of Old Plantation Creek, thrus with low tidal flushing it is subject to increased nutrient input in the form of commercial fertilizers. The Cape Charles station also had the highest productivity during the study, at 1,907 mg $C/m^3/hr$ during the 2011 fall season. The lowest average phytoplankton productivity rates were seen at the New Point Comfort station (avg. 141 mg $C/m^3/hr$), which, as noted earlier, is considered a more pristine location, with little surrounding human development, and has an unrestricted path of water exchange with Chesapeake Bay.

While much of the reported data regarding microphytobenthic productivity rates are reported as "mg $C/m^2/hr$", an aerial rate, data presented here is expressed as "mg

$C/m^3/hr$", a volumetric rate, since productivity was measured considering the entire algal community within the sediment core, instead of just the surface component. Comparison of aerial rates to volumetric microphytobenthic primary productivity rates is commonly accepted in microphytobenthic studies. Benthic microalgal primary productivity rates (0 – 21 mg $C/m^3/hr$), while significantly lower than rates for the neighboring phytoplankton, still are within the range of published results both in the intertidal Chesapeake Bay (1 – 90 mg $C/m^2/hr$), and worldwide (Cahoon 1999). When considering microphytobenthic biomass values measured in this study, benthic productivity rates recorded here are unexpectedly low (2-year average = 2.80 mg $C/m^3/hr$), particularly when compared with rates in the phytoplankton (2-year average = 390 mg $C/m^3/hr$). While microphytobenthic productivity rates were considerably lower than those of the phytoplankton, their biomass values were significantly higher than the phytoplankton, indicating an important role as a food source for benthic fauna. Evidence of an inverse relationship between biomass and productivity, similar to patterns seen in some terrestrial producers (Tilman et al. 1996) was explored, though no significant correlations could be made. Possibly explaining the high biomass/low productivity rates, much of the biomass quantified in this study may have been from sediment layers below the narrow euphotic zone, particularly in the muddy/silty sediment habitats, where many algal cells may not be photosynthetically active, or have reduced photosynthetic capacity. In general, microphytobenthic productivity rates remained static throughout the sampling period, having rates at most stations in the 0 – 5 mg $C/m^3/hr$ range, with little apparent divergence. However, data evaluation on a station by station basis indicated erratic patterns of productivity throughout the year regardless of biomass, season, or any other environmental variable, a

phenomenon similarly observed in other studies (Thornton 2002). Large scale and high frequency variations in biomass and productivity are a common feature of microphytobenthic communities (Kromkamp and Forster 2006). A review of annual rates by Cahoon (1999) highlight the extreme variability in estimates of microphytobenthic primary production , with an average rate of 104 g $C/m^2/yr$ with a standard deviation of 93 (North America only), with worldwide rates exhibiting similar variability. Both phytoplankton and microphytobenthic communities are patchy in their distribution, both at the meso- and microscale level, leading to significant variation in biomass values and primary productivity rates, complicating attempts at measuring these parameters. Phytoplankton patchiness, both on small and large scales is often the result of turbulent flow, shear, and tidal energy (Mitchell et al. 2008). In the benthos, this phenomenon may be more pronounced than in the fluid pelagic environment, as benthic habitats are subject to a wider range and magnitude of variables, both natural and human-influenced. Variability seen in microphytobenthic primary productivity rates may be the product of both actual variability and the differences in methodology used to measure those rates (Forster and Kromkamp 2006). In order to accurately evaluate trends in productivity, precise quantitative methodology must be employed. In the case of microphytobenthic communities, this may not be easy due to the complex set of changing interactions between the biological, chemical, and physical processes occurring in the benthic environment.

Though no clear productivity trends are apparent, some congruence with phytoplankton data was present, with productivity generally increasing with increasing temperature, yet no significant relationship was present. Also similar to the

phytoplankton, both the Lafayette and Cape Charles stations exhibited the highest average microphytobenthic productivity rates (2-year averages = 5.54 mg $C/m^3/hr$ and 10.33 mg $C/m^3/hr$, respectively) over the course of the study. This reinforces the concept of nutrient loading in these areas as a driver of increased algal productivity. The lowest average benthic productivity rate (0.05 mg $C/m^3/hr$) was observed at the Lynnhaven station. This site, is characterized by heavy wave action/disturbance plus large, coarse-grained sediment, and usually with little, or no obvious algal growth. This was consistently the benthic station with the lowest abundance and biomass values. Unlike evidence from previous studies summarized by Cahoon (1999), when compared with phytoplankton productivity rates, the current data does not suggest microphytobenthos as a large contributor to estuary-wide primary productivity for the entire Chesapeake Bay ecosystem, relative to phytoplankton productivity.

CHAPTER VIII

CONCLUSIONS

Results of this study have identified a significant microalgal biomass (microphytobenthos) within the benthic environment occurring year-round in the near shore waters of lower Chesapeake Bay. Unlike many estuarine macrophytes which enter dormancy during the colder fall and winter months, the microphytobenthos in these waters represent a continuous source of carbon to higher trophic levels of the common biota regardless of season. This study has identified specific relationships in this microalgal community and drivers of community composition and related dynamics. Productivity rates measured here indicate increased phytoplankton and benthic production in eutrophic habitats and other areas of high nutrient input. Based on these results, intertidal microphytobenthic primary production accounts for roughly 1% of the total microalgal production in the habitats surveyed. Although this percentage is low compared to the phytoplankton productivity, when considering the extent of the intertidal habitats in the Chesapeake Bay estuarine system, it represents a substantial amount of biomass available to constituents within the Bay complex.

These estimates do not include sub-tidal microphytobenthos or intertidal periphyton, and are restricted to the sediment-associated microalgae. Based on the sampling of only one benthic microalgal compartment, methodological constraints, and the characteristic patchiness of benthic microproducer communities, these results are believed to be an underestimate of benthic microalgal production in lower Chesapeake Bay.

As noted previously, phytoplankton and microphytobenthic populations are often generalized into a single group referred to as "microalgae". These findings

suggest that while some taxonomic overlap exists between these groups, their diversity, cell densities, biomass, productivity rates and community dynamics are very different, and reinforce the theory that they are indeed separate communities and should not be categorized as a single functional group. Considering the microphytobenthos alone, previous taxonomic studies of microphytobenthic communities often stress the presence of diatoms, and in many cases ignore the occurrence of other algal groups. Data presented here are to the contrary, in that a great diversity of benthic microalgal flora is present in these habitats. In several cases, other algal groups such as cyanobacteria and chlorophytes dominated the algal biomass at these benthic stations. As such, it is not recommended that all microphytobenthic communities be treated similarly, as these data reveal unique benthic microalgal assemblages, often showing site-specific diversity, significantly different from that in the neighboring phytoplankton.

While a number of factors interact to complicate microphytobenthic biomass and productivity measurements in the intertidal such as sediment type, light attenuation, spatial patchiness, and physiological variability driven by temperature, light, and other environmental gradients, it may be that microphytobenthic taxonomic diversity may itself account for much of the observed variability in primary productivity rates (Kromkamp and Forster 2006), with certain microalgal groups possessing unique physiological and photosynthetic capabilities.

While this project quantifies microphytobenthic properties on large scales, both spatially and temporally, small-scale variation must be explored as well. Evidence of daily oscillations of biomass, productivity, and highly localized species turnover may explain the high variability and lack of seasonal patterns in the biomass and primary

productivity measurements in this study. The heterogeneity observed in the benthic environment may be due to harsh and rapidly changing local or regional environmental conditions commonly associated with this algal community; the magnitude of which is not present in the pelagic environment. Intertidal benthic organisms, both flora and fauna, are subject to extreme physical, temperature, light, and salinity changes during ebb and flood tides, along with the obvious issues of daily periods of desiccation during emersion. Additionally, the benthos, and particularly the intertidal zone, may be more prone to human impacts than neighboring sub-tidal environments. Due to high human impacts in estuarine environments, and particularly in the shoreline areas where this study was focused, discerning natural microphytobenthic variability from that caused anthropogenically may be difficult. The presence both naturally-occurring and human-influenced disturbance-driven patchiness may affect these communities on a daily basis, thereby making broad conclusions regarding microphytobenthos dynamics across Chesapeake Bay not prudent.

Looking toward the future, predicted increased eutrophication of estuaries and coastal ecosystems worldwide will no doubt have a significant effect, not only on microphytobenthic communities, but the habitats in which they persist, and all associated local flora and fauna. What these effects may be however, are difficult to discern, and are hardly predictable. In one scenario, increased anthropogenic nutrient input would lead to extensive phytoplankton blooms, which may create a positive feedback, with a surplus of carbon entering the system, and eventually decomposing, thereby releasing nutrients back into the system. As noted earlier, microphytobenthic biofilms are adept at remineralizing nutrients bound in the sediments. Potentially, this would be advantageous for

microphytobenthic communities, allowing for increased productivity and extensive benthic microalgal biomass development. This situation would not only alter biomass and productivity rates, but could potentially affect the taxonomic makeup of these benthic microproducers. In the presence of recurrent dense phytoplankton blooms, turbidity becomes a factor, particularly in shallow near shore areas. In this case, temporary, yet frequent shading of the benthos would favor those algal taxa that either have an affinity for low-light conditions, or are otherwise better adapted at thriving in such an environment.

When considering eutrophication and habitat degradation in general, other human-influenced effects cannot be ignored. Coastal development and the hardening of shorelines is a serious threat to estuarine ecosystems, and particularly coastal wetlands, which are at the forefront of such development. A combination of rising sea levels and the construction of more bulkheads, seawalls, and other such non-natural shoreline structures, wetland vegetation is obstructed from a landward migration, thereby "drowning" such habitats. With the loss of wetlands, so comes the loss of those flora and fauna that inhabited these environments. In many cases, and especially in the vast wetlands of Chesapeake Bay and its associated tributaries, these coastal wetlands provide crucial habitat and rearing grounds for countless numbers of economically vital and ecologically essential marine and estuarine species.

While the specific role(s) and dynamics of microphytobenthos in these systems is still debatable, their importance is no longer in question. The results presented here, including biomass, abundance, productivity, and taxonomic information characterize the microphytobenthic communities and provides an essential framework for future

Chesapeake Bay microphytobenthic research, and identifies the importance of this crucial and significant component of the Bay's estuarine ecosystem.

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Selected Publications and Abstracts

Semcheski, M.R., T.A. Egerton, and H.G. Marshall. 2014. Comparative analyses of composition and productivity of phytoplankton and intertidal benthic microalgal communities in lower Chesapeake Bay. Ocean Sciences Meeting (American Society of Limnology and Oceanography). Honolulu, HI.

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