Nutrient Loading and System Response in the Coastal Lagoons of the Delmarva Peninsula

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A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Science

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by

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2009

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science

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PREFACE

Chapters 1 and 2 of this thesis were written as separate, independent manuscripts to be submitted for publication in peer-reviewed journals.

ACKNOWLEDGEMENTS

This master's thesis is the product of a significant amount of effort and dedication on behalf of numerous individuals. First, I want to thank my advisors, Dr. Mark Brush and Dr. Iris Anderson for their endless support, guidance, and motivation throughout my project and my time at VIMS. Dr. Brush's open door policy, endless patience with my "quick questions", and thoughtful advice were critical to the success of this project. Thank you both for providing me this tremendous opportunity. I am also very grateful to my committee members Dr. Karen McGlathery and Dr. Carl Friedrichs for their expertise and contributions to my project.

Secondly, I am indebted to all the people who made my field work possible by helping patiently with my long field days and late lab nights. Beth Condon, thank you for your patient assistance, advice, and, most importantly, your friendship as I developed my project and my life at VIMS. Ben Lawson and Heather Wiseman, I am entirely grateful for your tolerance and for your humor in dealing with leaking light boxes and endless nights in the lab. Jen Stanhope and Amber Hardison, thank you for your willingness to answer my numerous questions, offer advice, and generally help me through life at VIMS. Lisa Ott, Hunter Walker, and Sam Lake your assistance with my cold field days and lab work is much appreciated; YSIs do not calibrate themselves nor does the Lachat truly operate on its own. I also owe a huge thank you to Sean Fate and the Eastern Shore Lab crew and staff for making my field days possible and, more importantly, fun. Thank you, also, to my friends for providing much needed distractions and laughter.

To my family I am forever grateful. Mom and dad, I would not be where I am today without the amazing opportunities and encouragement you provided me over the years. Your lifelong love and support are the roots of my success. Jimmy and Val, thank you for being the best "big" little brothers and for always making me laugh and find humor in life. To Shawneen and Jacqui, I am so grateful Michael brought you into my life; thank you for your patience on holidays and vacations when I toiled away in your kitchen and living room. Finally, to Michael, my amazing husband and best friend, I cannot fully express my gratitude for your love, support, and encouragement over the last several years. You inspire me to be "great"- thank you.

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INTRODUCTION

Over half of the United States population resides in the coastal zone, making these regions the most developed in the nation (EPA, 2001). Growing development, population growth, and expansion of agricultural activities in coastal areas have increased loads of anthropogenic nitrogen to coastal marine systems (Nixon, 1995). This nutrient enrichment often results in eutrophication, or acceleration in the supply of organic matter (Nixon, 1995), which can lead to elevated concentrations of organic matter and phytoplankton in the water column (Valiela et *al.*, 1992; Taylor et *al.*, 1995a), increased biomass of macroalgae (Valiela et *al.*, 1992; 1997b), reduced dissolved oxygen levels (Bricker et *al.*, 2008), and losses of vegetated macrophytes (Valieal et *al.*, 1992, Duarte, 1995). Eutrophication can lead to degraded water quality and adverse shifts in ecosystem structure and function (Valiela et *al.*, 1992; Smith et *al.*, 1999).

Characterized by shallow depths (1-2 m) and well-mixed water columns, coastal lagoons are positioned at the land-sea margin and serve an important role as a filter for organic matter and nutrients traversing to the ocean (McGlathery et *al.*, 2001; Anderson et *al*., 2003). Nutrient enrichment and subsequent eutrophication is increasing nationwide (EPA, 2001; Bricker et *al.*, 2008), threatening the health of coastal ecosystems. Coastal lagoons are particularly susceptible to nutrient enrichment due to their close proximity to land, depth of the photic zone, and, in some cases, long residence times (Duarte, 1995; McGlathery et *al.*, 2007). Nitrogen loading per water body area to these littoral systems can be as high as loading to deep estuarine systems, illustrating the significant threat nutrient enrichment poses to shallow coastal bays (McGlathery et *al.*,

2007). Understanding the response of shallow systems to changes in nutrient regime is critical due to increasing anthropogenic pressure.

The effect of nutrient enrichment on deep estuarine systems has been widely studied and is well understood, though current understanding of the response of shallow marine systems to nutrient enrichment is limited (Boynton et *al*. 1996; Kinney and Roman, 1998; Nixon et *al.,* 2001; McGlathery et *al.*, 2007). In relatively deep estuarine systems where the benthos receives minimal, if any, light and stratified waters maintain phytoplankton within the photic zone, pelagic primary production dominates. Multi-year evaluations of nutrient enrichment in deep estuarine systems show a general trend of increasing water column chlorophyll (a proxy for phytoplankton biomass) with increasing nitrogen loading in systems with relatively low tidal energy (Monbet, 1992; Nixon et *al.*, 2001; Kemp et *al*., 2005).

A variety of physical and biological factors, however, can cause estuarine systems to deviate from this general trend. In Ythan Estuary and Bay of Brest, high tidal energy and rapid flushing of nutrients and phytoplankton out of the system resulted in stable phytoplankton concentrations despite increasing anthropogenic nutrient loading (Balls et *al.*, 1994; La Pape et *al.*, 1995; Cloern 2001). Large populations of benthic filter feeders exerting intense grazing pressure on phytoplankton biomass can also cause a system to diverge from the general trend as exemplified in the enriched San Francisco Bay (Alpine and Cloern, 1999; Cloern, 2001). Residence time also complicates the relationship between nutrient loading and phytoplankton concentrations (Valiela et *al.*, 1997b; Cloern, 2001). Additionally, light limitation (Cloern, 1999; 2001) can also complicate the positive relationship between nitrogen and phytoplankton. In the absence of confounding

factors, deeper estuarine systems tend to increase total system productivity in response to nutrient enrichment (McGlathery et *al.*, 2007).

Pelagic-benthic coupling in shallow systems complicates system response to nutrient enrichment. Light reaches the bottom in shallow coastal systems stimulating the growth of benthic micro- and macroalgae, and the benthos can contribute significantly to total system production. Nitrogen loading can thus stimulate the growth of both pelagic and benthic primary producers (i.e. seagrasses, macroalgae, microalgae). Competition between autotrophic groups for light and nutrients led to a conceptual model of shifting dominance of primary producers with increasing nutrient loads in shallow systems (Borum and Sand-Jensen, 1996; Valiela et *al*, 1997). According to the model, increases in nutrient enrichment cause shifts in autotroph dominance, from seagrasses and slow-growing macroalgae in high-light, low-nutrient conditions, to bloom-forming macroalgae and phytoplankton in low-light, high-nutrient conditions; shading effects and competition for resources fuel the shift in producers (Fig. 1- Duarte, 1995; Borum and Sand-Jensen, 1996; Valiela et *al.*, 1997). This model excludes benthic microalgae, which may obscure general trends in autotroph dominance.

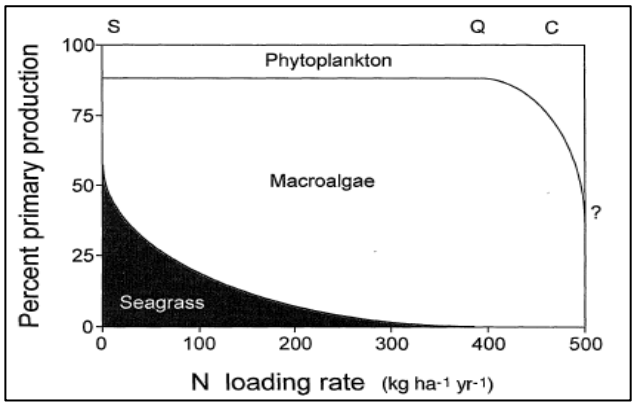

Figure 1 : Valiela et *al.*'s (1997b) conceptual model illustrating the shift in primary producers species in 3 systems of Waquoit Bay, MA with different loading rates; S- Sage Lot Pond; Q- Quashnet Pond; C- Childs River.

Complex interactions among primary producers complicate the use of the conceptual model as a paradigm for shallow system response to nutrient enrichment. While it appears seagrass declines at high nutrient loads due to light limitation by shading

from phytoplankton and macroalgae (Valiela et *al.*, 1992; Valiela et *al.*, 1997; Havens et *al.*, 2001), competitive outcomes between phytoplankton and macroalgae are inconsistent. Both phytoplankton (Taylor et *al.*, 1995b) and macroalgae (Fong et *al.*, 1993) have been shown to be the dominate producer at high nutrient loads, while others found no predictive pattern in the response of dominant autotrophic communities to nutrient enrichment (Taylor et *al.*, 1999; Nixon et *al.*, 2001). Additionally, attempts to link nitrogen loading to increases in primary producer biomass have been unsuccessful. In some cases, shallow systems demonstrate positive relationships between increased nitrogen loading and increases in water column chlorophyll (Boynton et *al.*, 1996), macroalgal biomass (Valiela et *al.*, 1997; Kinney and Roman, 1998), and net and gross primary production (Oviatt et *al.*, 1993; D'Avanzo et *al.*, 1996). However, other studies found no predictive relationship between nitrogen loading and primary producer biomass or production (Nixon et *al.*, 2001).

The inability to assign consistent predictive relationships between nutrient load and autotroph response is due to the suite of direct and indirect interactions with physical processes like residence time and flushing, light regime, and filter feeding populations (Cloern, 2001; Howarth and Marino, 2006). Simple predictive relationships do not seem to exist when evaluating nutrient loading compared to one component of the system such as pelagic primary production (Howarth and Marino, 2006). The importance of benthic producers in shallow systems also complicates the predictive relationship. An understanding of how changes in nutrient regime affect shallow systems requires broad ecosystem scale evaluations incorporating different processes mediating trophic response (Cloern, 2001).

Net Ecosystem Metabolism:

An easily measurable and integrative approach for assessing the trophic response of an entire system to nutrient enrichment is net ecosystem metabolism (NEM- Kemp and Boynton, 1980; D'Avanzo et *al*., 1996; Kemp et *al.*, 1997). Defined as the difference between gross primary production (GPP) and community respiration (R), NEM provides a measure of how a system processes nutrients and organic material (Smith and Hollibaugh, 1997). A system with positive NEM (in oxygen units) is net autotrophic and produces more organic matter than is consumed by a net assimilation of inorganic nutrients (Hopkinson and Smith, 2004). Conversely, a system with negative NEM (in oxygen units) is net heterotrophic with a potential net export of inorganic nutrients and a net import or storage of organic matter (Eyre and McKee, 2002; Hopkinson and Smith, 2004). Just as the metabolism of an individual organism is driven by numerous cellular components, an ecosystem's metabolism is an aggregate of numerous ecological processes (Odum and Hoskins, 1958). Therefore, system metabolism is a key measure of the functional activity of an ecological community (Boynton and Kemp, 1980), and quantifying this measure is a useful indicator of the

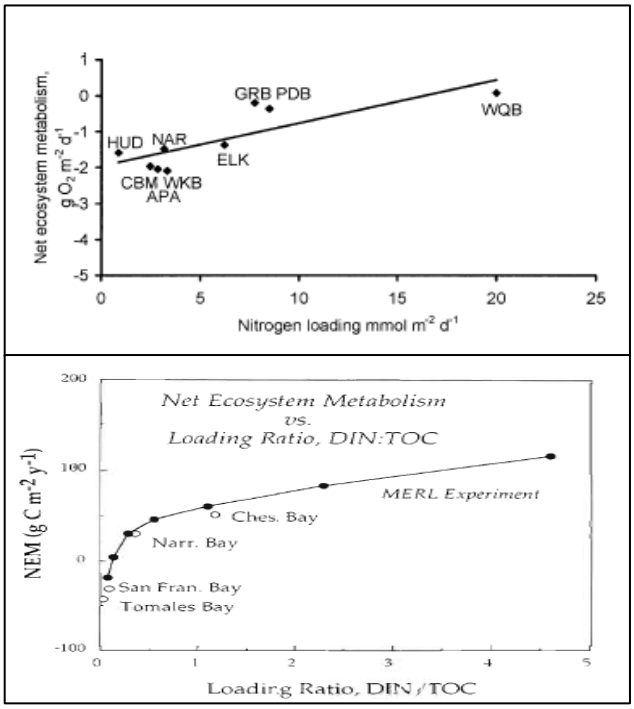

Figure 2: Relationship between nutrient enrichment and NEM in coastal systems; Top- from Caffrey (2004) showing increasing NEM with increasing nitrogen load in several national estuarine research reserve sites; Bottom- from Kemp et *al.* (1997) illustrating increasing NEM (measured by ^{14}C method) with the ratio of DIN to TOC load.

trophic status of the system (Caffrey, 2003). Net ecosystem metabolism measurements inherently incorporate complex processes influencing primary production and respiration, and are a great tool for assessing the trophic response of shallow ecosystems.

General trends in coastal zone NEM are unclear. A review by Smith and Hollibaugh (1993) concluded that terrestrial organic matter inputs to coastal systems fuel heterotrophy. Conversely, Gattuso et *al.* (1998) found that most coastal systems (i.e. macrophyte-dominated systems, coral reefs, salt-marshes, mangroves, and continental shelf) are net autotrophic, except for estuaries, which are net heterotrophic. Relatively deep estuarine systems are generally net heterotrophic and shallower systems, with a contributing benthic producer population trend towards autotrophy. A study of shallow sites in the Chesapeake Bay, found that the majority of sites were autotrophic (Schaffner and Anderson, *unpublished data*). Otherwise heterotrophic, macrophyte populations in shallow St. André lagoon pushed this system toward net autotrophy (Duarte et *al.*, 2002). Similarly, a study of 27 shallow National Estuarine Research Reserve Sites (NERRS) using historical dissolved oxygen data found that only eelgrass or macroalgae dominated sites were autotrophic on an annual basis (Caffrey, 2003). Though, Barron et *al.* (2004) found seagrass dominated systems can be heterotrophic due to the build-up of allochthonous organic matter. Other studies have also found seasonal patterns in the trophic status of shallow systems, with system heterotrophy in the fall and system autotrophy in the spring (Carmouze et *al.*, 1991; Smith and Hollibaugh, 1997; McGlathery et *al.*, 2001).

The loading ratio of inorganic nutrients to organic carbon (DIN:TOC) can control the NEM of coastal environments (Kemp et *al.*, 1997). For example, in Tomales Bay,

California, large influxes of oceanic carbon from coastal upwelling fueled system heterotrophy (Smith and Hollibaugh, 1997). In systems receiving high rates of inorganic nutrient loading though, NEM may shift towards autotrophy (Fig. 2). In Moreton Bay, Australia, nutrient loads from increased wastewater discharges resulted in system autotrophy (Eyre and McKee, 2002). Similarly, studies by Oviatt et *al.* (1986) and Caffrey (2004) show that as nutrient loading increases, NEM becomes more autotrophic. Thus, NEM appears to be a useful indicator for system response to nutrient enrichment.

The majority of studies measuring NEM in relation to nutrient loading have focused on estuarine systems or shallow tributaries and littoral zones of larger systems; few studies have concentrated on lagoon systems. Given that coastal lagoons comprise a notable percentage of the world's coastlines and provide vital ecological services (Boynton et *al.*, 1996), understanding the response of these systems to increasing nutrient enrichment is important.

Methods for Measuring Net Ecosystem Metabolism:

Several methods exist for measuring NEM, both oxygen and non-oxygen based. Two widely-used oxygen-based approaches for measuring total system metabolism are the open-water and component methods (Odum and Hoskins, 1958; Kemp et *al.*, 1997; Hopkinson and Smith, 2004). Open-water methods measure *in situ* metabolism, which is determined from changes in water column DO concentrations measured at dawn and dusk or net changes over a 24-hour period measured using a continuously recording datasonde. The component approach measures changes in dissolved oxygen concentrations in the water column and sediments separately, and aggregates them to obtain a measure of total system metabolism. A popular non-oxygen based method employs a mass balance for

NEM measurements. Mass balance methods calculate NEM using nutrient fluxes, input and outputs, and stoichiometry (Kemp et *al.*, 1997; Gazeau et *al.*, 2005). Budgets based on stoichiometry do not work in shallow systems, because benthic microalgal uptake and microbial processes complicate calculations of the nitrogen term (Anderson et *al.*, 2003). Relatively few studies comparing the different approaches have been done (Kemp et *al.*, 1997; Hopkinson and Smith, 2005); however, the comparative studies that do exist have found that different approaches can lead to different estimates of total system metabolism (Odum and Hoskins, 1958; Kemp and Boynton, 1980; Kemp et *al.*, 1997).

Oxygen-based NEM measurements are widely used because they are easy to apply and provide a reliable measure of NEM. However, the most appropriate method, open-water versus component, for measuring shallow ecosystem metabolism is still unclear (Hopkinson and Smith, 2005). An open-water method is useful because it accounts for all biological and physical factors affecting metabolic processes. This method is difficult to apply in shallow lagoons, however, because of the large influence of physical factors such as tides, currents, and winds (Kemp and Boynton, 1980), which influence atmosphere-water exchange of oxygen, nutrient fluxes, and system metabolism. Conversely, a component approach to total system metabolism excludes physical factors, but may lead to flawed measurements of metabolic processes because the experimental enclosures isolate the water and sediments from natural processes like nutrient flux and mixing occurring in the system (Kemp and Boynton, 1980). Additionally, component methods require large sample sizes to account for natural heterogeneity in the system. Component method measurements are beneficial, however, because they quantify the relative importance of different biotic components (Smith and Hollibaugh, 1997).

A recent study by Gazeau et *al.* (2005) conducted in Randers Fjord, Denmark, compared four methods of measuring NEM, oxygen incubations (component method), dissolved inorganic carbon (DIC) budgets, response surface difference (RSD), and dissolved inorganic phosphorous (DIP) budgets (also known as Land-Ocean Interaction in the Coastal Zone [LOICZ] budgets). Methods were compared between two months, April and August 2001. All of the methods gave similar values for NEM in both sign and magnitude, but the oxygen incubations underestimated metabolic rates compared to the other methods. Underestimation was largest in August when the spatial resolution of sampling decreased, because of fewer sampling sites (Gazeau et *al.*, 2005). Since the study only compared methods between two months, drawing conclusions about the accuracy of oxygen incubations is difficult.

Other studies have also found that component incubations underestimate system production and respiration (Kemp and Boynton, 1980; Smith and Hollibaugh, 1997; Santos et *al.*, 2004). Photoinhibition of primary producers may be a reason incubations underestimate primary production (Macedo et *al.*, 2002), but this should not be a problem in shallow systems since pelagic and benthic primary producers are adapted to saturating light levels. Macedo et *al.* (2002) found that short incubations (30 min - 1 hr) applied in shallow systems do not lead to underestimations of primary production. Despite the potential discrepancies of using component incubations, a variety of studies found that NEM values from component methods were similar to NEM estimated from other methods (Nowicki and Nixon, 1985; Santos et *al.*, 2004; Gazeau et *al.*, 2005).

Oxygen-based measurements can be problematic due to the potential underestimation of community respiration, as this method does not directly measure

anaerobic metabolism (Hopkinson and Smith, 2005). Sulfate reduction is an important anaerobic pathway in marine sediments, which does not utilize oxygen and creates sulfide as a major product. In systems with high rates of anaerobic respiration via sulfate reduction, oxygen measurements will not account for and underestimate this fraction of community respiration. Underestimation may be a greater problem in eutrophic systems with higher rates of anaerobic respiration (Hopkinson and Smith, 2005). Despite this potential issue, Santos et *al.* (2004) found that underestimation of community respiration from oxygen measurements is relatively low. Oxygen can reoxidize sulfide, the major product of sulfate reduction, which is then accounted for in oxygen flux measurements (Santos et *al.*, 2004). Therefore, oxygen-based rates can still provide a reliable estimate of NEM.

Objectives

The overarching objective of this thesis project was to assess the impact of nutrient loading on shallow coastal lagoons. The first objective was to establish a variation in nutrient loads among the four coastal lagoons of the VA/MD Eastern Shore chosen for this project. Second, we wanted to link watershed land use to eutrophication occurring within the system. The third objective was to determine how system metabolism changed as a response to nutrient enrichment. Our final objective was to compare two widely used methods for measuring system metabolism, an open water method and a component method, in a shallow coastal lagoon.

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CHAPTER 1: Extending the Delmarva Eutrophication gradient into Virginia's coastal lagoons using a combination of watershed modeling and nitrogen source tracking

ABSTRACT

Nutrient enrichment is an increasing threat to the health of coastal lagoons as coastal watersheds experience intensified development and population growth. A well-established large-scale eutrophication gradient exists among the coastal bays of the Delmarva Peninsula, particularly in MD and DE where extensive development and agriculture contribute to the nutrient enrichment of shallow systems. In VA, rural agriculture and forest dominate the landscape, suggesting these systems are relatively less impacted. Using a combination of modeling and nitrogen source tracking, we tested the degree to which the Delmarva nutrient enrichment gradient extends into the coastal bays of VA. Despite the rural character of VA's coastal watersheds, some of the shallow bays in VA appear to be quite nutrient enriched due to intensive agriculture in the watershed and high watershed to lagoon size ratio. Results of a nitrogen source tracking experiment confirmed the importance of recycled nutrients to primary producers. The response of VA lagoons to nutrient enrichment does not follow trends of eutrophication established in other shallow systems, particularly in MD, which exhibited positive relationships between nutrient loading and both water column chlorophyll and nutrient concentrations. Our results suggest VA's coastal bays respond differently to enrichment than the northern bays, perhaps due to more rapid flushing in the VA lagoons.

INTRODUCTION

Nutrient enrichment is an increasing threat to the health of coastal lagoons as coastal watersheds experience intensified commercial and residential development, population growth, and agricultural activities. This nutrient enrichment often results in eutrophication, a phenomenon defined by Nixon (1995) as "an increase in the rate of supply of organic matter". Eutrophied waters tend to have elevated concentrations of organic matter and phytoplankton (Valiela et *al.,* 1992; Taylor et *al.*, 1995), increased biomass of macroalgae (Valiela et *al.*, 1992, 1997b), reduced dissolved oxygen levels, and losses of vegetated macrophytes (Valiela et *al.*, 1992, Duarte, 1995). Eutrophication ultimately leads to degradation of water quality and loss of ecosystem function (Valiela et *al.*, 1997b).

Nitrogen is the primary stimulus for eutrophic conditions in temperate, marine systems due to the nitrogen limited nature of marine primary producers (Howarth, 1988; Taylor et *al.*, 1995; Howarth and Marino, 2006). Coastal lagoons are particularly susceptible to nitrogen enrichment because of their proximity to land, photic zone depths, and high residence times (Duarte, 1995; McGlathery et *al.*, 2007). Bio-available nitrogen enters marine systems through both external, anthropogenic inputs ("new nitrogen") and internal nitrogen fixation, and is retained in the system through internal recycling processes. Introduction of new nitrogen into marine systems stimulates and maintains eutrophic conditions.

Various sources contribute anthropogenic nitrogen to coastal marine systems. Atmospheric deposition to the watershed and water surface contributes inorganic and organic nitrogen to coastal systems, and can represent an important external source of

nitrogen (Spokes and Jickells, 2005). Freshwater input in the form of runoff from the land, riverine inputs, or groundwater flow is also an important source of anthropogenic nitrogen. If the dominant freshwater input is groundwater, as is the case for the coastal lagoons of the VA Eastern Shore, the water quality of the receiving bays or lagoons is tightly linked to the land use occurring in the watershed (Reay et al. 1992), though the importance of groundwater depends on the ratio of watershed to lagoon volume. Agriculture and residential development can contribute significantly to groundwater nitrogen loads due to fertilization of crops and lawns and leaching of nitrogen from wastewater effluent.

Coupling of land-derived nitrogen and eutrophication implies that primary producers assimilate the new nitrogen entering the system. Since different nitrogen sources have different $\delta^{15}N$ signatures, primary producers also incorporate the ^{15}N isotopic signature of the new nitrogen source (Martinetto et *al.*, 2006). Evaluating stable nitrogen isotope signals in marine primary producers is a useful method for determining the sources of anthropogenic nitrogen in marine environments (Peterson and Fry, 1987; Macko and Ostrum, 1994; McClelland et *al.*, 1997; Martinetto et *al.*, 2006). Macroalgae have been shown to be sensitive indicators of anthropogenic nitrogen loading (Costanzo et *al.*, 2001; Cole et *al.*, 2004; Martinetto et *al.*, 2006). A new technique, nitrogen source tracking, relies on macroalgal incorporation of the enrichment signal to determine systems impacted by septic tanks, sewage wastewater, or livestock agriculture (Costanzo et *al.*, 2001; Savage, 2005; Deutsch and Voss, 2006).

Atmospheric nitrogen has a light $\delta^{15}N$ signature at 0‰. Synthetic fertilizers and ammonium (NH_4^+) produced from nitrogen fixation have isotopic signatures ranging

from 0 to 4‰, due to the conversion of atmospheric N_2 into a bio-available nitrogen form (Sharp, 2007). Alternatively, nitrogen derived from groundwater influenced by wastewater has a heavier $\delta^{15}N$ around +10‰ to +20‰ (McClelland et *al.*, 1997). Nitrogen from animal waste, particularly poultry, also has an enriched $\delta^{15}N$ signal around 8‰ (Macko and Ostrum, 1994; Wassenaar, 1995). Fractionation, due to the preferential reaction of isotopically light nitrogen (^{14}N), creates the enriched signal of nitrogen derived from waste (Macko and Ostrum, 1994; Sharp, 2007).

A gradient of nutrient enrichment exists among the coastal bays of the Delmarva Peninsula (Table 1), with generally higher loading in the northern lagoons and lower loading in the southern lagoons. Extensive agriculture and commercial and residential development in the DE and MD coastal watersheds contributes to the large annual nitrogen loads to receiving coastal lagoons (Boynton et *al.*, 1996; Table 1). Virginia's Eastern Shore is an area characterized by minimal development, large-scale agriculture and abundant natural vegetation. Development is beginning to alter VA's rural watersheds, however, and the high nutrient loads of the MD and DE bays has important implications for the VA coastal bays as development increases.

Using complimentary techniques of watershed modeling and stable nitrogen isotopes, we test the degree to which the regional eutrophication gradient extends into VA's coastal lagoons. We focus on four Delmarva lagoons, three in VA and one in MD. Compared to the more nutrient enriched lagoons of MD and DE, we expect the VA systems to receive lower nutrient loads given the surrounding rural watersheds. Annual nitrogen loads for each system were quantified, and we used a modified-nutrient loading model (NLM- Valiela et *al.* 1997; Cole, 2003) for systems with no previous estimates. A

nitrogen source tracking study was done to determine sources of anthropogenic nitrogen entering the coastal lagoons. We hypothesized that systems with larger nitrogen loads and more influence from animal or human waste will have heavier isotopic signatures.

METHODS

Study sites

The four coastal lagoons selected for the study are Hog Island Bay, Burton's Bay and Gargathy Bay, VA and Isle of Wight Bay, MD. All four bays are located on the Atlantic side of the Delmarva Peninsula (Fig. 1a). Isle of Wight Bay has an average depth of 1.2 m and a surface area of 21.1 km^2 and is estimated to be moderately impacted (Wazniak et *al*., 2004). Extensive development in the watershed and inputs from the highly impacted St. Martin's River contribute to the high nutrient and chlorophyll concentrations in the bay (Maryland Coastal Bays Program, 2004), resulting in an annual load of 6.5 g N m^{-2} y^{-1} (Boynton et *al.*, 1996). Gargathy Bay and Burton's Bay were chosen because they are estimated to be moderately impacted based on a previous study by Stanhope (2003). Agricultural operations including poultry and tomato farms and moderate residential development exist within the Gargathy and Burton's watersheds and contribute to the nutrient enrichment of these systems. Hog Island Bay is the least impacted member of the four sites, due to the lack of extensive development and comparatively low annual areal nutrient load (Stanhope, 2003). The annual nitrogen load to HIB is 1.4 g N m^{-2} y^{-1} (Stanhope, 2003).

Nitrogen Loading Model (NLM)

A watershed nutrient loading model was used to calculate the annual nitrogen load (kg N y^{-1}) entering Gargathy and Burton's Bay from the surrounding watershed. The model, originally developed for Waquoit Bay in Cape Cod, Massachusetts (Valiela et al. 1997a) and recently adapted for the Virginia/Maryland Chincoteague Bay (Cole 2005), can be applied to watersheds characterized by rural to suburban land use where the main source of freshwater to the estuary is groundwater. Accomack County has unconsolidated sandy sediments (EPA, 1997) which is characteristic of watersheds dominated by groundwater inputs, including Waquoit Bay where the NLM was developed. Given Accomack County's rural landscape, sediment type, and freshwater source from groundwater, the NLM is appropriately applied in this region.

Nitrogen in the model enters the system via three inputs: atmospheric deposition, fertilizer application (both agricultural and residential), and wastewater from septic systems. Once the nitrogen inputs reach the watershed surface they are subject to a series of reductions as they travel through different land covers, the vadose zone, and the aquifer (Table 2), eventually arriving at a total nitrogen load entering the receiving water body from the groundwater (Valiela et al. 1997a). Inherent in the model calculations are the addition/losses of nitrogen from processes occurring in the soil, vadose zone, and aquifer such as nitrogen fixation, nitrification, denitrification, and remineralization of organic matter.

Nitrogen inputs (kg ha^{-1}) in the model are deposited onto four different land covers: agriculture, residential turf, natural vegetation and impervious surfaces

(impervious surfaces were broken into urban, streets and driveways, and barren, open undeveloped). Land cover in Burton's and Gargathy watersheds was determined using GIS ArcMap and datasets from numerous sources including the 2007 Regional Earth Science Applications Center, the Chesapeake Bay Program, the Virginia Soil and Water Conservation District of Accomack County, and WorldView Solution, in addition to aerial digital photographs of the watersheds and personal observation. Given the dense agriculture in the Gargathy watershed, the modified version of the NLM (Cole, 2005) was used because it specifies agricultural land by major crops. Agricultural land use in the watersheds includes tomatoes, soybeans, corn grown for grain (Virginia Agricultural Statistics 2003, 2004), and poultry operations. We made an additional modification to the model to account for tomato plasticulture. Agricultural modifications to the model included using crop specific fertilization rates, areal extent of crop, and calculations for crop nitrogen removal and attenuation for additional nitrogen (Cole, 2005). Crop data were taken from National Resource Conservation Service (NRCS), Stanhope (2003), Virginia Agricultural Statistics (2003, 2004), and Virginia Cooperative Extension (2000)

Application of the NLM

The reliability of the model output was verified by applying the NLM to small, gauged sub-watersheds in Burton's and Gargathy Bay watersheds, for Nickawampus and Gargathy Creeks, respectively (Fig.1b,c). Modeled nitrogen loads of the sub-watersheds were then compared to measurements of Stanhope (2003), who computed annual base flow nitrogen loads for the sub-watersheds from, 2001-02 with monthly measurements of stream discharge rates and in-stream nutrient concentrations at the gauged stations. After establishing the reliability of the model in the sub-watersheds, we applied the NLM to the

entire watershed for Burton's and Gargathy Bay to estimate the current annual groundwater nitrogen load to the bay. Manipulation of model parameters allowed the simulation of different land use scenarios such as, residential and agricultural expansion and increased poultry production, to project potential changes in the annual nitrogen loads to the bays and the implications for resultant water quality.

All input values used in the model are specific to Virginia or Accomack County except for parameters measured on a regional basis (i.e. atmospheric deposition). Atmospheric nitrogen deposition rates were obtained from Meyers et al. (2001) and include both wet and dry deposition. Wastewater nitrogen inputs were calculated using population and housing densities obtained from the US Census Bureau (TIGER 2000). For all agricultural scenarios, a three-crop rotation of corn followed by winter wheat (as a cover crop) followed by soybeans was assumed (Jim Belote, *personal communication*; Stanhope 2003). As noted, tomato plasticulture was added to the NLM because of the additional fertilizer the crop contributes and its presence in both watersheds. Areal extent of tomato plasticulture in the watersheds was calculated using aerial photos in ArcMap. The nitrogen content in the crops was calculated on a dry matter basis using the Crop Nutrient Calculator from the NRCS website. Agricultural fertilizer nitrogen inputs were calculated using crop-specific fertilization rates (Stanhope, 2003; Virginia Cooperative Extension, 2000). Turf fertilization rates used in Valiela et al. (1997a) and Cole (2005) were also used in this study.

Limitations of the model must be considered, because no matter how complex or simple a model's design, all models are simplifications of natural systems and include some range of error and uncertainty in the calculations. The model is spatially

aggregated and may miss small scale heterogeneity. Valiela et al. (1997a) estimated that their NLM predicted nitrogen loads within 37-38% of measured loads; therefore, the NLM predictions are interpreted as estimations and not absolute values. Despite the NLM's limitations, several studies including this one have shown the NLM provides reliable estimations comparable to actual measured loads and is a useful management tool for forecasting future scenarios (Heberlig et al. 1997; Valiela et al. 2000).

Nitrogen Source Tracking

Nitrogen source tracking was conducted in the three VA coastal lagoons, Gargathy Bay, Burton's Bay, and Hog Island Bay (Fig.1a); time and travel constraints limited our study to the VA lagoons. A similar tracking study was completed in July 2004 for the Maryland coastal bays (Jones et *al.*, 2004). In the 2004 study, macroalgae were collected from a low-nutrient site and deployed in clear, perforated chambers (similar to the ones used in this study) at various sites throughout Isle of Wight Bay. Deployments were not done in duplicate in the MD study, however, more deployments sites were used within each bay. We patterned our study after the 2004 MD study so we were able to compare results.

Source tracking in the three VA bays was done along a creek to inlet transect within each bay. In mid-June, *Gracilaria* and site water were collected from a low-nutrient site, the inlet of Hog Island Bay. Macroalgae were returned to the lab and starved for 12 days in 10-gallon, glass aquarias filled with bubbled site water in a greenhouse located at the Virginia Institute of Marine Science, Gloucester Point.

Deployment chambers for the algae were clear, 250 ml Nalgene containers with 25 8 mm holes drilled along the sides and bottom to allow water flow through the

chamber. Prior to deployment, approximately 5 g of wet algae were placed into pre-labeled containers, and put into coolers filled with incubation water for transfer to the field. Algae were assessed for uniformity before being used for deployment (i.e. similar number of fronds). Ten sub-samples of algae were collected for assessment of initial isotopic signatures.

Algal containers were deployed in duplicate along creek to inlet transects in the three bays (see Appendix I, Table 1). Chambers were deployed at a constant depth of 0.5 m below the water surface and deployments lasted 7-9 days.

At the end of the deployment, macroalgae were collected in 1 gallon Ziploc bags filled with site water, put on ice and returned to the lab. Macroalgal tissue was rinsed in distilled water and dried in a drying oven at 40˚C until reaching a constant weight. Once dry, the samples were ground into a homogenous powder by mortar and pestle, 0.2-0.3 grams of homogenized tissue were packaged into tin capsules (5x9 mm; Costech) and weighed. Samples were sent to the University of California at Davis Stable Isotope Facility for analysis on a Europa Scientific Integra isotope ratio mass spectrometer.

Statistical Analysis

All statistical tests were run in Minitab 15 software. Analysis of variance (ANOVA) was used to determine significant differences for the nitrogen source tracking experiment. Tukey's pair-wise comparison was used to determine statistical differences between groups. All statistical significance was assessed at the $\alpha = 0.05$ level. Regression analyses were also completed in Minitab 15.

RESULTS

Model Calibration

The measured annual nitrogen load for Burton's sub-watershed was 1,660 kg N y^{-1} (Stanhope, 2003). The NLM estimated a nitrogen load of 1,640 kg N y^{-1}. Values for measured and estimated loads in Burton's sub-watershed are quite similar, and vary by less than 1%. Model estimates for Burton's sub-watershed fall well within the variability of the model reported by Valiela et *al.* (1997). The measured annual nitrogen load for Gargathy sub-watershed was 2,150 kg N y^{-1} (Stanhope 2003); the NLM estimated load was 1,640 kg N y^{-1}. The difference between these values is 24%, but still within the variability range of the model. The overall close values of the model estimates and measured loads indicate that the NLM reliably predicts actual nitrogen loads of the Eastern Shore systems. In both Burton's and Gargathy sub-watersheds, the model underestimated the annual load, which is consistent with another NLM verification study that obtained lower modeled loads compared to actual loads (Heberlig et al. 1997).

Despite underestimation of modeled loads at the sub-watershed level, NLM predictions possibly overestimated nitrogen loads to the non-tidal creeks. Sediment and riparian zone uptake and denitrification of nitrogen, particularly NO_3^-, is important at the groundwater-surface water interface (Gu et *al.*, 2007), and can reduce stream nitrogen loads. The model, while it accounts for nitrogen losses in the watershed, does not specifically identify riparian or in-stream losses. However, the model estimates baseflow loads and when compared to measured baseflow loads in the creeks, which already account for the riparian or in-stream uptake processes, model loads compare well. Thus, overestimation is likely not an issue.

Whole Watershed Load Estimates

Applying the NLM to the entire Burton's Bay watershed resulted in an annual groundwater nitrogen load of 80,600 kg N y^{-1} (Table 3). Agricultural fertilization contributed almost 60% to the annual nitrogen load. Atmospheric deposition to the water body (both creeks and bay) contributed 27% of the annual nitrogen load. Contributions from residential nitrogen sources were relatively small. The NLM predicted wastewater contributed roughly 3% to the annual load and turf fertilizer less than 1%. Relative contributions of nitrogen sources break down differently in the sub-watershed. In Burton's sub-watershed, agricultural fertilizer was still the dominant nitrogen source contributing one-third of the annual load, but residential sources comprised a larger percentage. Wastewater comprised a quarter of the annual nitrogen load, and atmospheric deposition to urban and barren areas combined contributed almost 40%.

Applying the model to the entire Gargathy watershed estimated an annual groundwater nitrogen load of 29,300 kg N y^{-1} (Table 3). A large percentage of the nitrogen load, 75%, entering Gargathy Bay is estimated to result from agricultural fertilization. Residential inputs were again small with roughly 3% of the annual load estimated from wastewater and less than 1% estimated from turf fertilization. In the Gargathy sub-watershed, agricultural fertilizer was again the dominant nitrogen source (47% of the load). As in Burton's watershed, residential sources were more pronounced at the sub-watershed level, as wastewater was predicted to contribute almost 13% of the load. Atmospheric deposition contributed more to the annual load at the sub-watershed level (~ 14%) as compared to the whole Gargathy watershed (9.2%). The importance of

residential sources at the sub-watersheds level illustrates the impact of cluster developments characteristic of Accomack County.

The magnitude of annual loads entering the receiving watersheds seems quite different between the two bays. Burton's Bay watershed had a much higher annual load than Gargathy, but Burton's Bay also has larger watershed and a larger receiving water body. Normalizing the annual load to water body area provides a better comparison between the two systems. Burton's Bay was estimated to receive around 4.4 g N m^{-2} y^{-1}, whereas Gargathy Bay was estimated to receive around 25 g N m^{-2} y^{-1} (Table 4). Gargathy Bay is smaller than Burton's Bay, 1.2 x 10^6 m^{-2} and 18 x 10^6 m^{-2} respectively. The higher areal nitrogen load suggests Gargathy Bay is likely to be a more impacted system than Burton's Bay.

Model Sensitivity Analysis

Sensitivity analysis was conducted on the NLM in both watersheds (see Appendix I, tables 2,3). The model was most sensitive to changes in percent attenuation in the vadose zone and aquifer. Reducing vadose zone attenuation by 10% resulted in a 7% increase in Burton's annual load and an 8% increase in Gargathy's annual load. Decreasing the amount of attenuation in the aquifer by 10% increased the amount of nitrogen reaching Burton's and Gargathy Bay by 8% in both watersheds. Model sensitivity to these parameters is important, because the coefficients for attenuation in the vadose zone and aquifer are estimates (Valiela et *al.*, 1997a). Data regarding the amount of nitrogen lost in the aquifer are limited (Valiela et *al.*, 1997a), and changes to this parameter could influence NLM estimates.

The model was also sensitive to changes in the nitrogen content of corn and soybean crops. Sensitivity was greatest in the Gargathy watershed. Increasing the amount of nitrogen in corn crops and soybean crops by 25% decreased the annual loads by 12% and 16%, respectively. Greater nitrogen removal in crop harvests likely caused this reduction in load. The model was not quite as sensitive in Burton's watershed, but a 25% increase in nitrogen content in corn decreased the annual load by 8%, and a 25% increase in soybean nitrogen content decreased the annual load by 9%. In both watersheds, the model was relatively insensitive to changes in tomato nitrogen content. Increasing the tomato nitrogen content by 100% changed the load by less than 1%. This is likely due to the minimal amount of nitrogen in tomato plants, 0.002 kg N kg dw^{-1} vs 0.014 kg N kg dw^{-1} for corn and 0.059 kg N kg dw^{-1} for soybean . The sensitivity of the model to changes in corn and soybean nitrogen content illustrates the importance of using accurate nitrogen values for the crop being grown in the watershed. For most sensitivity analyses, estimated loads were within the reported variability range (40%), except when testing variations within vadose zone and aquifer attenuation (50%).

Nitrogen Source Tracking

Results of the nitrogen source tracking performed in the VA coastal bays indicate that dissolved nitrogen in these systems had enriched $\delta^{15}N$ values relative to potential nitrogen sources (Fig. 2). The initial average $\delta^{15}N$ signature of starved macroalgae was 12.42‰ (std. dev= 0.21). Bay-wide average post-deployment $\delta^{15}N$ signatures in Hog Island, Burton's, and Gargathy Bays were 14.7‰ (1.7), 13.2‰ (0.88), and 12.0‰ (0.53), respectively (Fig. 2). Jones et *al.* (2004) reports a mean range of $\delta^{15}N$ values for Isle of Wight between 14-18‰, similar to the values found in Hog Island, but more enriched

than Gargathy or Burton's Bays. The 2004 MD study did not include initial values for deployed macroalgae, but the study reported latitude-longitude coordinates with the corresponding $\delta^{15}N$ signatures, and we were able to calculate a mean initial $\delta^{15}N$ value of 11.7‰ for macroalgae collected from Greenbackville on the VA/MD border used in their deployments. The post-deployment average $\delta^{15}N$ signature for Isle of Wight Bay was 15.2‰. Focusing on the three VA bays, only Hog Island Bay mean macroalgal $\delta^{15}N$ was found to be significantly different ($F=12.24$, $p<0.001$) from the mean $\delta^{15}N$ of the other bays and the pre-incubation algae.

We were not able to relate macroalgal enrichment to a particular source of nitrogen (sewage or animal waste to the VA bays). Macroalgal $\delta^{15}N$ values were similar along creek to inlet transects, and showed no indication of enrichment from wastewater, and no significant differences existed among the sites within each bay (See Appendix I, Fig. 1). In Burton's Bay and Hog Island Bay, $\delta^{15}N$ values demonstrated increased enrichment along the creek to inlet transect. This trend was statistically significant in Burton's Bay, with the creek site $\delta^{15}N$ values significantly below mid and inlet sites ($F=11.74$, $p=0.002$).

Results from the MD Coastal Bays nitrogen source tracking also indicated no clear trends in $\delta^{15}N$ values within Isle of Wight. Saint Martin's River feeds into Isle of Wight Bay and a gradient of $\delta^{15}N$ values existed within the river. Values within the bay, however, were consistent ranging between 14-18‰, with a few sites below that range and a few sites, close to the developed Ocean City, exceeding that range at over 18‰.

Build-out scenario 1: Residential Impacts on Nitrogen Loads

Population increases

Accomack County's 2008 comprehensive plan predicts an annual increase in population of 0.65% and an annual increase in housing density of 2% (Accomack County, 2008) over the next 30 years. These predicted population and housing density increases were used to determine the impact of increasing residential development and to estimate the changes in nitrogen loading from the two watersheds. By increasing watershed populations, we can estimate how important septic systems become to the annual nitrogen load. Model estimates showed that strictly increasing populations in both watersheds had minimal impacts on the annual load.

Using County estimates of population increases, Burton's watershed population was predicted to increase from 1,874 people to 2,242. Model results indicate that the annual load will not change appreciably by adding the projected population to Burton's watershed; the estimated load increased from 80,600 kg N y^{-1} to 81,000 kg N y^{-1} (Appendix I, Table 4). Increased watershed population in Burton's watershed represented an estimated 0.025 g N m^{-2} y^{-1} increase to the water body over 30 years. Daily export loads from the watershed area increased from 0.265 mmol m^{-2} d^{-1} to 0.267 mmol m^{-2} d^{-1}, indicating that each additional person in the watershed contributed a nominal amount of nitrogen to the daily load (Fig. 3).

Increasing Gargathy population to the 2030 predicted population of 878 people also had a minimal impact on the predicted annual load. The annual nitrogen load increased nominally over the 30 year period from 29,300 kg N y^{-1} to 29,500 kg N y^{-1}. The predicted daily export load from the watershed increased marginally from 0.20 mmol N m^{-2} d^{-1} in 2000 to 0.21 mmol N m^{-2} d^{-1} in 2030 (Fig. 3). Overall, the changes in annual loads to both systems in this scenario are low.

Maximum build-out scenarios

Population increases bring about changes in land use as areas expand and develop into residential and urban locales to accommodate the increasing population. It is necessary to account for these land use changes to fully understand the impact of an increasing population and development. Accomack's comprehensive plan predicted housing density increases almost three times that of population increases (Accomack County, 2008). As development increases, especially in the northern seaside areas, existing land will undergo a conversion from its current land use, be it agriculture or natural vegetation, to residential land. To capture this land use change, the NLM was run using three maximum build-out scenarios: (1) conversion of all existing agricultural land in the watersheds to residential land (low-impact); (2) conversion of all existing natural vegetation in the watersheds to residential land (high-impact); (3) conversion of half of the agricultural area and half of the natural vegetation to residential land (moderate-impact). While these scenarios are extreme, they nevertheless serve to forecast the likely upper limit of nitrogen loading under different build-out conditions.

In the different build-out scenarios, the NLM was run using housing densities, populations, and turf and impervious surface areas associated with the different densities of residential development; we incorporated different lot sizes ranging from a quarter acre to 10 acres. The assumption used in the development scenarios was that an 1/8-acre in the lot is fertilized turf, an 1/8-acre is impervious surfaces (houses, driveways, etc), and the remainder of the lot is natural vegetation (this is likely a low estimate of development on lots larger than half-acre). To determine housing density, total residential area was divided by the lot size assuming one house per lot. The population

under the different development scenarios was determined by multiplying the number of houses by 2.2 (the current average residences per house).

In Burton's watershed, if all the created residential land were developed into houses on quarter acre lots under a moderate-impact scenario, the estimated annual nitrogen load would increase from 80, 600 kg N y^{-1} to 142,000 kg N y^{-1} (Fig. 4). The annual load estimate under a high-impact scenario would increase to 188,000 kg N y^{-1} and to 124,000 kg N y^{-1} under a low impact scenario. Assuming lot sizes of one-acre reduced the estimated load to 94,600 kg N y^{-1} (moderate-impact), 108,000 kg N y^{-1} (high-impact), and 56,800 kg N y^{-1} (low-impact). Estimated loads in the moderate- and high-impact scenario were 14,000 and 27,800 kg N y^{-1} above currently estimated loads. Even in the lowest density build-out scenario (10 acres), the annual load was estimated to be 4,000 kg N y^{-1} above the current estimate in the high-impact scenario.

The Gargathy watershed responded slightly differently to changes in housing density and conversion scenarios (Fig. 4). Assuming quarter acre lots, the annual nitrogen load was estimated to be 61,200 kg N y^{-1} for the moderate-impact, 62,000 kg N y^{-1} for high-impact and 48,200 kg N y^{-1} for the low-impact conditions. Assuming half-acre lots, high- and moderate-impact conversions predicted nitrogen loads well above the current estimate and low-impact conversion estimated loads below the current estimate. With 10-acre lots, all development scenarios predicted nitrogen loads below or similar to the current estimate.

The response of the NLM in the two watersheds under different conversion scenarios highlighted the varying importance of agriculture in the two watersheds. In Gargathy watershed, the model predicted similar loads in high- and moderate-impact

conversion conditions and much lower loads in the low impact scenario (Fig. 4). In Burton's watershed, however, estimated nitrogen loads responded more sharply to changes in conversion scenarios (Fig. 4). As agriculture in the watershed increased, the difference in load estimates between high- and moderate-impact conversions decreased.

Build-out Scenario 2: Agricultural Impacts on Nitrogen Loads

Agriculture in both watersheds was the main nitrogen source to groundwater. Most of the agricultural nitrogen comes from fertilization of crops and the leaching of excess nitrogen into the groundwater. Nutrient management plans and the use of cover crops have undoubtedly proven successful at reducing nitrogen leaching into the groundwater. In Accomack County, most farmers follow nutrient recommendations given the high cost of fertilizer and the low price of crops (Jim Belote, *personal communication*). Despite the use of nutrient management plans and best management practices, nitrogen still manages to leach into the ground water. Poultry operations are the other agricultural input of nitrogen to the groundwater, and they comprise a significant, and increasing, portion of agricultural land in the county. Given that agriculture is a significant portion of Accomack's landscape and an important industry to the county, the model was run using various agricultural scenarios to help quantify the impacts of increased agricultural development on the annual nitrogen loads.

Accomack County has many poultry operations, so the first agricultural scenario estimated the impact of increasing poultry populations on annual nitrogen loads in both watersheds. Three assumptions were used for the poultry analysis: (1) no poultry manure was imported into or exported out of the watershed, based on information obtained from the Virginia Waste Transfer Report (VA DEQ 2002; 2003; 2004); (2) all poultry manure

from an operation is applied on-site; (3) when poultry manure alone does not meet crop nutrient needs it will be supplemented with synthetic fertilizer; (4) Cole's (2005) assumption of six flocks per poultry house per year. Under current conditions there were only around 1,350,000 and 750,000 birds each year in Burton's and Gargathy watersheds, respectively, and model results implied no significant impacts from poultry practices because the poultry waste produced was less than total crop nutrient requirements.

The model was not sensitive to poultry until the number of birds equaled or exceeded 5 million birds per year in Burton's watershed and 3.1 million birds per year in Gargathy watershed, at which point the waste produced exceeded crop fertilizer requirements. In Burton's watershed, the addition of 5 million birds, equivalent to having 33 chicken houses in the watershed, increased the estimated annual load to 82,000 kg N y^{-1}. In Gargathy watershed, an additional 3.1 million birds per year, equivalent to 20 poultry houses, increased the predicted annual nitrogen load to 29,900 kg N y^{-1}. With 20 million birds, equivalent to 133 poultry houses, the annual nitrogen load increased to 185,000 kg N y^{-1} in Burton's watershed and 146,000 kg N y^{-1} in Gargathy watershed. Daily watershed export increased with the number of birds in both watersheds, though it increased at a greater rate in Gargathy watershed (Fig. 5a).

The second agricultural scenario estimated the amount of nitrogen that a hectare of corn, soybean, and tomato plasticulture leached into the watershed. The model was run holding all residential and agricultural parameters constant, except for the crop of interest. One hectare of tomato plasticulture was predicted to leach 433 kg N y^{-1} compared to 35 and 22 kg N y^{-1} for corn and soybeans, respectively. The tomato value seems excessively high, but we believe this is driven by three factors: the relatively small

amount of nitrogen in the tomato plant, the fertilization of tomato crops at their roots, and the multiple fertilizations of tomato crops during their growing cycle. A wide range of values exists in the literature regarding the nitrogen content in these crops, and, as previously discussed, the NLM was sensitive to this range of values. Ultimately, we used the NRCS calculation tool because it provided a reliable, national average of nitrogen crop content.

The final analysis considered an incremental conversion of all available agricultural area into tomato plasticulture. We assumed corn and soybean equally represented the remainder of agricultural area. The results were similar in both watersheds, as the area of tomato plasticulture increased, the annual load, and daily watershed export of nitrogen increased (Fig 5b). Gargathy watershed showed slightly greater sensitivity to the tomato conversion, with an increase in daily export just over 1 mmol N m^{-2} d^{-1} at 100% tomato plasticulture. This represents an increase in the annual load up to 178,000 kg N y^{-1}. Burton's watershed responded similarly to this build-out analysis, and daily watershed export increased by an additional 0.8 mmol N m^{-2} d^{-1} at 100% tomato plasticulture, and the annual load increased to 319,000 kg N y^{-1}. At 100% tomato plasticulture, Burton's annual load was equivalent to 18g N m^{-2} y^{-1} and the annual load to Gargathy Bay was estimated at 155 g N m^{-2} y^{-1}, illustrating the susceptibility of small bays to extreme nutrient enrichment under intensive land uses.

DISCUSSION

Lagoon Nitrogen Loading Range

Based on estimated annual nitrogen loads to each system, a range of nitrogen loading levels exist among the four bays. Results of the NLM projections suggested that despite similar land use in the Burton's and Gargathy watersheds, annual nitrogen loads to the two systems was quite different. The small size of Gargathy Bay and the relatively large load qualifies it as the most impacted end member of the four coastal lagoons in this study. Annual nitrogen loads normalized to water body area in Gargathy Bay were greater than loads to the other systems, including Isle of Wight, which originally was thought to be the most impacted (Table 3). Intensive agriculture, including tomato plasticulture, and poultry operations in the Gargathy watershed likely contributed to the enrichment of Gargathy Bay. On an areal loading basis, Isle of Wight Bay was the next most nitrogen enriched system, then Burton's Bay, and, finally, Hog Island Bay with the smallest areal nitrogen load. Our results indicated that small VA systems, like Gargathy, may be highly enriched despite the rural landscape.

Nitrogen source tracking

Results of the nitrogen source tracking experiment failed to identify notable differences in nitrogen sources among the VA bays, but suggested that nitrogen recycling was important in the shallow lagoons (McGlathery et *al.*, 2001; Tyler et *al.*, 2001; Anderson et *al.*, 2003). Two issues likely complicated the relationship between nitrogen sources and isotopic signatures in the VA coastal lagoons, the relatively small contribution of septic wastewater reaching the bays and the fractionation of nitrogen during transport through the system. Other studies using stable nitrogen isotopes to detect sewage influences studied systems receiving significant contributions from a wastewater source, such as a treatment plant or numerous septic systems (McClelland et

al., 1997; Valiela et *al.*, 2000; Costanzo et *al.*, 2001). Establishing a source-signature relationship requires that nitrogen not be fractionated by biological processes in the system (Macko and Ostrom, 1994). Recycled nitrogen is an important source for primary producers in these coastal lagoons (Tyler et *al.*, 2001; McGlathery et *al.*, 2001; Anderson et *al.*, 2003), and this nitrogen is likely highly fractionated.

Nitrogen source tracking using macroalgae was successfully applied in Moreton Bay, Australia where treated sewage was directly discharged into several river estuaries (Costanzo et *al.*, 2001). Another conducted in the estuaries of Waquoit Bay determined a gradient of wastewater influence using estimates of wastewater loading from the NLM (used in this study) and $\delta^{15}N$ signatures of existing *Gracilaria tikvahiae* (McClelland et *al.*, 1997). The study established a strong linear relationship between the percent of wastewater entering a system and the $\delta^{15}N$ signature of macroalgae. Wastewater contributions ranged from 0-65% of annual nitrogen loads to the different estuaries, but a wastewater signal was only detectable after it comprised more than 16% of the nitrogen load (McClelland et *al.*, 1997).

In the VA coastal lagoons, wastewater did not contribute significantly to the annual loads comprising only 3% of the annual load to Burton's and Gargathy Bays. The lack of development in HIB watershed also suggests a small contribution of wastewater nitrogen as well. Isle of Wight Bay receives more influence from wastewater which may explain the comparatively heavier signature of the system. A treatment plant discharges directly into St. Martin's River (Jones et *al.*, 2004), though the main contribution of nutrients to Isle of Wight is agriculture (Boynton et *al.*, 1996; Wazniak et *al.*, 2007). Contributions by wastewater were likely too small in the VA coastal lagoons for

detection by stable nitrogen isotopes. Additionally, in systems where other nitrogen sources can influence the $\delta^{15}N$ value of macroalgae, detection of residential sources may not be accurate (Cole et *al.*, 2004).

Enriched initial values of macroalgae could have distorted the nitrogen source – signature link. Nitrogen sources to the VA coastal bays include atmospheric deposition, nitrogen fixation, and nitrogen transported in groundwater from fertilizer and animal and human waste, as well as nitrogen fixation and atmospheric deposition in the watershed. Atmospheric deposition has a $\delta^{15}N$ signature of 0‰ and nitrogen fixation and synthetic fertilizers have a signature of 0 to +4‰ (Sharp, 2007). Poultry excrement has a $\delta^{15}N$ signature around +8‰ (Wassanaar, 1995). If macroalgae were assimilating nitrogen directly from the source, we would anticipate lower signatures. Establishing a signature-source link requires a high ratio of new to recycled nitrogen. Thus, heavy initial $\delta^{15}N$ signatures of macroalgae indicated enriched dissolved nitrogen in the system, confirming the importance of coastal lagoons as transformers of anthropogenic nitrogen (Anderson et *al.*, 2001).

Fractionation of nitrogen results from the preferential reaction of isotopically light nitrogen (^{14}N) during biological and chemical processes, leaving remaining reactant species enriched in ^{15}N (and the product isotopically light- Peterson and Fry, 1987; Sharp, 2007). Nitrogen availability and degree of nutrient limitation affect fractionation. Greater availability of nitrogen allows organisms to preferentially take-up or assimilate isotopically light nitrogen. Thus in nutrient replete conditions, nitrogen cycling processes fractionate nitrogen, leading to nitrogen enriched in $\delta^{15}N$ relative to the source (Macko and Ostrum, 1994). High mineralization rates and the occurrence of coupled

nitrification-denitrification in HIB (Anderson et *al.*, 2003), suggest nitrogen recycling drove the heavier $\delta^{15}N$ signatures in the least nutrient-enriched HIB. Nitrogen cycling processes may have also enriched signatures in Burton's Bay given the significant trend of increasing $\delta^{15}N$ values from creek to inlet in Burton's Bay (Fry et *al.*, 2003).

Reduced fractionation in Gargathy Bay may be driving the slightly lighter macroalgal $\delta^{15}N$ signatures in this system. Gargathy Bay sediments are rich in organic matter, and often smelled strongly of sulfide, which can inhibit coupled nitrification-denitrification (Joye and Anderson, 2008), suggesting these processes may not control macroalgal $\delta^{15}N$ values. Dissimilatory reduction of nitrate to ammonium (DNRA) controls nitrogen cycling in systems experiencing hypoxia with high sediment organic matter content (Joye and Anderson, 2008) and fractionation effects associated with DNRA are expected to be small (Macko and Ostrum, 1994), which may explain the comparatively low $\delta^{15}N$ signatures. Extensive macroalgal blooms in Gargathy Bay may also reduce fractionation, as macroalgae rapidly assimilate available nitrogen.

We conducted the nitrogen source tracking experiment to link land-use and eutrophication, and our results did not really confirm our hypothesis that the most heavily loaded systems would have the most enriched signals. Though Isle of Wight, one of the more nutrient loaded systems had the heaviest $\delta^{15}N$ signatures, the most nutrient loaded system had the lightest $\delta^{15}N$ signatures and the least loaded system had the heaviest $\delta^{15}N$ signature. Nitrogen recycling processes likely drove the $\delta^{15}N$ signatures in VA lagoons, whereas in MD, nitrogen source potentially had more influence on $\delta^{15}N$ signatures.

Eutrophication and implications for future development

Understanding results of the NLM predictions requires discussing these estimates in the context of their potential affects on water quality. A study completed by Boynton et al. (1996) in the coastal lagoons of MD's Eastern Shore found a positive relationship between nitrogen loads and two parameters, measured concentrations of chlorophyll-*a* and total nitrogen in the water. According to this study, the total nitrogen concentrations in the water column increased by 0.53 μM for each one unit increase in nitrogen load (g N m^{-2} y^{-1}), and chlorophyll-*a* concentrations increased by 0.7 mg m^{-3} for each one unit increase in nitrogen load (Fig 6; Boynton et al. 1996).

The Boynton et *al.* (1996) relationships are good first order estimates for determining potential chlorophyll-*a* and nitrogen concentrations in the two bays from various NLM projections. Predicted nitrogen loads for Burton's Bay and Gargathy Bay fall in the low to middle range of estimated loads for the MD Bays, suggesting that these lagoons fall in the middle of this regional enrichment gradient. In other words, the VA Bays are moderately impacted. Using the Boynton relationships, the annual average chlorophyll-*a* concentration estimated for current conditions in Burton's Bay was 20 mg m^{-3} and for Gargathy Bay was 35 mg m^{-3}. Estimated total nitrogen concentrations for Burton's and Gargathy Bays were 53 μM and 42 μM, respectively.

The potential impacts of the various projection scenarios on chlorophyll-*a* concentrations can be estimated using the relationship between nitrogen loads and chlorophyll-*a*. Projected increases in Burton's and Gargathy Bays populations do not significantly change the estimated chlorophyll-*a* concentrations. Maximum potential land-use changes, however, can be very significant in terms of the predicted increases in

chlorophyll-*a* in the system, particularly in Gargathy Bay (Fig. 6). Under a moderate-impact maximum build-out scenario, a quarter acre lot size would potentially increase chlorophyll-*a* concentrations to 52 mg m^{-3} in Gargathy Bay, indicative of very eutrophied waters and at the upper end of the MD eutrophication gradient. Even a lot size of one acre could potentially raise chlorophyll-*a* concentrations to 45 mg m^{-3}, a value that falls on the higher end of the Maryland eutrophication gradient (Boynton et al. 1996; Fig.6). Similarly, increases in the poultry population could significantly increase chlorophyll-*a* concentrations to 20-24 mg m^{-3} in Burton's Bay and to 44-105 mg m^{-3} in Gargathy Bay.

Annual average chlorophyll-*a* concentrations measured as part this study for Burton's and Gargathy Bays are below predicted values using the Boynton et *al.* (1996) relationships. The Boynton et *al.* (1996) relationship also appears to overestimate total nitrogen (TN) in the system. We only measured total dissolved nitrogen (TDN) as part of our study, but we estimated particulate nitrogen to get TN. We converted chlorophyll-*a* concentrations into nitrogen using two carbon:chl-*a* ratios (a high- 60g C g chl^{-1} and low-30 g C g chl^{-1} ratio- Brush et *al.*, 2002) and assumed Redfield ratio for converting carbon into nitrogen. We report TN based on the higher C:Chl as we believe that phytoplankton in these systems have higher carbon content. Despite the rough calculation, our estimate of TN in Gargathy and Burton's Bays still fall below predicted concentrations.

We performed similar regressions as the Boynton et *al.* (1996) study, of annual nitrogen loads with measured average values of DIN, TDN, TN (estimated) and chlorophyll-a collected over the annual sampling period in Gargathy Bay, Burton's Bay, Hog Island Bay, and Isle of Wight Bay. We found moderate, but not significant relationships between nitrogen loading and water quality parameters (Fig. 7a-c). The

strength of the relationships of DIN and chlorophyll-*a* concentrations with annual nitrogen loads have R^2 values of 0.79 and 0.47, respectively. Despite the strong R^2 values, these regression were not statistically significant (DIN, p=0.107; chlorophyll-*a*, p=0.313); however, regressions using estimated TN in the system were significant (p=0.025), suggesting that organics drove the relationship between nutrient concentrations and loading in the MD bays.

The failure of predictive patterns developed in one study to apply to other shallow systems is not surprising given that Nixon et *al.* (2001) found predictive relationships do not necessary hold in shallow marine systems. Data used in the 1996 study relied on water quality data and nutrient loading data collected at two different times, and the chlorophyll-*a* concentrations were measured during warmer seasons which may bias concentrations upward (Boynton et *al.*, 1996).

Observed differences in relationships between water quality parameters and nutrient loads between the VA and MD bays suggest dissimilarities between the systems. A shift in nutrient regime may be one factor driving the differences between the Boynton et *al.* (1996) and the current study. Relationships in the Boynton et *al.*(1996) study are based on data collected by Fang et *al.* in 1977. For Isle of Wight Bay, included in both studies, we found differences in mean annual chlorophyll-*a* and DIN concentrations between the two studies indicating a possible regime shift (Fig 7b). Alternatively, biological and physical factors may be driving the differences in the VA bays. The coastal lagoons of VA may be more rapidly flushed than the MD Bays. Faster flushing times in the VA systems may remove nutrients and phytoplankton from the system more quickly causing lower water column concentrations of nutrients and chlorophyll. Also,

the influence of macroalgae could, potentially, cause the VA lagoons to respond differently. Macroalgae can outcompete phytoplankton in rapidly flushed systems (Fong et *al.*, 1993), resulting in low water column chlorophyll and nutrient concentrations due to macroalgal retention of nutrients (Nixon et *al.*, 2001; McGlathery et *al.*, 2007). However, the influence of macroalgae on water quality would be greater in systems with more macroalgal biomass and it is unclear if VA systems have higher macroalgal biomass than the MD lagoons. A larger scale study evaluating water quality parameters along the greater Delmarva nutrient loading gradient may help elucidate the reasons for the departure of VA bays from the established relationships.

CONCLUSIONS

Using a combined technique of modeling and nitrogen source tracking, we were able test the extension of an established regional nitrogen load gradient in DE and MD lagoons into VA. Validation of the nitrogen loading model (NLM) against measured data, showed the model produced reliable estimates. Using the results from the NLM, we were able to quantify annual nitrogen loads to two VA coastal lagoons, and combined with existing data for the MD lagoons and a relatively pristine system in VA, confirmed a significant range of nutrient loading among the study bays.

Watersheds of VA lagoons are generally rural and undeveloped relative to the more developed watersheds of MD and DE. Despite the overall rural land use, some of the VA bays are still highly enriched. However, patterns of increasing concentrations of chlorophyll-*a* and TDN with increasing nitrogen load indicative of eutrophication in the MD bays (Boynton et *al.*, 1996) are not evident in the VA lagoons. Among the four bays

of this study, annual concentrations of chlorophyll-*a* and DIN did not significantly increase with increasing annual nitrogen load. A significant relationship of nitrogen load and estimated TN in the bays of this study, consistent with the Boynton et *al.* (1996) study, suggests organic nitrogen drives this trend. The different eutrophication responses in the VA systems were likely due to more rapid flushing of the VA lagoons as compared to the MD lagoons.

Results from the nitrogen source tracking experiment in VA produced no clear patterns in $\delta^{15}N$ signatures for identifying nitrogen sources. Enriched signatures in the VA bays suggest nitrogen cycling processes dominate $\delta^{15}N$ signatures. A heavier isotopic signature in Isle of Wight was consistent with a wastewater signature-source relationship, though we cannot rule out the influence of nitrogen recycling processes.

Finally, the model projections for the different build-out scenarios imply that extensive development or agriculture in coastal watersheds can greatly increase annual groundwater nitrogen loads. Increased annual nitrogen loads at levels attained under maximum build-out scenarios can also have detrimental effects on coastal water quality. Despite the relatively undeveloped nature of VA coastal watersheds, Gargathy Bay provides a good example of how intensive agriculture can still lead to highly enriched systems.

Table 1. Annual nitrogen loads (total nitrogen) for the DE and MD coastal bays.

[1]Nixon et *al.* (2001)
[2]Boynton et *al.* (1996)

Bay	Latitude	Annual Nitrogen Load (g N m^{-2} y^{-1})	Nitrogen load (mmol N m^{-2} d^{-1})
Rehoboth Bay, DE[1]	38°39.7	12.3	2.4
Indian River Bay, DE[1]	38°35.9	27.6	5.4
Assawoman Bay, MD[2]	38°25.1	4.1	0.80
Isle of Wight Bay, MD[2]	38°22.1	6.5	1.27
Newport Bay, MD[2]	38°14.9	17.5	3.42
Sinepuxent Bay, MD[2]	38°13.4	2.4	0.47

Table 2. Breakdown of the four main nitrogen inputs used in the NLM and the percentage of nitrogen removed in each watershed component as it travels through the watershed ending with a summation of all nitrogen inputs and total annual groundwater nitrogen load reaching the receiving bay (adapted from Valiela et al. 1997a).

Type of Land Cover	Watershed Loss Component	% of N removed
NITROGEN INPUT 1: ATMOSPHERIC DEPOSITION		
Natural vegetation	Watershed surface/soils	65%
Agriculture	Watershed surface/crops	62%
Turf	Watershed surface/soils	62%
Impervious Surface	Watershed surface/soils	62%
NITROGEN INPUT 2: FERTILIZER APPLICATION		
Agriculture	Watershed surface/crops	Variable with crop harvest
- Corn	Volatilization	39%
- Soybean		
- Tomato		
Residential turf	Watershed surface/soils	39%
(34% of lawns fertilized)	Volatilization	39%
NITROGEN INPUT 3: WASTEWATER FROM SEPTIC SYSTEMS		
ISDS Tanks	Septic Tank/Leach Field	30%
	Plume Leachate	33%
NITROGEN LOSSES IN VADOSE ZONE AND AQUIFER		
Contributing Inputs		
Nitrogen input 1+2	Vadose Zone	61% lost
Total nitrogen inputs (1+2+3)	Aquifer	35% lost
Total annual nitrogen load	Bay	

Table 3. Breakdown of nitrogen inputs to the annual groundwater load for entire Burton's Bay and Gargathy Bay watersheds. First and third columns, estimate current nitrogen yields for Burton's and Gargathy watersheds; second and forth columns, the percent contribution of different nitrogen sources to the annual load for each watershed.

	Burton's Load (kg N y^{-1})	**% of Burton's load**	**Gargathy Load (kg N y^{-1})**	**% of Gargathy load**
1. Atmospheric Deposition				
Natural Vegetation	2,990	3.7	1,120	3.8
Turf	130	0.2	40	0.1
Agricultural	2440	3.0	1,520	5.2
Urban	3180	3.9	1,420	4.9
Barren	1060	1.3	410	1.4
Water surface	21,640	26.8	1,910	6.5
2. Fertilizer				
Excess Poultry Litter (Fertilizer) [1]	0	0	0	0
Turf (Fertilizer)	650	0.8	170	0.6
Agricultural Land (Fertilizer)	46,780	57.3	21,840	74.5
3. Septic system				
Wastewater	2,340	2.9	900	3.1
Total N-Load to Estuary[2]	80,560	100	29,330	100

[1]At the watershed scale, poultry litter produced was not in excess of crop nutrient needs, thus, there was no contribution to the annual nitrogen load.
[2] Values may not sum due to rounding

Table 4. Annual areal nitrogen loading rates per square meter of water body area for the four bays in this study. Loads include atmospheric deposition

Bay	Annual N load ($g\ N\ m^{-2}\ y^{-1}$)
Isle of Wight Bay, MD[1]	6.5
Gargathy Bay, VA[2]	25
Burton's Bay, VA[2]	4.4
Hog Island Bay, VA[3]	1.4

[1]Boynton et *al.* 1996
[2]This study
[3]Stanhope, 2003

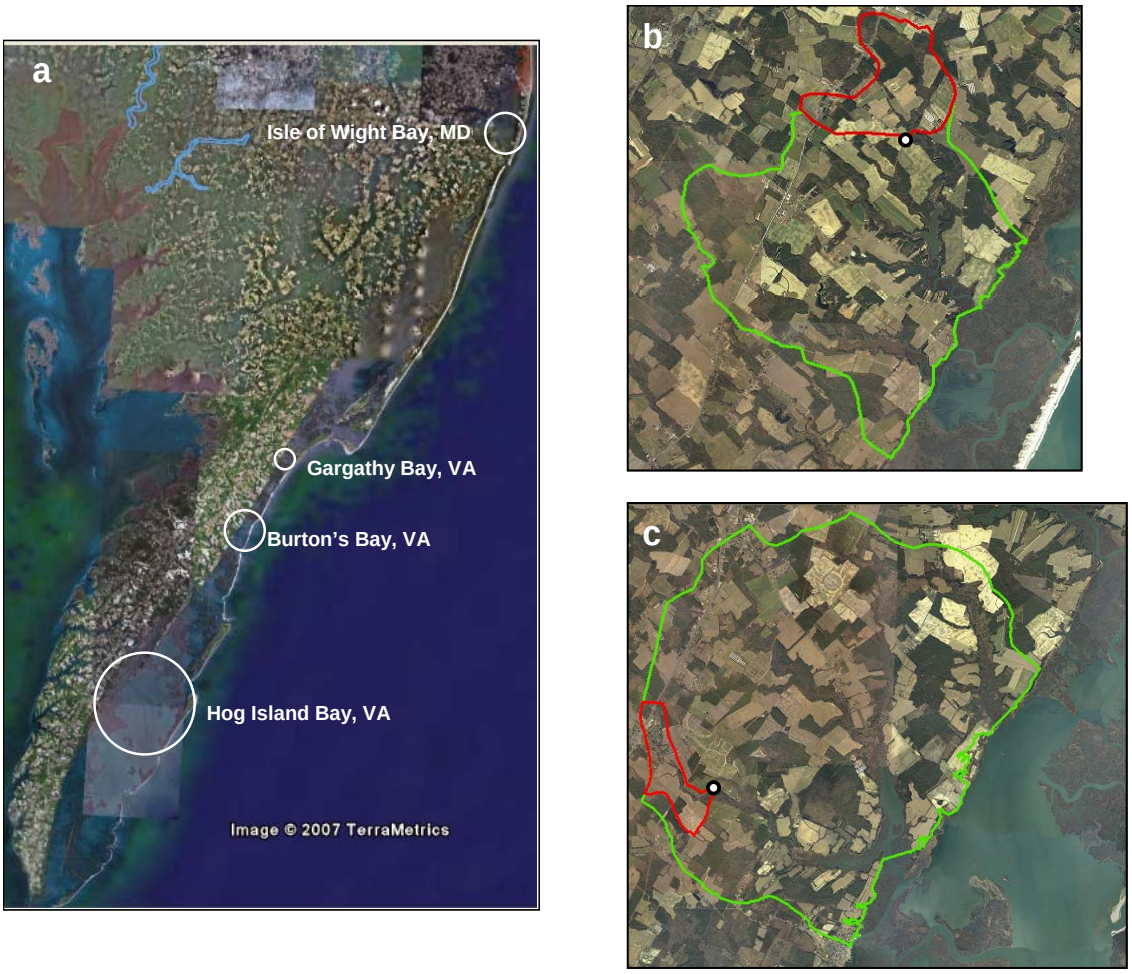

Figure 1. **(a)** Location of the four bays selected for this study on the MD/VA Eastern Shore. Digital images of Gargathy Bay watershed **(b)** and Burton's Bay watershed **(c)**; watersheds are delineated in green and sub-watersheds are delineated in red. Black and white points represent the locations of Stanhope's (2003) sites at which base flow nitrogen loads were measured.

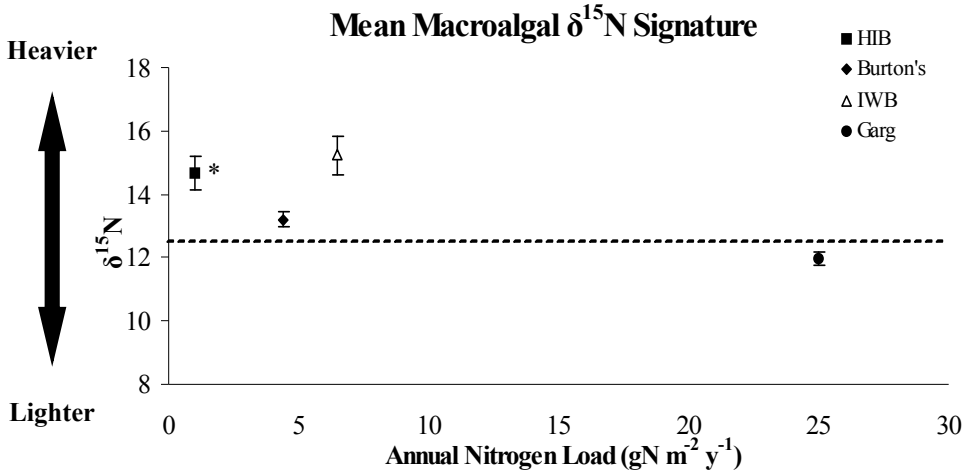

Figure 2. Bay-wide average macroalgal $\delta^{15}N$ signatures for the four study systems. Isle of Wight Bay values were calculated using reported lat-long coordinates and corresponding $\delta^{15}N$ signatures reported in Jones et *al.* (2004). The dashed line represents the pre-incubation $\delta^{15}N$ signature for macroalgae deployed in VA bays. Error bars represent standard error (n= 6- Gargathy Bay; n= 13- Burton's Bay; n= 10- Hog Island Bay).
*Denotes statistical significance among VA bays at α= 0.05 level.

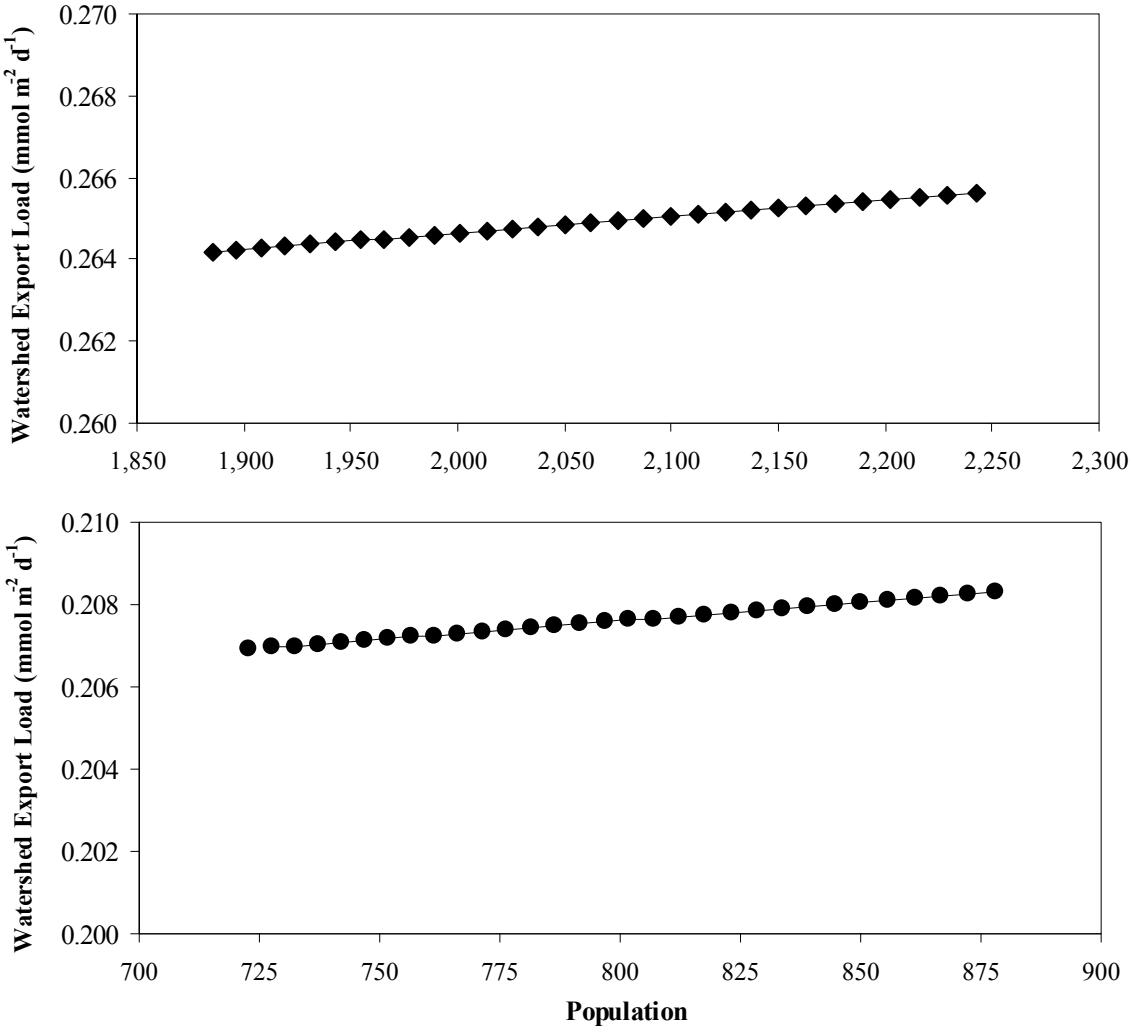

Figure 3. Residential build-out scenario increasing just the population and housing density within Burton's watershed (top) and Gargathy Bay watershed (bottom) illustrating the predicted increases in daily watershed nitrogen export as populations in the watersheds increase.

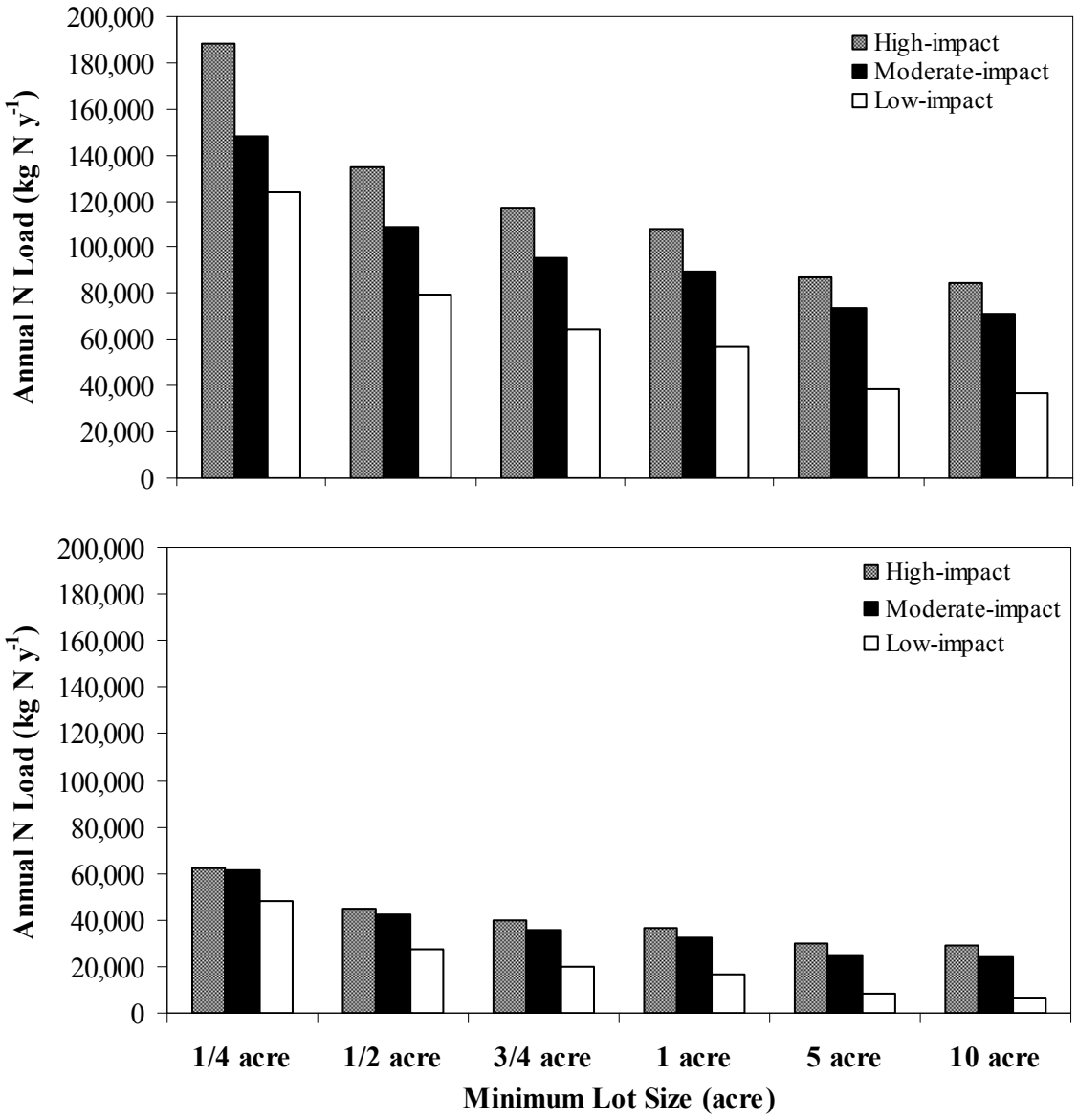

Figure 4. Residential build-out scenarios of the three conversion scenarios under different housing densities in Burton's watershed (top) and Gargathy watershed (bottom). The build out scenarios captured the increases in population and the associated increases in impervious surfaces and turf area, along with the corresponding loss of natural vegetation and agricultural land.

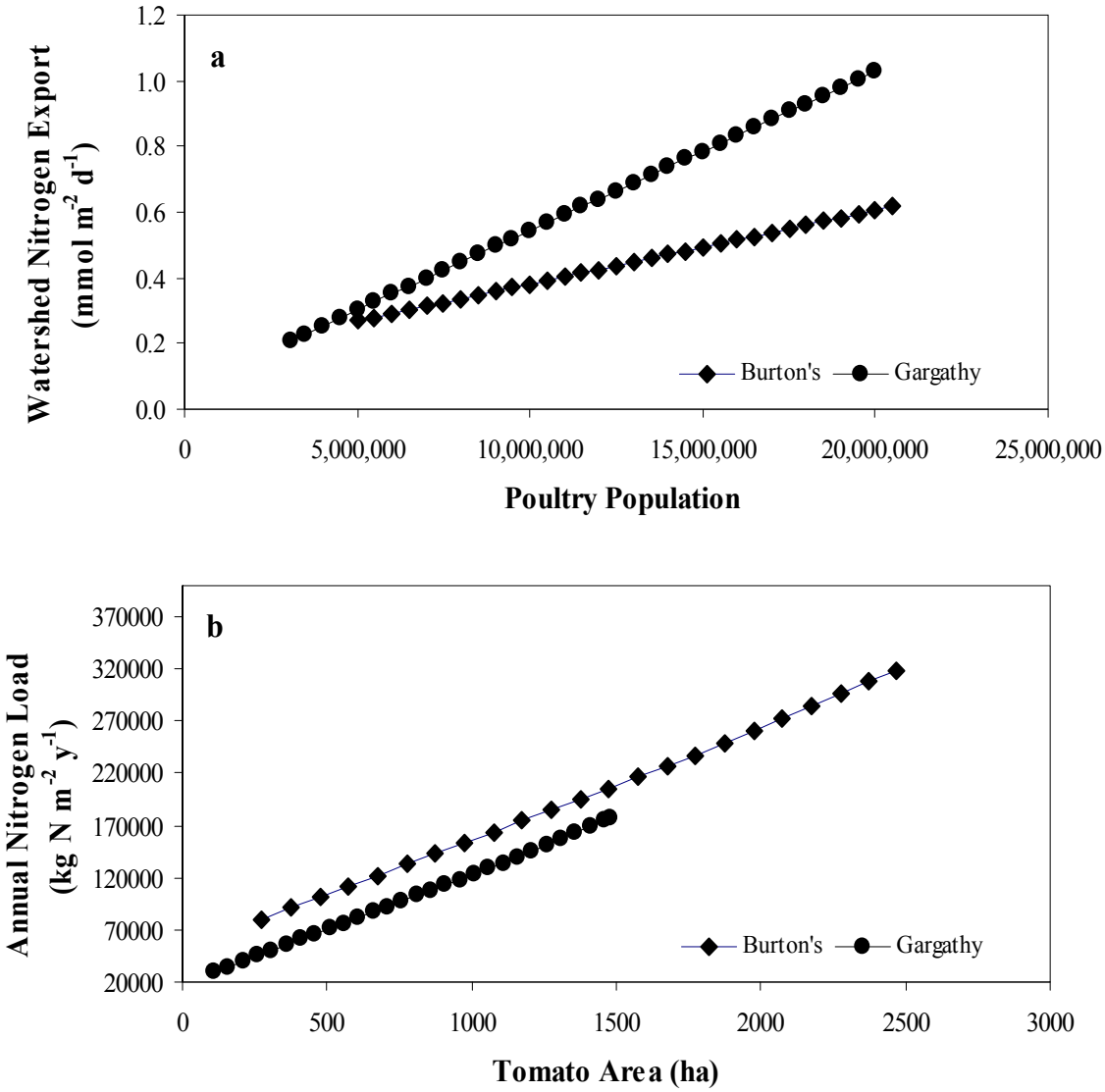

Figure 5a. Agricultural build-out scenario increasing the number of chickens in Burton's Bay and Gargathy Bay watersheds and the predicted increases in daily watershed export. **(b)** Agricultural build-out scenario increasing the hectares of tomato plasticulture in the two watersheds and the estimated increases in annual nitrogen load. This analysis assumes tomato crop replaces corn and soybean.

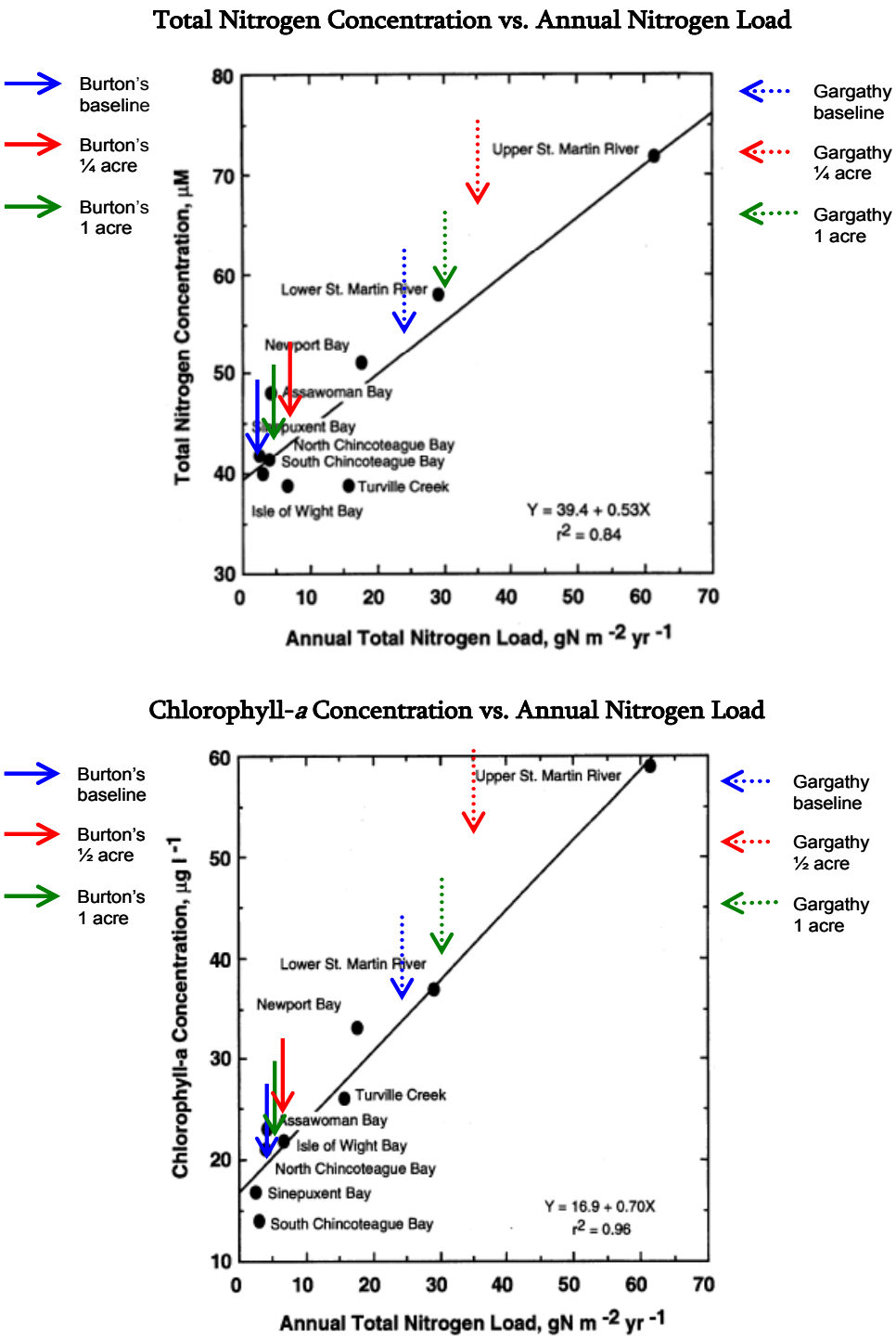

Figure 6: Relationships between the annual total nitrogen load and the annual average total nitrogen concentration in the water column (µM- top) and the annual average chlorophyll-a concentration (µg l^{-3}- bottom) in the water column for the Maryland Coastal Bays (figure from Boynton et al. 1996). Arrows denote estimated values for Burton's Bay (solid arrows) and Gargathy Bay (dotted arrows) for the annual current loads and the moderate-impact conversion residential build-out scenario.

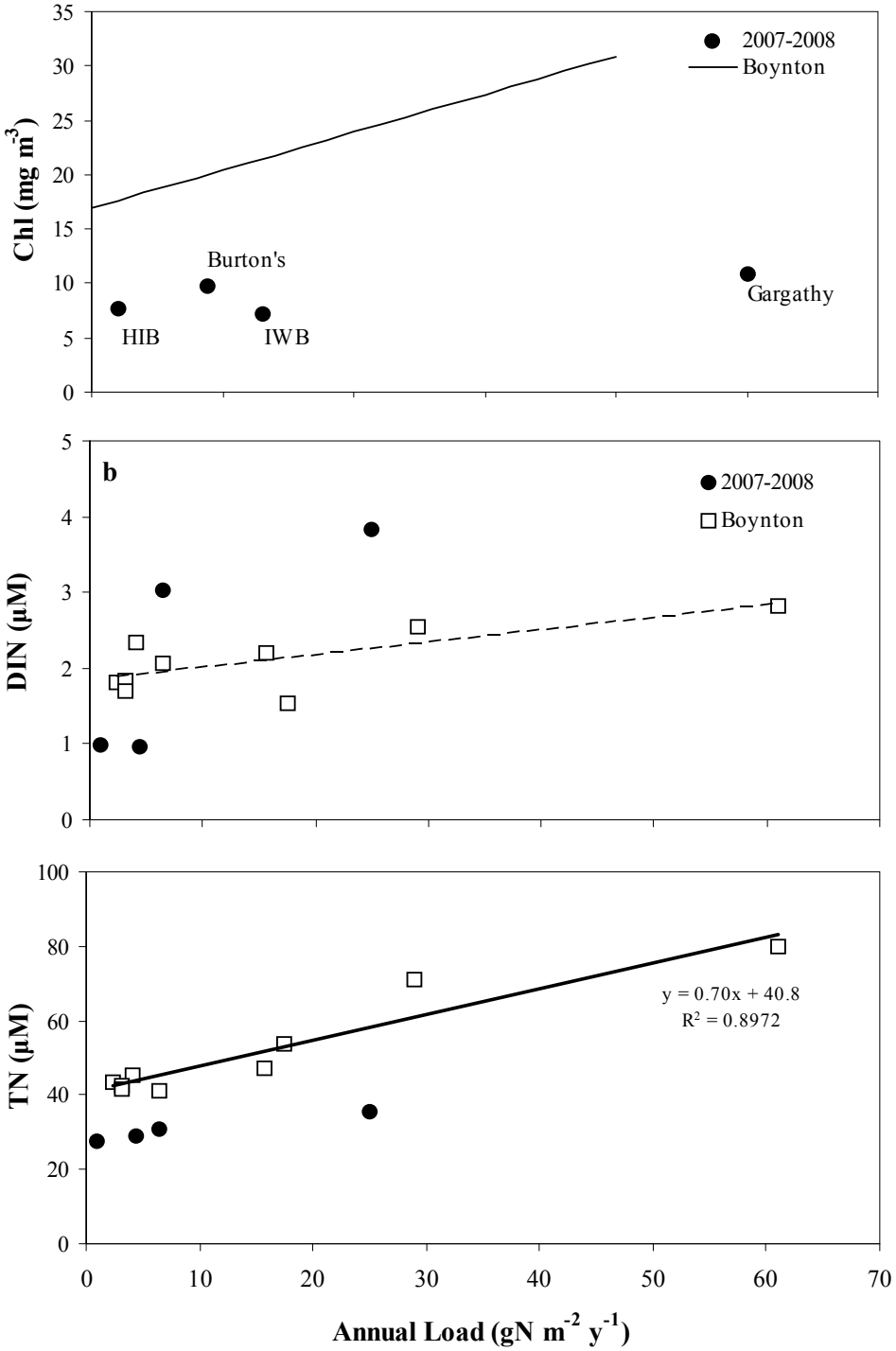

Figure 7a: Annual mean water column chlorophyll-*a* concentration for each bay in the current study regressed against annual nitrogen load. Line represents regression from Boynton et *al.* (1996). **(b)** Annual mean DIN concentration and **(c)** estimated TN concentration for bays in the current study and in the Boynton et *al.* (1996) study regressed against annual nitrogen loading. Fang et *al*. (1977) data was used to re-create Boynton et *al.* (1996) regression.

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CHAPTER 2: Metabolic responses to nutrient enrichment in temperate shallow coastal lagoons

ABSTRACT

Shallow coastal lagoons are susceptible to adverse effects of nutrient enrichment due to their proximity to land, photic depths, and long residence times. Net ecosystem metabolism (NEM) is a quantifiable and integrative method for assessing the ecological response of a system. NEM has also been shown to be positively related to nutrient enrichment in shallow systems, thus we used NEM as an indicator of system response to nutrient enrichment in four coastal lagoons receiving different nutrient loads on the VA/MD Eastern Shore. From July 2007 to July 2008, we measured NEM (and other metabolic parameters) monthly during the growing season and bi-monthly during the winter using light-dark incubations of water column and sediment cores; macroalgal incubations were added in the summer of 2008. We also measured NEM using short-term deployments of data sondes for an independent estimate.

Average metabolic rates for March to October from component incubations indicated that the lagoons were net autotrophic. We found a no trend in NEM in the less loaded systems, but the most nutrient enriched system demonstrated statistically significantly reduced autotrophy. System NEM in summer 2008, which included macroalgal metabolism, was again net autotrophic in all lagoons. A shift to reduced autotrophy along the loading range occurred at a lower nutrient load during this period. Open water and component NEM did not follow the same trends, which is likely due to the assumptions inherent in the two methods. Though we found patterns in system metabolism with nutrient enrichment, additional factors like light regime, sediment organic content, primary producer biomass, and temperature were important regulators of NEM.

INTRODUCTION

Over half of the nation's population resides in the coastal zone, making these regions the most developed in the nation (EPA, 2008). Intensified development, population growth and expansion of agricultural activities have increased anthropogenic nitrogen loading to coastal marine systems resulting in reduced water quality (Nixon, 1995). Systems receiving enhanced nutrient loads tend to experience an increased rate of supply of organic matter, or eutrophication, which has serious implications for the health of coastal ecosystems (Nixon, 1995) and can lead to adverse shifts in ecosystem structure and function (Valiela et *al.*, 1992; Smith et *al.*, 1999).

Shallow marine systems are particularly susceptible to nutrient enrichment due to their close proximity to land, penetration of light to the benthos, and long residence times (Duarte, 1995; McGlathery et *al.*, 2007). Coastal lagoons, characterized by shallow depths of 1-2 m and well-mixed water columns, serve an important role as a filter for organic matter and nutrients traversing to the ocean (McGlathery et *al.*, 2001; Anderson et *al*., 2003). They support a wide variety of primary producers and substantial benthic communities (Boynton et *al*., 1996), and serve as critical habitats, spawning grounds and nurseries for numerous fish and shellfish species (Valiela, 1995; EPA, 2008).

Although nitrogen loads to coastal lagoons are of a similar magnitude as those to deeper estuaries, the response appears to be quiet different, perhaps due to benthic-pelagic coupling (McGlathery et *al.*, 2007). An illuminated benthos results in a significant contribution of benthic micro- and macroalgae to total system production. Interactions between autotrophic communities are complex and predictive patterns between nutrient loading and a single component of the system often do not hold in

shallow systems as they do in deeper systems (Nixon et *al.*, 2001; Cloern, 2001; Howarth and Marino, 2006). An understanding of how changes in nutrient regime affect shallow systems requires broad ecosystem scale evaluations incorporating different processes mediating trophic response (Cloern, 2001).

Net ecosystem metabolism is an easily quantifiable and integrative approach for assessing the trophic response of an entire system to nutrient enrichment (NEM- Kemp and Boynton, 1980; D'Avanzo et *al*., 1996; Kemp et *al.*, 1997). Defined as the difference between gross primary production (GPP) and community respiration (R), NEM provides a measure of how a system processes nutrients and organic material (Smith and Hollibaugh, 1997). A system with positive NEM (in oxygen units) is net autotrophic, producing more organic matter than is consumed through net assimilation of inorganic nutrients. Conversely, a system with negative NEM (in oxygen units) is net heterotrophic with a potential net export of inorganic nutrients and a net import or storage of organic matter (Eyre and McKee, 2002; Hopkinson and Smith, 2004). Net ecosystem metabolism measurements inherently incorporate complex processes influencing primary production and respiration and are a useful tool for assessing the trophic response of shallow ecosystems. Shallow system NEM can be driven by organic matter loading (Smith and Hollibaugh, 1997), inorganic nutrient loading (Oviatt et *al.*, 1986; Eyre and McKee, 2002; Caffrey, 2004), or the ratio of inorganic to organic nutrient loads (Kemp et *al.*, 1997). Regardless of the precise driver, NEM has been found to respond predictably to nitrogen load in shallow systems if light and other required nutrients are not limiting (Nixon et *al.*, 1986; Nixon et *al.*, 2001).

The majority of studies measuring NEM in relation to nutrient loading have focused on estuarine systems or shallow tributaries and littoral zones of larger systems; few studies have concentrated on shallow, coastal lagoon systems. Given that coastal lagoons comprise a notable percentage of the world's coastlines and provide vital ecological services (Boynton et *al.*, 1996), understanding how these systems respond to increasing anthropogenic nutrient enrichment is important. Therefore, we used metabolic measurements as an indicator of system response to nutrient enrichment. We measured metabolic processes in four temperate coastal lagoons with disparate nutrient loads from July 2007 to July 2008. Both oxygen-based component and open-water methods were employed. The ultimate goal of this project was to determine if ecosystem metabolism varied with increasing nitrogen loading and anthropogenic influence. We hypothesized that as nutrient enrichment increased, system NEM would increase up to some threshold level of loading, above which the system would trend towards net heterotrophy. We also hypothesized that as nutrient enrichment increased, the water column would trend towards autotrophy and sediments towards heterotrophy and that the benthic:pelagic GPP ($GPP_{B:P}$) would decrease.

METHODS

Site description

Four coastal lagoons on the Delmarva Peninsula characterized by a range of nutrient loading were selected for the study (Fig. 1). These systems have shallow water depths (~1 m), illuminated sediments and well-mixed water columns. Varying land use within the watersheds contributes to the different nitrogen loads entering each system

(Table 1). We estimated residence times in Burton's and Gargathy Bays using calculations based on calculated freshwater input from the watershed, average salinity of the lagoons, and an ocean salinity of 34 ppt following Geyer and Signell (1992 - Table 1). Using previously estimated residence times for Hog Island (Fugate et *al.*, 2006) and Isle of Wight Bays (Wazniak et *al.*, 2004) we were able to calculate a conversion constant for freshwater input as a function of watershed and bay area. Using this constant, we estimated fresh water input into Burton's Bay and Gargathy Bay and associated residence times. We used estimated residence times to look for enhanced relationships between metabolism and nutrient loading by normalizing annual loads to residence time.

Field monitoring and sampling

From July 2007 through July 2008, we sampled the four lagoons, monthly during the growing season and bi-monthly during the winter. Time and resource constraints limited resulted in seasonal sampling in Isle of Wight Bay. Within each lagoon, sampling occurred across a creek to inlet gradient with stations at the mouth of the contributing creek, at mid-bay, and near the inlet (see Appendix II, Table 1 for precise locations). Only one mid-bay sampling site was used in Gargathy Bay due to its small size.

Temperature (°C), salinity (‰), and dissolved oxygen (DO) were measured at each site using a handheld MS5 Hydrolab. A LiCor 2π underwater Quantum sensor was used to determine irradiance at the surface, at the bottom, and at 10-20 cm increments through the water column depending on depth. Light data were used to determine attenuation coefficients, k_D, at each site.

Water and sediment samples were also collected to determine site characteristics at the time of sampling. We measured a suite of water quality parameters including

chlorophyll-*a* concentrations, dissolved inorganic and organic nitrogen and dissolved inorganic phosphorous (DIN, DON, DIP) concentrations, chromophoric dissolved organic matter (CDOM), and total suspended solids (TSS). Water samples were collected into 1-liter amber Nalgene bottles and immediately put on ice until processing in the lab. Water column chlorophyll-*a* was determined by filtering 10 mL of sample water onto Whatman 0.7 μm GF/F filters and extracting for 24 hours in the dark in 45:45:10 dimethyl sulfoxide:90% Acetone:1% diethylamine extract (Shoaf and Lium, 1976), followed by measurements of fluorescence (10 AU Turner Design) before and after acidification. Nutrient samples were filtered through 0.45 μm Gelman Supor filters into Whirlpack bags and frozen until analysis. A Lachat auto analyzer was used to measure concentrations of NO_3^-, NO_2^-, and NH_4^+; TDN was analyzed by persulfate digestion in sealed ampules (Knepel and Bogren, 2001, revised 2002; Liao, 2001, revised 2002; Smith and Brogen, 2002, revised 2002). DON was determined by subtracting DIN (NO_2^-, NO_3^-, NH_4^+) from TDN. CDOM concentrations were measured by filtering sample water through 0.2 μm Nucleopore membrane filters into scintillation vials, which were then frozen until analysis. Samples were read at wavelengths from 400-800 nm on a scanning spectrophotometer (Beckman Coulter DU 800). Finally, TSS was determined by filtering 200 mL of sample water onto pre-combusted and weighed Whatman 0.7 μm GF/F filters, which were dried to a consistent weight at 50˚C, combusted at 500˚C for five hours, and re-weighed for quantification of ash free solids.

Sediment chlorophyll concentrations, bulk density and percent organics were used to characterize sediments at each site. Using a 10 ml syringe with the top removed samples were taken in triplicate at each site for determination of sediment chlorophyll-*a*,

b, *c*, and phaeophytin. Depth segments of 0-3 mm and 3-10 mm were placed in 20 ml centrifuge tubes on ice in the dark and frozen until analyzed; all analyses were done no later than one month post-sampling. Ten ml of 90% acetone (Dr. I.C Anderson, Dr. J. Pickney, and Dr. C.A. Currin, *pers. comm.*) were added to each centrifuge tube, which were then vortexed and sonicated for 30 seconds each. After extraction in the dark for 24 hours, sample extractant was filtered through a 0.45µm PTFE filter and read on a spectrophotometer (Beckman Coulter DU 800) at 630, 647, 664, 665, and 750 nm. Samples were acidified using 10% HCl and read again at the same wavelengths for determination of phaeophytin. Triplicate sediment samples to a depth of 10 mm for percent organics and bulk density were taken at each site using a 60 ml syringe core (i.d. 26 mm), placed into pre-weighed foil envelopes, dried to a constant weight at 50˚C (~ 2 weeks), combusted at 500˚C for five hours, and weighed again.

During the summer of 2008, macroalgae were collected for biomass calculations in Gargathy and Burton's Bays to compliment existing measurements in Hog Island and Isle of Wight Bays made during May-September 2006-2007 (A. Hardison, *unpublished data*). Since Hardison's measurements were reported in dry weight, we used an average of reported literature wet weight:dry weight ratios to convert these measurements into wet weight (Brush, 2002) for comparison to our measurements. Macroalgae, using a 0.14 m^2 ring, were randomly sampled in triplicate at each station and upon return to the lab were rinsed in distilled water, separated by genus (i.e. *Gracilaria, Ulva,* Other), and weighed fresh. All biomass estimates included samples with zero biomass to account for the spatial patchiness of the macroalgae.

System Metabolic Measurements

Several oxygen and non-oxygen based methods exist for measuring NEM. Commonly used mass balances based on the stoichiometry of nutrient fluxes, inputs and outputs (Kemp et *al.*, 1997; Gazeau et *al.*, 2005), can be difficult to apply in shallow systems, because benthic microalgal uptake and microbial processes complicate calculations of the nitrogen term (Anderson et *al.*, 2003). Oxygen-based methods like open-water and component incubations are easy to apply and provide a reliable measure of NEM (Odum and Hoskins, 1958; Kemp et *al.*, 1997; Hopkinson and Smith, 2004). In the open-water method, *in situ* metabolism is determined from changes in water column DO concentrations measured at dawn and dusk or net changes over a 24-hour period measured using a continuously recording datasonde. *In situ* methods account for all factors influencing metabolism, but can be difficult to apply due to the impact of physical processes on atmosphere-water exchange of oxygen (Kemp and Boynton, 1980), as well as the influence of physical processes like currents and waves on sediment metabolism. Component incubations separately measure changes in DO in the sediments and water column and aggregate them to obtain a measure of total system metabolism. Component methods may underestimate metabolic rates due to bottle effects and the isolation of the water column from the sediments (Kemp and Boynton, 1980; Smith and Hollibaugh, 1997; Gazeau et *al.*, 2005), but component estimates of NEM have been shown to parallel trophic trends found by other methods (Nowicki and Nixon, 1985; Santos et *al.*, 2004; Gazeau et *al.*, 2005).

Component Method

We used changes in DO concentrations from light-dark incubations to estimate system metabolism and quantify the contributions from different parts of the system

(Smith and Hollibaugh, 1997). Water samples were collected in 2 liter, blackened Nalgene bottles and placed on ice until returning to the lab. Thirteen sediment cores to a depth of 7 cm (i.d. 4.1 cm) were also collected at each site and kept on ice until return to the lab. Cores were then left uncovered in the dark overnight in a circulating seawater bath to equilibrate. The top few cm of the cores were darkened with black electrical tape exposing only the surface sediments to light. *Graciliaria* and *Ulva* spp. were collected from each site (when present) from May-July 2008 to determine macroalgal metabolism. Upon collection, macroalgae were placed into clear, Ziploc bags full of site water and placed on ice in the dark until incubation in the lab.

Short-term incubations were conducted in a flow-through light gradient box maintained at *in situ* temperatures (Fig. 2) with light (PAR) ranging from ~60 μE m^{-2} s^{-1} to ~2000 μE m^{-2} s^{-1} creating a range of low to saturating irradiance. Ten samples from each site were incubated in the light box and three samples were simultaneously incubated in a temperature-controlled dark box. Dissolved oxygen concentrations were measured before and after incubations using a Hach HQ40d meter with luminescent DO probes.

Immediately upon return to the lab, water was incubated in 60 ml biological oxygen demand (BOD) bottles in the light for approximately 1 hour; dark incubations were incubated over 24 hours to obtain a measurable change in oxygen. On the day following sample collection, we incubated sediment cores. Immediately before incubation, overlying water was siphoned out of each core, replaced with filtered seawater, and sealed with Saran Wrap (low oxygen permeability- 1.5 ml • 100 in^{-2} • 24 h^{-1}; Pemberton et *al.*, 1996). Sediment samples from each site were incubated in the light

and dark for 1-2 hours. Before taking final DO measurements, we gently stirred overlying water to break-up any oxygen gradients, as cores were not stirred during incubations.

We conducted separate incubations of *Gracilaria* and *Ulva*. Macroalgal incubations were similar to water column incubations and performed on the same day as collection. Prior to incubation, macroalgae were removed from the dark and allowed to acclimate in the light for ~30min -1hr. Approximately 100-150 mg (wet weight) of macroalgal biomass was placed into 60 mL BOD bottles with filtered seawater, and incubated in the light and dark. All algal samples were weighed post-incubation to normalize rates to biomass.

Changes in DO concentrations over the incubation period for each component were used to develop production-irradiance curves (Fig. 3). We used information theory statistics to determine the best production-irradiance model for our data (see *Statistical Analysis* for more details). Based on these results, we fit hourly water column, sediment, and macroalgae production data from each month to the Jassby and Platt (1976) model:

$$\text{Production} = P_{\max} \cdot \tanh\left(\frac{\alpha \cdot I}{P_{\max}}\right) - R \qquad (1)$$

where P_{max} is the maximum rate of photosynthesis, α is photosynthetic efficiency or the initial slope of the curve (change in photosynthesis relative to the change in light), I is irradiance ($\mu E\ m^{-2}\ s^{-1}$), and R is respiration. Using model estimates of α, $P_{max,}$ and R and a mean hourly irradiance (PAR) each month (Chesapeake Bay National Estuarine Research Reserve of Virginia- CBNERRVA) we calculated average daily gross primary production (GPP), R, net community production (NCP), NEM, and other metabolic parameters for each month. Water column metabolism was depth integrated and assessed

for a 1 m water column, assuming a constant respiration rate for the 24-hour period. Sediment metabolism was determined for a water depth of 1 m assuming a constant 24-hour respiration rate.

To assess the impact of macroalgae on system metabolism we estimated mat thickness using field biomass estimates and a relationship of mat thickness to biomass for *Gracilaria tikvahiae* (Peckols and River, 1996); for all macroalgal calculations, we assumed mat thickness was equivalent to the estimated thickness of *Graciliaria* mats. Second, we used mean hourly irradiance values for each month to compute the average hourly PAR ($\bar{I}$) experienced within the mixed assemblage mat of *Ulva* and *Gracilaria* as:

$$\bar{I} = \frac{I_M \left(1 - e^{-(k_D \cdot z_{mat} + k_t \cdot Thalli + k_g \cdot Grac_{dw})}\right)}{(k_D \cdot z + k_t \cdot Thalli + k_g \cdot Grac_{dw})} \qquad (2)$$

where I_M is irradiance at the top of the mat, k_D is attenuation by the water within the mat, z_{mat} is mat thickness, k_t is attenuation per thallus of *Ulva* (Brush and Nixon, 2003), *Thalli* is the number of *Ulva* thalli (Brush and Nixon, 2003), k_g is the attenuation of light through the *Gracilaria* mat calculated based on a relationship between percent light transmission and biomass of *Gracilaria* (Brush, 2002), and *Grac* is *Graciliaria* biomass. These hourly light levels, $\bar{I}$, were combined with biomass-normalized macroalgal α, P_{max} and R to scale up to daily mat metabolism in each month. To extrapolate to in field metabolism, we used measured biomass estimates.

Finally, we adjusted sediment production in May, June, and July 2008 to account for macroalgal shading of the sediment surface based on average macroalgal biomass

each month. We used the following equation to calculate light at the sediment surface (I_{sed}) under a 1 m water column and a given mat thickness:

$$I_{sed} = I_o e^{-(k_D \cdot z + k_t \cdot Thalli + k_g \cdot Grac)} \quad (3)$$

Where I_o is light at the surface, k_D is the water column attenuation, z is water depth and the other variables are as defined for equation (2).

Site specific irradiance was unavailable, so we used hourly PAR data from Taskinas Creek, VA collected by the Chesapeake Bay National Estuarine Research Reserve of Virginia (CBNERRVA). To ensure CBNERRVA data were applicable to the VA Eastern Shore, we tested a regional irradiance relationship using daily PAR collected at the University of Maryland Horn Point Lab located on Maryland's Eastern Shore (T. R. Fisher and A. B. Gustafson- *pers. comm.*; Fisher et *al.*, 2003). The relationship between daily PAR records from these two sites was evaluated for 2006, 2007 and 2008. Regression analyses found strong relationships between PAR values for the two sites each year (2006- R^2= 0.74, p=0.000; 2007- R^2=0.82, p=0.000; 2008- R^2=0.81, p= 0.000), thus we felt comfortable using hourly PAR from Taskinas Creek.

Open Water Method

Open water measurements of system metabolism were conducted for comparison to the component approach in Burton's and Gargathy Bays seasonally over the sampling year. At the time of sampling, we deployed a continuously recording data sonde 0.5 m below the water surface near mid-bay in the lagoons. An important assumption of the open water method is that the water mass measured is homogenous and has a similar metabolic history (Odum and Hoskins, 1956; Kemp and Boynton, 1980). Previous studies found that a mid-bay deployment site measures water representative of the system

(D'Avanzo et *al.*, 1996; Caffrey, 2003; Caffrey, 2004). Hach Hydrolab DS5X and YSI 6600 V2 sondes were used to record DO concentration, percent saturation, temperature, and salinity every 15 minutes. From July 2007 to July 2008 there were 7 deployments that lasted 7 – 18 days each, though instrument malfunction and sonde damages sustained in the field resulted in only 5 recorded deployments in Burton's Bay and 4 in Gargathy Bay and only 3 simultaneous measurements.

Net ecosystem metabolism was calculated using hourly averages of DO and percent saturation collected every 15 minutes. We calculated an air-sea exchange coefficient to correct oxygen fluxes for atmosphere-water exchange using the regression of Howarth and Marino (1993), which calculates the transfer velocity as a function of wind speed:

$$y = \frac{(1.09 + 0.249x)}{100} \tag{4}$$

Where y is the oxygen transfer velocity (m h^{-1}) and x is wind speed (m s^{-1}). We used wind data recorded at the nearby Wallops Island Flight Facility Airport and obtained from the NOAA National Climatic Data Center. We then calculated an air-sea exchange correction (g O_2 m^{-3} h^{-1}):

$$Air - SeaFlux = \left(y \cdot \left(DO_{sat} - DO_{conc} \right) \cdot \frac{t}{z} \right) \tag{5}$$

where, y is the same as in equation (4), DO_{sat} is the DO concentration under saturated conditions (mg l^{-1}), DO_{conc} is the measured DO concentration (mg l^{-1}), t is the time interval (h), and z is water depth (m). When there was no sonde recorded depth, we assumed a 1 m water column. Net ecosystem metabolism was determined by the change in oxygen between each time step corrected for air-sea exchange, and integrated to daily

values. The correction for air-sea exchange often accounted for up to half of the daily NEM; thus calculation of NEM is very sensitive to potential errors in estimations of air-sea exchange.

Statistical Analyses

We used information theory (Burnham and Anderson, 2003) to determine the best P-I model for the hourly production data collected each month. Information theory is based on how well a single model fits given data, and ranks the different models according to the Akaike Information Criterion (AIC). Models that have a smaller AIC value are considered to have a better fit. Sediment and water column production data from each site (10 sites total) measured in August 2007 were fit to ten different production-irradiance models using a non-linear function in SAS 9.1 (see Appendix II, Tables 2,3,4). Using the residual sum of squares (RSS) from each model output we calculated the AIC for each model and corrected the AIC for small sample size (AIC_c). These AIC_c values were weighted based on the other minimum AIC_c values for each model to determine the overall best model. Several models fit the data well (Appendix II), but the Jassby and Platt (1976) model consistently ranked the highest.

General linear model analysis of variance (GLM ANOVA) was used to determine statistical significance of the metabolic parameters. Factors included in the model were bay, sampling date, and sampling location (i.e. creek, mid bay, inlet). We tested for differences of daily GPP, R, and NCP and hourly R and P_{max} values for the water column and sediments, as well as NEM, production:respiration (P:R), and benthic:pelagic metabolism. We also tested for differences between metabolic parameters on daily values extrapolated for March-October. Differences were considered significant at the

α= 0.05 level. Tukey's pair-wise comparison was used to determine differences between factors from significant ANOVA tests. Data were also tested for normality using an Anderson-Darling test and for homogeneity of variance using Levene's test. All data met the homogeneity of variance assumption, though not all data were normally distributed; transformation of the data did not improve the distribution. ANOVAs are robust to non-normality, however, and the assumption of homogenous variance is more important to reduce the potential of Type I error (Quinn and Keough, 2002). Regression analyses of metabolic parameters were also conducted; analyses were again considered significant at the α=0.5 level. All ANOVA and regression analyses were performed in Minitab 15.0.

We calculated daily metabolism as a bay wide average using the three sampling stations as a single replicate. No statistical differences were found by site for average daily water column GPP ($p=0.885$), water column NCP ($p=0.075$), sediment GPP ($p=0.880$), sediment R ($p=0.160$) or sediment NCP ($p=0.715$) and we found no interaction effects of site. The GLM ANOVA found a statistical difference in water column R among sites ($p=0.012$), but the lack of statistical difference of net water column metabolism among sites indicates this difference in respiration does not significantly influence the overall metabolic balance of the water column. There was also no interaction effect of site within a bay, indicating pelagic respiration does not differ among sites within a single bay. An additional ANOVA with just site as the factor and a Tukey's pair-wise comparison found that there were no significant differences ($p=0.133$) for pelagic respiration among sites. Based on this additional test, we felt comfortable using pelagic respiration from the three sites as an estimate for the whole bay. To test for differences in daily metabolism across bays, we assumed the values obtained for

Gargathy's mid-bay site held for a creek and inlet station, though we did not actually sample such sites. This assumption was again substantiated by the lack of statistical differences between locations within a bay. For all analyses, we therefore treated the three sites within each bay as replicates.

RESULTS

Water quality

Nutrient concentrations were similar among the bays throughout the year. Dissolved inorganic nutrient concentrations were persistently low over the annual cycle, though concentrations spiked in October 2007 in the three VA bays and again in the spring (Fig. 4). Ammonium was the predominant DIN species in the fall in all bays and NO_3^- was the dominant DIN species in the spring.

Dissolved organic nitrogen was the main species of TDN present in all the lagoons. Concentrations of DON were highest at the creek site in Isle of Wight ranging from 18-40 μM. Gargathy Bay DON concentrations had the largest range from a low of 12 μM in August 2007 to a high of 34 μM in March 2008. In Hog Island, the creek and mid-bay sites had the highest DON concentrations relative to the inlet, ranging from a low in October 2007 of 15 μM to a high of 26 μM at the mid-bay site in September 2007. Similarly, the creek site in Burton's Bay had the highest DON concentrations throughout the sampling year, ranging from 14-28 μM. Concentrations of DIN and DON followed an opposing pattern in the 3 VA bays in the fall; the spike of DIN in October is consistent with a relative decrease in DON. Such a pattern is consistent with the remineralization of organic matter.

Water column chlorophyll concentrations were generally low and followed similar patterns among the bays over the year (Fig. 5). In Hog Island, chlorophyll concentrations followed a seasonal pattern, with higher concentrations in the warmer months and lower concentrations in the winter months (Fig. 5a). Burton's Bay followed a similar trend, though an increase in chlorophyll at the creek site in March indicates a possible phytoplankton bloom in the creek; a trend not evident in the other systems (Fig. 5b). Gargathy Bay chlorophyll concentrations also followed a seasonal pattern, though it had higher concentrations in the winter than the other systems (Fig. 5d). In Hog Island, Isle of Wight, and Burton's, water column chlorophyll concentrations peaked in the late summer coincident with the August sampling; a similar peak occurred a month later in Gargathy.

Throughout the year, sediment chlorophyll concentrations in the first 3 mm of sediments were lowest in Burton's and Gargathy (Fig. 5f,h). Gargathy Bay experienced two pronounced peaks in sediment chlorophyll-a concentrations in October 2007 and May 2008 (Fig. 5h). The peak in May was likely detrital macroalgal material as there was a significant bloom of *Gracilaria* in this month which produced thick mats that shaded the entire benthos, and is further supported by the lack of measurable benthic production. Sediment chlorophyll concentrations were highest throughout the year in the sediments of Hog Island and Isle of Wight (Fig. 5e,g). In all bays, sediment chlorophyll concentrations peaked in the fall, the month following the peak in water column chlorophyll, though the trend in Burton's was only evident at the inlet (Fig. 5f). Benthic chlorophyll concentrations also peaked at the creek site in Burton's in March, concurrent with the water column chlorophyll peak (Fig. 5f).

Daily Gross Primary Production and Respiration

All bays experienced increased pelagic GPP in the fall. In Gargathy, the water column GPP peaked concurrently with the spike in water column chlorophyll, but the spike in GPP in the other systems occurred the month following the peak in chlorophyll. Burton's appeared to have the highest rates of GPP and R throughout the year (Fig. 6b), though differences in water column GPP and R were only significant among bays on a few sampling dates. Daily pelagic metabolism oscillated between net autotrophy and net heterotrophy in all the bays over the annual sampling period, though overall the water column was net autotrophic in all systems (Fig.6). Daily pelagic respiration values were relatively low throughout the annual sampling period. In some months, we had difficulty getting a measurable change in oxygen in our dark incubations, thus we may have underestimated pelagic respiration in some months. However, the greater measured rates of R in some months, suggest that water column R was generally low in these systems. Despite the low respiration measurements, in many cases pelagic respiration tended to follow water column GPP.

Sediment metabolism in Hog Island and Burton's were in balance much of the time, with net heterotrophy in the late summer, shifting to slight autotrophy in the fall, slight heterotrophy in the spring and slight autotrophy in the summer (Fig. 6e). Burton's Bay experienced a peak in benthic GPP in June shifting the sediments to slight autotrophy (Fig. 6f); this also occurred in Hog Island in July (Fig. 6e). Benthic metabolism in Isle of Wight was net autotrophic to balanced over the annual cycle (Fig. 6g). Sediment metabolism in Gargathy was net heterotrophic most of the time, with a period of balanced metabolism from October through March (Fig. 6h). Gargathy Bay

had the lowest rates of sediment GPP and highest rates of sediment R over the annual cycle. There was no measurable benthic production in May or June and GPP was highest in July 2007 with 0.9 g O_2 m^{-2} d^{-1}; sediment respiration ranged from a low of -0.2 g O_2 m^{-2} d^{-1} in March to a high of -3.7 g O_2 m^{-2} d^{-1} in May (Fig. 6h).

Net ecosystem metabolism was slightly net autotrophic in all four bays over the annual cycle (Fig. 7). In Hog Island Bay, daily NEM was slightly heterotrophic in July and September 2007, shifted toward net autotrophy in October and remained slightly autotrophic throughout the winter, with peak autotrophy occurring in June at 12.6 g O_2 m^{-2} d^{-1} (Fig. 7a). Burton's Bay NEM followed a more seasonal pattern with net autotrophy in summer and net heterotrophy in the winter (Fig. 7b). Similar to Hog Island, peak autotrophy in Burton's occurred in June with NEM equivalent to 11.7 g O_2 m^{-2} d^{-1}. Isle of Wight Bay was net autotrophic, except in August when NEM was slightly heterotrophic at -0.8 g O_2 m^{-2} d^{-1}; NEM became increasingly autotrophic during the warmer months of May and July, peaking in July 2008 and again in September with similar rates of 5.4 and 5.6 g O_2 m^{-2} d^{-1} (Fig. 7c). Similar to Burton's Bay, daily NEM in Gargathy fluctuated over the annual cycle. Gargathy was net heterotrophic in July 2007 shifting to net autotrophy in September of 6.8 g O_2 m^{-2} d^{-1} (Fig. 7d). Like Burton's, Gargathy was net heterotrophic in March and shifted to slight autotrophy in the summer (Fig. 7d).

March-October Metabolism

We scaled our daily measurements to the entire growing season (March to October) by weighting each estimate with the number of days between sampling events. We were unable to extrapolate over the entire annual cycle due to temperature regulation

problems during our January incubations resulting in samples incubated above the ambient temperature of 1°C. Graphs in figure 8 for March to October are arranged to illustrate changes in system metabolism with increasing nutrient load (Table 1). Mean growing season water column GPP, R, and NCP rates were similar among the bays and each system had a net autotrophic water column (Fig. 8a).

Sediment metabolism was significantly different among the bays over the study period (Fig. 8d). Mean daily rates of benthic GPP differed significantly among the bays ($p>0.000$), with Isle of Wight experiencing the highest rate of benthic GPP and Gargathy the lowest. Average daily benthic R was not statistically different among the bays, except for Gargathy, which had a rate of -1.5 g O_2 m^{-2} d^{-1} ($p>0.000$). The difference in rates of benthic NCP among the bays was also significant ($p>0.000$), with Isle of Wight experiencing the greatest autotrophy and Gargathy the greatest heterotrophy.

The $GPP_{B:P}$ was below one in all systems indicating water column GPP, extrapolated to a 1 m water column, dominated total system GPP (Fig. 8b). Isle of Wight Bay, which had an intermediate nitrogen load, had the highest $GPP_{B:P}$ and Gargathy Bay with the highest nitrogen load, had the lowest $GPP_{B:P}$ (Fig. 8b); overall, there was no obvious pattern with nutrient load. The $R_{B:P}$ was highest in Isle of Wight and Gargathy Bay, the two systems receiving the highest nutrient loads (Fig. 8e). The ratio of $R_{B:P}$ was below one in Hog Island and Burton's and slightly above one in Isle of Wight and Gargathy (Fig. 8d). This trend suggests an increasing contribution of benthic respiration to total system respiration with increasing nutrient loads. .

Overall, all four bays were net autotrophic during March to October (Fig. 8c,f). Net ecosystem metabolism was lowest in Hog Island with a mean daily rate of 2.8 g O_2

m^{-2} d^{-1}. Burton's and Isle of Wight Bays had similarly high NEM of 3.3 and 3.4 g O_2 m^{-2} d^{-1}, respectively; Gargathy had the lowest NEM, 0.8 g O_2 m^{-2} d^{-1}. Differences in NEM were only significant between Isle of Wight and Gargathy ($p=0.04$). There was no significant trend of NEM with nutrient load, except in the most enriched system which demonstrated reduced autotrophy. We also evaluated the production:respiration (P:R) ratio for each bay and found it showed a pattern similar to that of NEM.

Normalizing loads to residence times did not improve the relationship of any metabolic parameter with nutrient load. Normalizing to residence time only switched the relative ranking of Gargathy and Isle of Wight Bays, making Isle of Wight the most enriched system.

Open Water Net Ecosystem Metabolism

Open water measurements in both bays illustrated daily fluctuations in rates of NEM (Fig. 9). Average daily PAR (μE m^{-2} s^{-1}) was sometimes a good predictor of NEM, as average PAR was in some cases directly related to increased autotrophy. For all five deployments, Burton's was net heterotrophic, though the degree of heterotrophy fluctuated on a daily and monthly basis (Fig. 9). Open water measurements in Gargathy show shifts between net autotrophy and heterotrophy over a single deployment. On average, NEM was slightly net heterotrophic in July and September 2007, net autotrophic in February 2008 and net heterotrophic in July 2008. Results of the open water measurements were not consistent with NEM calculated using the component method.

May-July Macroalgal and Sediment Metabolism

Average daily *Ulva* GPP and R over the May- July sampling period indicated that *Ulva* metabolism was net autotrophic in all four bays, though only slightly in Isle of

Wight (Fig. 10). *Graciliaria* metabolism was net autotrophic in Isle of Wight, Hog Island and Burton's, but net heterotrophic in Gargathy, where the maximum rates of GPP and R were found (Fig. 10). An extensive bloom of *Gracilaria* occurred in Gargathy during May and June, which likely caused the mat to become net heterotrophic due to self-shading. Higher rates of macroalgal GPP and R in Burton's and Gargathy reflect the high macroalgal biomass observed in these systems.

Benthic and system metabolism were re-calculated with the presence and absence of macroalgae for May to July 2008, to estimate the impact of macroalgae on benthic and system NEM. Scaling macroalgal metabolism to the full system is difficult due to the spatial variability of macroalgal biomass and its unknown distribution bay-wide. Thus, our estimates of macroalgal metabolism do not represent integrated rates across the full lagoon, but only at those sites where we made measurements.

Inclusion of macroalgae reduced sediment GPP in all systems by at least 50%, except in Isle of Wight, and there was no significant difference in GPP among the systems ($p=0.141$; Fig. 11b). Sediment respiration did not appear to respond to the presence of macroalgae. In incubations in which we sampled sediments from underneath macroalgal mats in June and July, no differences were observed in benthic respiration in cores from between or underneath mats. Macroalgae shifted NCP in sediments towards increased heterotrophy, although only Burton's sediments changed from net autotrophic to net heterotrophic (Fig. 11b).

Average daily NEM from May to July, without macroalgae, showed a significant trend of decreasing NEM with increasing nutrient loads in the two most enriched systems ($p<0.000$ – Fig. 11c). The addition of macroalgal metabolism had varying affects on

system metabolism in the four bays, but results followed the same overall trend with a peak in autotrophy at an intermediate load and then reduced autotrophy at higher loads ($p<0.000$). The P:R ratio in May to July with and without macroalgae was greater than one in Hog Island, Isle of Wight, and Burton's Bays indicating greater production than respiration in these systems (Fig. 11d), whereas in Gargathy, P:R was slightly greater than one, with and without macroalgae, suggesting a balance between production and respiration. Overall, trends in P:R mirrored trends in NEM (Fig. 11d); the low P:R observed in the presence of macroalgae in all systems was likely due to reduction in benthic GPP .

DISCUSSION

Water column dissolved inorganic nitrogen concentrations followed similar patterns in all four systems, peaked in the fall and in the spring, but otherwise remained relatively low (Fig. 4). Ammonium was the primary DIN species in the fall, which is consistent with the remineralization of organic matter at the end of the growing season (Tyler et *al.*, 2001). Nitrate was the dominant species in the spring, which is consistent with enhanced freshwater delivery of nutrient input from the land in the spring. Peaks of NO_3^- in the spring are comparatively higher in Gargathy and Isle of Wight than in Burton's or Hog Island suggesting that the former bays receive greater influence from land derived nitrogen. Despite the seasonal peaks of DIN, DON drove TDN dynamics in the four systems.

Temporal trends in pelagic chlorophyll concentrations (Fig. 5) showed higher concentrations in the warmer months and lower concentrations in the winter months,

though values were both temporally and spatially variable. All bays experienced a late summer peak in water column chlorophyll, which is likely due to a phytoplankton bloom fueled by the senescence of macroalgae and the release of nutrients into the water column. McGlathery et *al.* (2001) reported a similar trend in Hog Island, where a macroalgal die off in July stimulated increased water column productivity in August. The peak in NH_4^+ in the four bays in late summer and fall further supports this idea. Water column chlorophyll concentrations increased progressively from May to July following the spring peak in DIN, suggesting warmer temperatures and increased light enhanced phytoplankton growth.

Benthic chlorophyll concentrations and rates of GPP were persistently low throughout the year, especially in Burton's and Gargathy, suggesting limitation of BMA by light or, possibly, nutrient availability or both. Distinct peaks in the fall of benthic chlorophyll further corroborate that critical resources limited BMA. Following the peak and subsequent decline of water column chlorophyll, benthic chlorophyll concentrations in all bays spiked (Fig. 5). Macroalgae present in the system from early to mid-summer can out compete BMA, intercepting water column nutrients and shading the benthos. Phytoplankton production fueled by nutrients from senescing macroalgae further reduced light and nutrient availability for BMA upon the decline of macroalgae (McGlathery et *al.*, 2001; Tyler et *al.*, 2001). Thus, BMA were likely limited by light and potentially nutrients until the fall. Of the systems studied, benthic chlorophyll and GPP were the highest through the year in Isle of Wight Bay, as might be expected since Isle of Wight had the lowest measured light attenuation, and, thus, better able to support an active BMA community.

Temporal patterns in pelagic metabolic rates do not always follow patterns of measured phytoplankton biomass. In the fall, all bays experienced peaks in water column chlorophyll and peaks in pelagic GPP (Fig. 5, Fig. 6). In Gargathy, the peaks occurred simultaneously, which is expected given the link between biomass and primary productivity (Valiela, 1995). Peaks in water column chlorophyll in Hog Island and Isle of Wight occurred prior to the peak in GPP, and in Burton's, pelagic GPP remained constant throughout the fall regardless of phytoplankton biomass. Periodic high rates of GPP and low biomass suggest heterotrophic or physical controls on producer biomass at these times. Local conditions in the lagoon may be suitable for high rates of growth, but large-scale transport processes, which component methods do not measure, may reduce accumulation of biomass and uncouple growth rates and biomass measurements (Lucas et *al.*, 1996).

The variability in our water column respiration is difficult to explain, as there does not appear to be a clear trend with producer biomass or season. A review of coastal system respiration by Hopkinson and Smith (2005) concluded that pelagic respiration rates are highly variable among and within coastal systems and parameters such as temperature and chlorophyll concentrations are not always good predictors of R (Hopkinson and Smith, 2005). In some systems, water column respiration has been shown to be correlated to pelagic production (Kemp and Smith, 2003; Hopkinson and Smith, 2005), and this appeared to be the case in our study at some times but not others. Additionally, pelagic respiration can vary with inorganic nutrient availability, as this can limit heterotrophic bacterial activity (Smith and Kemp, 2005).

Water column net metabolism drove the daily NEM fluctuations within our systems. For a given irradiance, areal sediment GPP exceeded that in the water column, but after depth-integrating water column GPP & attenuating irradiance to the bottom, water column GPP exceeded sediment GPP. Similarly, Hopkinson and Smith (2005) found pelagic signals dominated when they depth integrated literature values of pelagic respiration, though they integrated over a deeper water column. Another study found that standardizing water column depth to compare two study sites of different depths reduced the contribution of the benthos to system metabolism (Meyercordt et *al.*, 1999).

Daily NEM in the four bays fluctuated seasonally over the annual cycle (Fig. 7). Burton's and Gargathy Bays demonstrated net autotrophy in the warmer months and reduced autotrophy and heterotrophy in the fall and winter months. Hog Island and Isle of Wight demonstrated net autotrophy throughout the year and decreased autotrophy in the fall and winter, which is consistent with heterotrophic patterns identified in Gargathy and Burton's Bays. Similar seasonal patterns have been observed in other coastal lagoon systems and are consistent with patterns in previous studies in Hog Island (Carmouze et *al.*, 1991; Reyes and Merino et *al.*, 1991; Smith and Hollibaugh, 1997; McGlathery et *al.*, 2001). Seasonal NEM fluctuations may be due to effects of temperature and light availability on primary producers (Carmouze et *al.*, 1991; Caffrey, 2003, 2004) or from enhanced heterotrophic activity from wind induced turbulence and re-suspension of organic matter (Reyes and Merino et *al.*, 2001). As discussed below, macroalgae may also drive the seasonal changes in NEM, as they can reduce benthic GPP through shading and influence water column metabolism by controlling the availability of nutrients to the water column (McGlathery et *al.*, 2001; Tyler et *al.*, 2001).

March – October Metabolism

By scaling our daily rates to monthly values and averaging over a period from March to October, we can examine the metabolic balance of the lagoons over a longer temporal scale (Fig. 8). Trends in average daily rates for March-October for pelagic, benthic and system metabolism were similar to the trends in daily rates. Water column NCP was net autotrophic from March to October. Some studies found pelagic metabolism in coastal systems to be net heterotrophic (McGlathery et *al.*, 2001, Gazeau et *al.*, 2005), while other studies have reported net pelagic autotrophy. In the coastal lagoon, Ria Formosa, net community production was autotrophic in the water column (Santos et *al.*, 2004). Similarly, Tomales Bay, CA was found to have a strongly autotrophic water column (Smith and Hollibaugh, 1997). Water column in the littoral zones of the Chesapeake Bay have also been shown to be seasonally net autotrophic and respiration rates in these regions were also lower than in the deeper regions of the bay (Kemp et *al.*, 1997; Smith and Kemp, 2001).

One factor that may be driving net autotrophy in the water columns of our lagoons is the high rates of nitrogen loading. Rates of nitrogen loading to the lagoons in this study are within the range of loadings that spurred greater pelagic production over benthic production in a mesocosm study (Taylor et *al.*, 1995). Sediment resuspension, an important process in these wind-driven lagoons (Lawson et *al.*, 2007), and the subsequent resuspension of benthic microalgae could have driven net autotrophy in the water column as well. Resuspended benthic microalgae can contribute to water column productivity, increasing autotrophy. Low rates of respiration also contributed to the net autotrophic nature of the water column. Finding a net autotrophic water column was different from

previous studies in Hog Island Bay (McGlathery et *al.*, 2001; Anderson et *al.*, 2003), and could be due to inter-annual variability or a long-term shift in the system. Long-term measurements of pelagic metabolism could help decipher the differences between studies.

Benthic metabolism from March to October was slightly net autotrophic in Hog Island and slightly net heterotrophic in Burton's Bays. The variability associated with these measurements however suggests benthic NCP was generally balanced. Previous studies in Hog Island found net metabolism in the benthos to be both net autotrophic (McGlathery et *al.*, 2001) and net heterotrophic (Tyler et *al.*, 2003), highlighting the temporal variability of the system driven by differences in macroalgal biomass and shading of sediments. Our finding of a slightly autotrophic benthos in Hog Island Bay agreed with findings from McGlathery et *al.* (2001), though the differences in sediment metabolism from the various studies supports the idea of a metabolically balanced benthos. Benthic metabolism in the other two systems was different however, with significant net autotrophy in Isle of Wight and heterotrophy in Gargathy.

Light availability, a small BMA community, and sediment organic matter likely drove the differences in sediment metabolism among the study bays. Gargathy Bay had, on average, the highest vertical light attenuation coefficient at 2.9 m^{-1}, the highest sediment organic content of 4%, and low concentrations of benthic microalgae (Fig. 5h). The combination of low light, high sediment organic content, and a small producing BMA community likely maintained net heterotrophy in the sediments. Conversely, lower vertical light attenuation (1.7 m^{-1}), low sediment organic content (0.9%), and high benthic chlorophyll concentrations likely drove net autotrophy in Isle of Wight Bay sediments.

Benthic NCP was not significantly different in Burton's or Hog Island Bays. Despite greater average light attenuation in Hog Island of 2.3 m^{-1} (compared to 1.8 m^{-1} in Burton's), it trended toward net autotrophy and Burton's toward net heterotrophy. Burton's Bay, however, had greater sediment organic matter content of 2.7% (compared to 1.7% in Hog Island) and lower BMA biomass (Fig. 5f). Light availability is an important determinant of benthic GPP (Meyercordt and Meyer-Reil, 1999; Stutes et *al.*, 2006) and results from our study are consistent with this finding, as rates of benthic GPP were highest in Isle of Wight and lowest in Gargathy. Dalsgaard (2003) found sites with a large BMA community to be net autotrophic as compared to a net heterotrophic site with low BMA biomass. Thus, net metabolism of the benthos in our bays appeared to be driven by a combination of light, BMA biomass, and organic matter content.

Over the March to October period, GPP in the water column was greater than GPP in the benthos, thus explaining the benthic:pelagic GPP ratios ($GPP_{B:P}$) below 1 in all systems. No clear or significant trends in $GPP_{B:P}$ with loading were identifiable, though Gargathy had the lowest ratio. With the exception of Isle of Wight, $GPP_{B:P}$ ratios followed a decreasing trend with increasing load among the VA bays, a pattern consistent with the shift in primary producers towards phytoplankton dominated systems at high nutrient loads (Valiela et *al.*, 1997). Gargathy Bay had the largest contribution of pelagic GPP to total GPP. D'Avanzo et *al.* (1996) also found a larger contribution of phytoplankton to system production in the highly enriched Child's River. Isle of Wight Bay had the highest $GPP_{B:P}$, which does not match the trend towards a phytoplankton based system at higher nutrient loads. This deviation of Isle of Wight Bay was likely due to the greater degree of benthic production relative to the other systems as explained

above. Regardless, pelagic GPP in all systems dominated the $GPP_{B:P}$, suggesting that phytoplankton are important producers in these shallow lagoons.

The ratio of $R_{B:P}$ from March to October in the four systems shows that benthic respiration contributed more to total system respiration in the highly loaded lagoons of Isle of Wight and Gargathy. In Gargathy Bay, this is not surprising given the high rates of sediment respiration and organic content. However, respiration rates in the other three systems were comparable, thus the high $R_{B:P}$ in Isle of Wight is likely due to the low rates of pelagic respiration. In Gargathy, over 44% of system GPP was respired by the benthos as compared to only 13 – 14% in the other systems. Pelagic respiration, as indicated by the $R_{B:P}$ dominated in Hog Island and Burton's Bays.

During March to October NEM was net autotrophic in all four systems. We hypothesized that NEM would become more autotrophic as nutrient loading increased (Oviatt et *al.*, 1986, Kemp et *al.*, 1997; Caffrey, 2004), except for a potential increase in heterotrophy at the highest load. Our results partially supported our hypothesis. There was no significant change in NEM in the three least loaded systems; however, in the highly loaded system NEM became less autotrophic. Differences in NEM were significant between Isle of Wight and Gargathy Bays, suggesting a threshold level of loading between 6.5 g N m^{-2} y^{-1} and 25 g N m^{-2} y^{-1} where NEM shifted towards reduced autotrophy. Gargathy Bay experienced the least autotrophic NEM, suggesting that other factors, such as sediment organics and light availability influenced the trophic status of this system in addition to nutrient load.

No clear relationships existed between NEM or P:R and nutrient load with or without normalizing to residence time. Residence time can be important in regulating

system metabolism, as it can control the exposure of primary producers to nutrients, the length of time an autotroph is in the system, and light availability (Monbet, 1992; Lucas et *al.*, 1996; Valiela et *al.*, 1997). In systems with shorter residence times, nutrients and primary producers are more rapidly flushed from the system, reducing pelagic primary productivity, but this can increase benthic primary production as macroalgae have been shown to dominate under these conditions (Fong et *al.*, 1993; Valiela et *al.*, 1997), and benthic microalgae may also benefit. For this reason, it is unclear if the system would become more autotrophic or heterotrophic in systems with faster residence times. Reduced light availability can also occur in systems with faster residence times as this can increase turbidity through resuspension or alter the position of phytoplankton in the water column (Lucas et *al.*, 1996). Under these conditions, benthic and pelagic production may decrease due to light limitation, which can reduce system autotrophy and shift the system to net heterotrophy.

The lack of an improved relationship between NEM and nutrient load after normalizing to residence time was not surprising as the residence time of nitrogen in these systems may be different from that of the water (Nixon et *al.*, 2001). Phytoplankton and macroalgae rapidly take up nitrogen and the large biomass and comparatively slower turn-over time of macroalgae allows nitrogen to be retained in the system (Valiela et *al.*, 1997; Nixon et *al.*, 2001). Similarly, benthic microalgae also take up and retain nitrogen in the system, further uncoupling the relationship of residence time and nutrient load. Thus, the retention of nitrogen by primary producers and the likely different relative residence times of water and nutrients may lessen the influence of water residence time on NEM.

The ratio of inorganic nutrient loading to organic nutrients has been shown to ultimately drive NEM in coastal systems (Kemp et *al.*, 1997). As the ratio of DIN to total organic carbon (TOC) loading increases, the system will become increasingly autotrophic (Kemp et *al.*, 1997). Additionally, a recent study found that DOC concentrations (in conjunction with temperature and depth) were a better predictor of P:R than inorganic nutrient concentrations (Rochelle-Newall et *al.*, 2008). Total organic carbon loading has not been quantified to these shallow systems; however, Stanhope (2003) found DOC and DON in base flow to be low relative to DIN. Thus, organic loading may not be driving the reduced autotrophy in Gargathy as much as the storage of organic matter within the system. Model simulations of a eutrophic estuary found flocculation and particulate settling can increase the residence time of organic matter within a bay and drive it towards net heterotrophy (Hopkinson and Vallino, 1995); this may be occurring in Gargathy Bay. Extensive macroalgal blooms in Gargathy can also reduce the benthic production contributing to the reduced autotrophy.

Open Water Net Ecosystem Metabolism

Results for open water system metabolism contrasted to those based on the component method. Both Burtons and Gargathy Bays appeared to be net heterotrophic over the various sampling periods, with the exception of February in Gargathy where the system shifted to net autotrophy. Within a single deployment, Burton's was always heterotrophic with the exception of one or two days. Open water measurements in Gargathy captured a larger degree of daily variability in system metabolism with shifts between net autotrophy and net heterotrophy in a single deployment.

It is not surprising that calculations of NEM using the component and open water methods differ. In a comparison of methods, Gazeau et *al.* (2005) found that open water measurements estimated a larger degree of heterotrophy than bottle incubations and in some cases estimated net autotrophy, similar to this study. Caffrey (2004) also found most coastal systems to be net heterotrophic using the open water method. Different NEM estimates calculated by the two methods likely resulted from differences in the hydrodynamics and physical nature of the systems in addition to the temporal and spatial scales upon which the methods are based (Gazeau et *al*., 2005).

Assumptions inherent in both methods may also drive differences in NEM results. The open water method assumes that biological processes dominate DO dynamics over physical process; the water mass being measured is homogeneous and has a similar metabolic history over a diel period; metabolic rates within the system are high; and the correction for air-sea exchange is accurate (Kemp and Boynton, 1980; Caffrey, 2003, 2004). Biases in component method calculations arise because of isolating biological components from natural processes like nutrient fluxes and mixing (Kemp and Boynton, 1980); excluding larger organisms from the experiment; and the multiple calculations associated with aggregating component methods.

The coastal lagoons in this study are physically dynamic systems, with significant influence from wind and tides. Thus, the physical nature of these systems may have violated the assumption of minimal influence of physical processes on DO levels in the system. Similarly, it is difficult to know if we accurately corrected for air-sea exchange. Our wind data came from a single monitoring station inland and north of the coastal bays; thus we are not able to capture exact wind conditions at our study sites, which has been

shown to be important in quantifying air-sea exchange at local scales (Kremer et *al.*, 2003). Sensitivity analysis of the effects of wind speed on computed NEM indicated that increased or decreased wind speeds did not change the trophic status of NEM (i.e. net heterotrophic, net autotrophic), but changed the magnitude of daily NEM. However, the air-sea exchange correction varied between 50-70% of total NEM highlighting the importance of the air-sea correction to overall NEM calculations. A single monitoring station may also not accurately reflect system NEM due to spatial variability, though this is more of a problem in larger systems (Russell and Montagna, 2007). Spatial variability is also a problem for component methods. Additionally, our sondes were located in deeper, channel sites so we may have captured more water column heterotrophy in the open water samples.

Despite the potential issues with the different methods, the results of the open water study illustrated the daily variability of NEM. PAR may be a potential driver of this daily variability. In both Gargathy and Burton's Bays, trends in daily NEM appeared to be related to average daily PAR (Fig. 9); in some months, NEM became less heterotrophic or net autotrophic as average PAR increased. While this suggests greater production over respiration on days with higher PAR, we cannot be certain that respiration did not change as well.

Macroalgal Influence on Sediment and System Metabolism

Up to this point, we have only discussed the metabolism of the water column and sediments without including the influence from macroalgae. Our analysis of the affects of macroalgal metabolism on system metabolism is limited to the months of peak macroalgal growth, May to July 2008, in which we measured metabolic rates and took

biomass estimates. In addition, because of the unknown spatial distribution of macroalgal biomass throughout the lagoons we limited our analysis to represent only areas from which we took measurements and not to the entire lagoon.

Macroalgae in May to July reduced benthic GPP and shifted the sediments of Hog Island, Isle of Wight and Burton's Bays from balanced or slightly autotrophic to net heterotrophic (Fig. 11). Macroalgae reduced light availability to the sediments decreasing rates of benthic GPP (Stutes et *al.*, 2006). While we did not detect differences in respiration rates as expected from cores taken directly under macroalgal mats we may have sampled under mats that were not thick or stationary. Gargathy experienced significantly greater benthic respiration rates in May during a *Gracilaria* bloom. We also measured greater benthic respiration rates at the Hog Island creek sampling station in June during an extensive macroalgal bloom. Thus, greater respiration rates under macroalgal mats would further reduce benthic net metabolism resulting in heterotrophic sediments in all bays (Trimmer et *al.*, 2000). Overall, there was no significant trend in benthic metabolism in May to July with nutrient load, with or without macroalgae, except for greater benthic heterotrophy in Gargathy.

Macroalgal metabolism, based on the areas where we sampled biomass and measured growth, had variable affects on NEM and P:R. In Burton's, macroalgae shifted NEM towards greater autotrophy. Macroalgae in Hog Island and Isle of Wight had virtually no affect on NEM, maintaining the lagoons at a similar level of net autotrophy, but in Gargathy macroalgae made the system less autotrophic. Our results were unexpected as we anticipated macroalgae would increase the degree of autotrophy in all the systems. Macroalgal reduction of NEM in Gargathy was due to the large biomass of

Graciliaria, which was likely beginning to undergo decomposition due to self-shading within the mat. Light limitation from self-shading within macroalgal mats can reduce photosynthetic and respiratory rates, shutting down algal metabolism (Brush and Nixon, 2003), leading to heterotrophy of the mat and system (D'Avanzo and Kremer, 1994; Viaroli et *al.*, 2003). The greater degree of water column GPP in Gargathy in May may be a response to the release of nutrients into the water column from decomposing macroalgae stimulating phytoplankton production (McGlathery et *al.*, 1997, 2001).

Minimal changes in NEM from macroalgae in Hog Island and Isle of Wight Bays may be due to the succession of benthic microalgae to macroalgae as the dominant autotroph in the system, supporting the model that changes in primary producers under different nutrient regimes do not increase total system productivity (Borum and Sand-Jensen, 1996; McGlathery et *al.*, 2007). Burton's Bay, however, experienced greater system autotrophy because of the high macroalgal biomass combined with greater macroalgal GPP. Given that our calculations only represent the areas in which we took macroalgal metabolism measurements, we may have under or overestimated the influence of macroalgae on system and sediment metabolism at the scale of the entire lagoon.

In May to July, we found NEM behaved similarly to our hypothesized trend with an increase and decline in system autotrophy with nutrient load. The peak in autotrophy occurred at an intermediate nutrient load, both with and without the inclusion of macroalgae. Including macroalgae, however, provides the best estimate of whole-system NEM. Warmer average temperatures during May to July likely increased respiration relative to production, causing NEM to peak and then decline in response to nutrient load

relative to March through October when there were no significant trends with nutrient enrichment.

CONCLUSIONS

Current literature regarding the trophic status of coastal systems is mixed. Some find coastal systems to be heterotrophic (Smith and Hollibaugh, 1993; Caffrey, 2004; Gazeau et *al.*, 2005), while others find net autotrophy (Gattuso et *al.*, 1998; D'Avanzo et *al.*, 1996; Kemp et *al.*, 1997). The temperate Virginia coastal lagoons in this study were autotrophic and dominated by pelagic producers. The dominance of pelagic producers in these shallow lagoons is contrary to the idea that benthic producers dominate shallow system production (Valiela et *al.*, 1997; McGlathery et *al.*, 2007). Light availability (Meyercordt et *al.*, 1999; Stutes et *al.*, 2006) and a small benthic microalgal community (Dalsgaard, 2003) may be driving the predominance of pelagic production over benthic production in our study. Additionally, macroalgae did not appear to have a significant effect on overall system NEM or P:R, as the system with the highest rates of macroalgal GPP and biomass did not demonstrate significantly increased system NEM. Distribution of macroalgae throughout the lagoons is not well known however, and we may have overestimated the contribution of macroalgal metabolism based on our biomass estimates.

Differences in system metabolism measurements from open water and component methods highlighted the importance of the assumptions associated with both methods. Component methods have been shown to underestimate metabolic rates due to bottle effects and can result in too much variability to accurately assess system metabolism

(Kemp and Boynton et *al.*, 1980; Smith and Hollibaugh, 1997, 1993; Gazeau et *al.*, 2005). Despite the potential problems with the component method, the use of short-term incubations minimized bottle effects. Open water methods operate on multiple assumptions that may have been violated in the physically dynamic coastal lagoons. Differences in results may also be due to the different time and spatial scales upon which the methods are based (Gazeau et *al.*, 2005).

The results of our study clearly illustrate the complex controls on component and whole system metabolism. We found statistically significant trends between NEM and nutrient enrichment in the summer, with maximum NEM at an intermediate load. However, there were no clear patterns NEM during March to October as a function of nutrient loading, except in the most nutrient loaded system, which exhibited reduced autotrophy. The variation of nutrient loading within our study should be adequate to detect changes in NEM, as other studies found differences in NEM at equivalent nitrogen loads (Oviatt et *al.*, 1986; D'Avanzo et *al*., 1996; Kemp et *al.*, 1997; Caffrey, 2003, 2004). Thus, factors aside from nutrient loading appeared to control NEM in our study, complicating the simple relationship with nitrogen load. Light availability, organic matter content, primary producer biomass, and temperature appeared to influence the metabolic rates and balance of benthic and pelagic metabolism within the systems. These factors, in combination with nutrient loads likely mediate the trophic response of shallow coastal lagoons to nutrient enrichment.

Table 1. Watershed and bay characteristics of the four bays in this study. Calculations of residence time are detailed in the text and annual areal nitrogen loads are normalized to the calculated residence times.

Bay	Annual N Load ($g\ N\ m^{-2}\ y^{-1}$)	Water Body Surface Area (m^2)	Watershed Surface Area (m^2)	Average Bay Salinity (ppt)	Fresh-water input ($m^3\ d^{-1}$)	Residence Time (d)	N Load adjusted to residence time ($mmol\ N\ m^{-2}$)
Isle of Wight Bay, MD[1,5]	6.5	$1.58 \cdot 10^7$	$1.75 \cdot 10^7$	30.8	$1.90 \cdot 10^5$	9.5	12
Gargathy Bay, VA[2]	25	$1.17 \cdot 10^6$	$2.77 \cdot 10^7$	32.5	$9.49 \cdot 10^4$	0.54	2.5
Burton's Bay, VA[2]	4.4	$1.82 \cdot 10^7$	$5.97 \cdot 10^7$	32.9	$2.04 \cdot 10^5$	2.8	2.4
Hog Island Bay, VA[3,6,7]	1.4	$1.5 \cdot 10^8$	$9.22 \cdot 10^7$	33.1	$2.75 \cdot 10^5$	15	1.9

[1] Boynton et *al.*, 1996
[2] This study
[3] Stanhope, 2003
[5] Wazniak et *al.*, 2004
[6] Fugate et *al.*, 2006
[7] Oertel, 2001

Figure 1: Selected bays along the MD/VA Eastern Shore. Sampling occurs along a creek to inlet transect within each bay, except for Gargathy Bay which has a single mid-bay site due to its small size

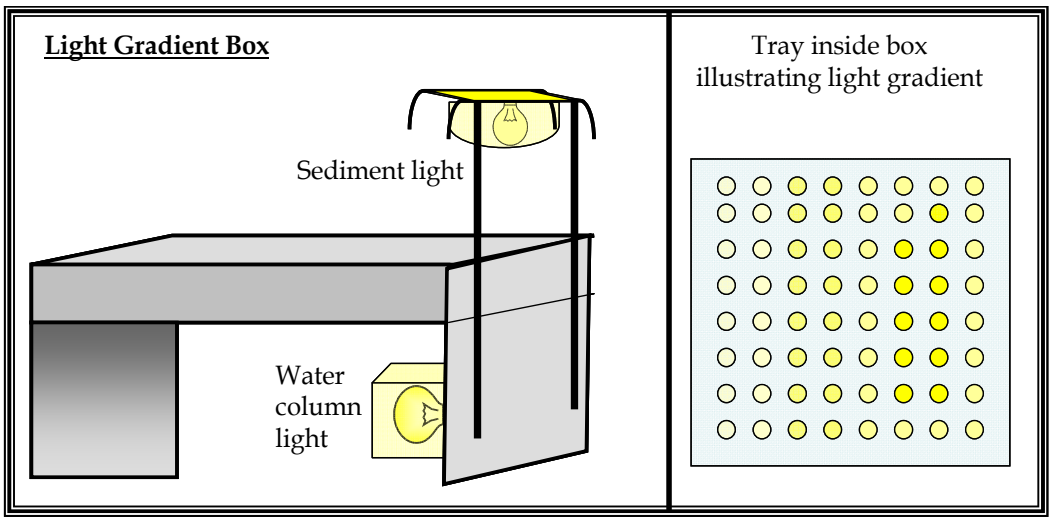

Figure 2: Depiction of a light gradient box used for incubation samples. Left panel: Light box experimental set up illustrating placement of lights used for water and sediment incubations (lights are not used simultaneously); box is flow-through temperature controlled. Right panel: Light grid inside box during incubations (10 light levels); shading gradient is the same for sediment and water incubations.

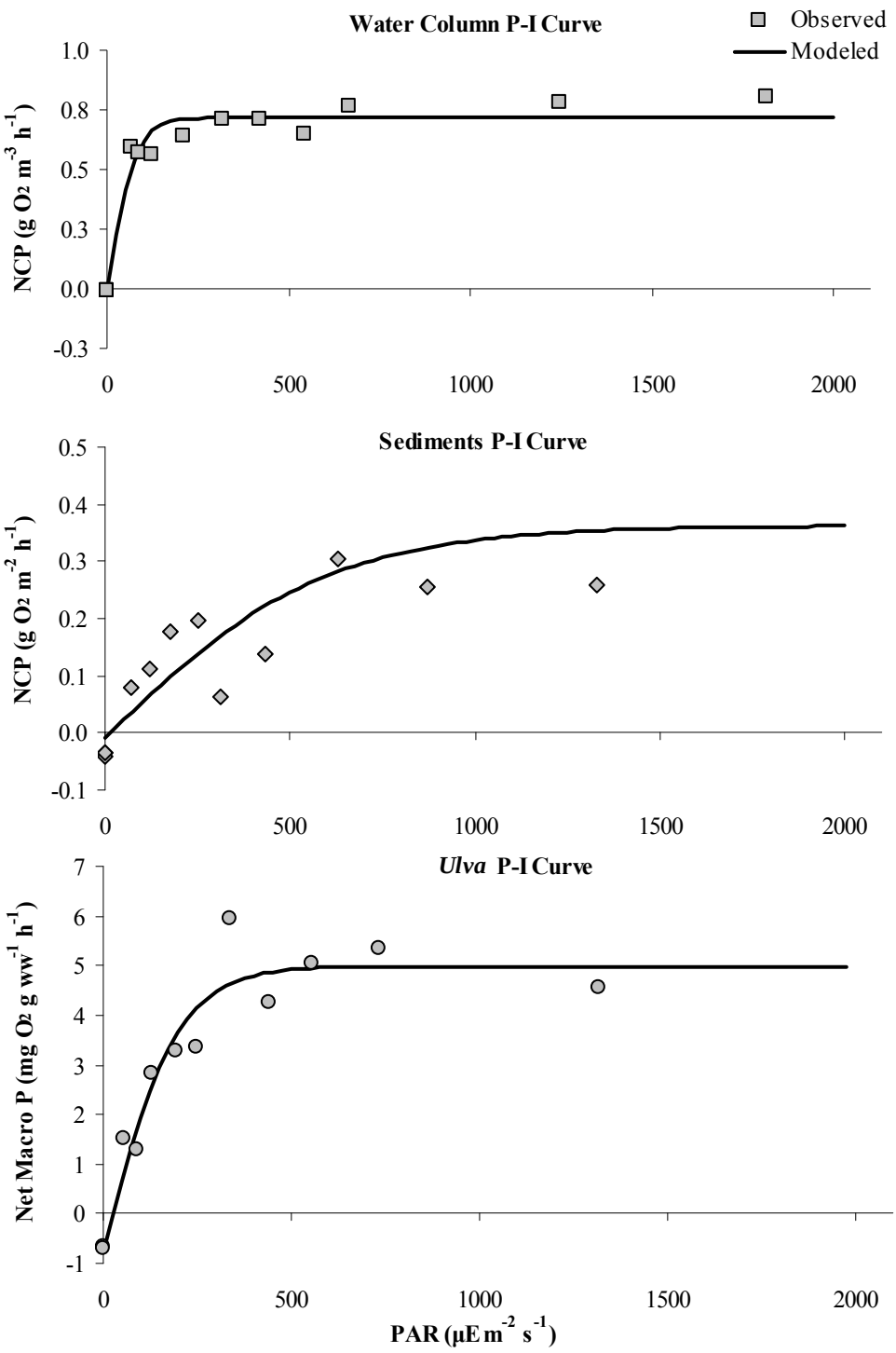

Figure 3. Example P-I curves taken from July 2008 sampling in Burton's Bay at the mid-bay sampling station. Graphs represent water column (top), sediment (middle), and *Ulva* (bottom) incubations.

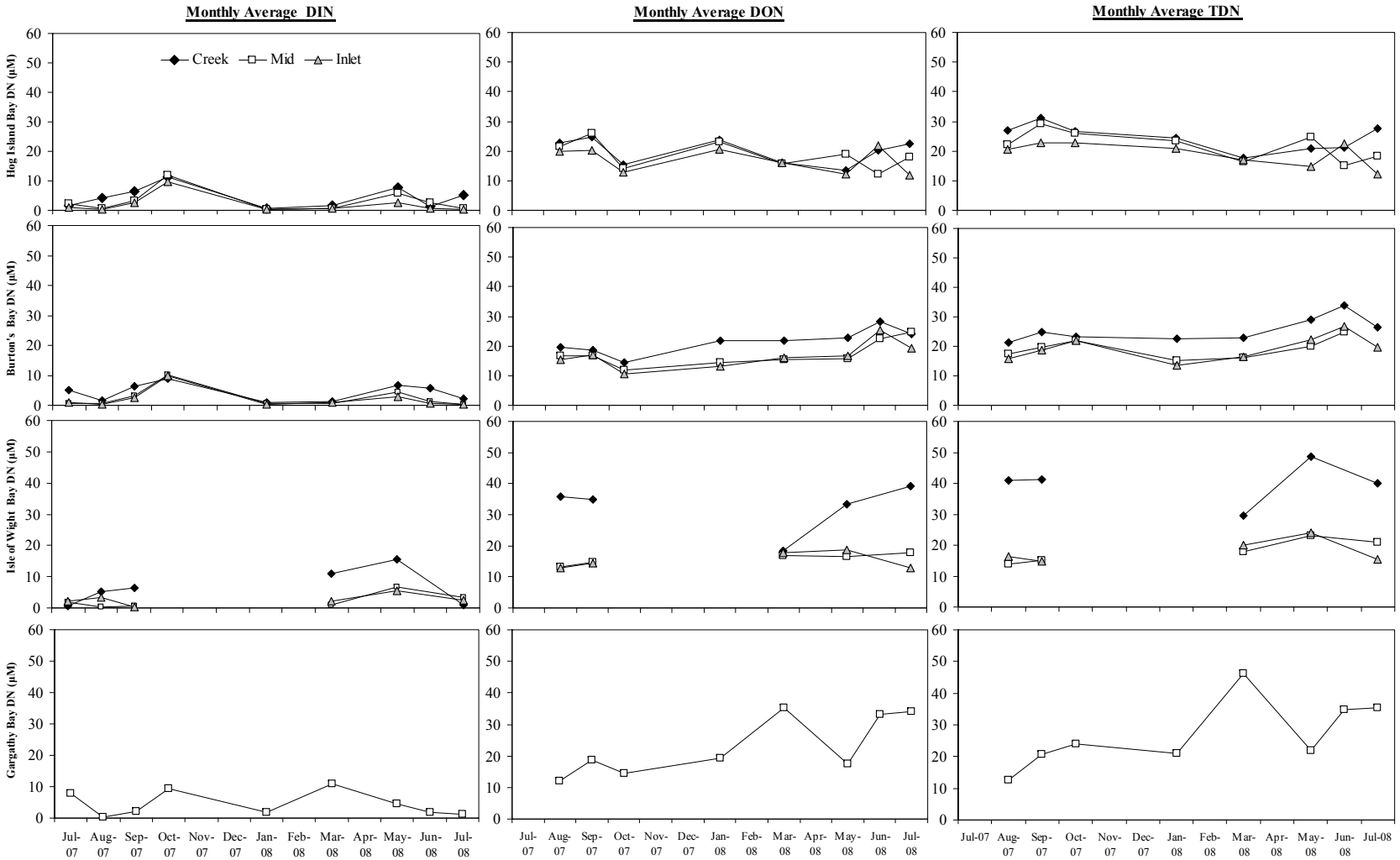

Figure 4. Times series of monthly average dissolved inorganic nitrogen (left), dissolved organic nitrogen (middle), and total dissolved nitrogen (right) concentrations measured by site for, Hog Island Bay, Burton's Bay, Isle of Wight Bay and Gargathy Bay (listed in order of increasing nutrient loading).

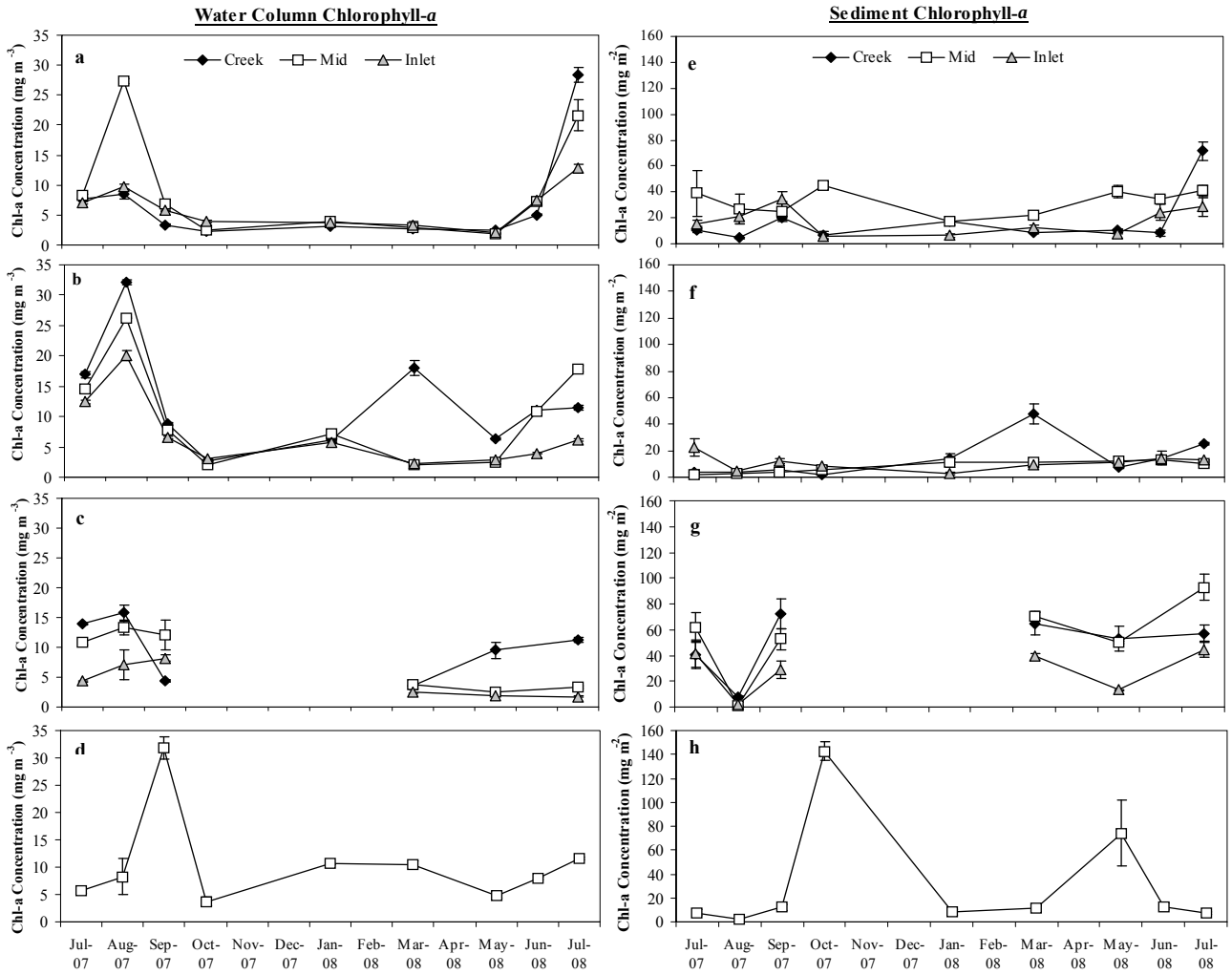

Figure 5. Time series of chlorophyll-a concentrations in the water column (left panel) and in the sediment to a depth of 3mm (right panel) over the annual sampling period for, (a) HIB, (b) Burton's Bay, (c) IWB, (d) Gargathy (listed in order of increasing nutrient loading). Error bars represent standard error (n=3 for each site).

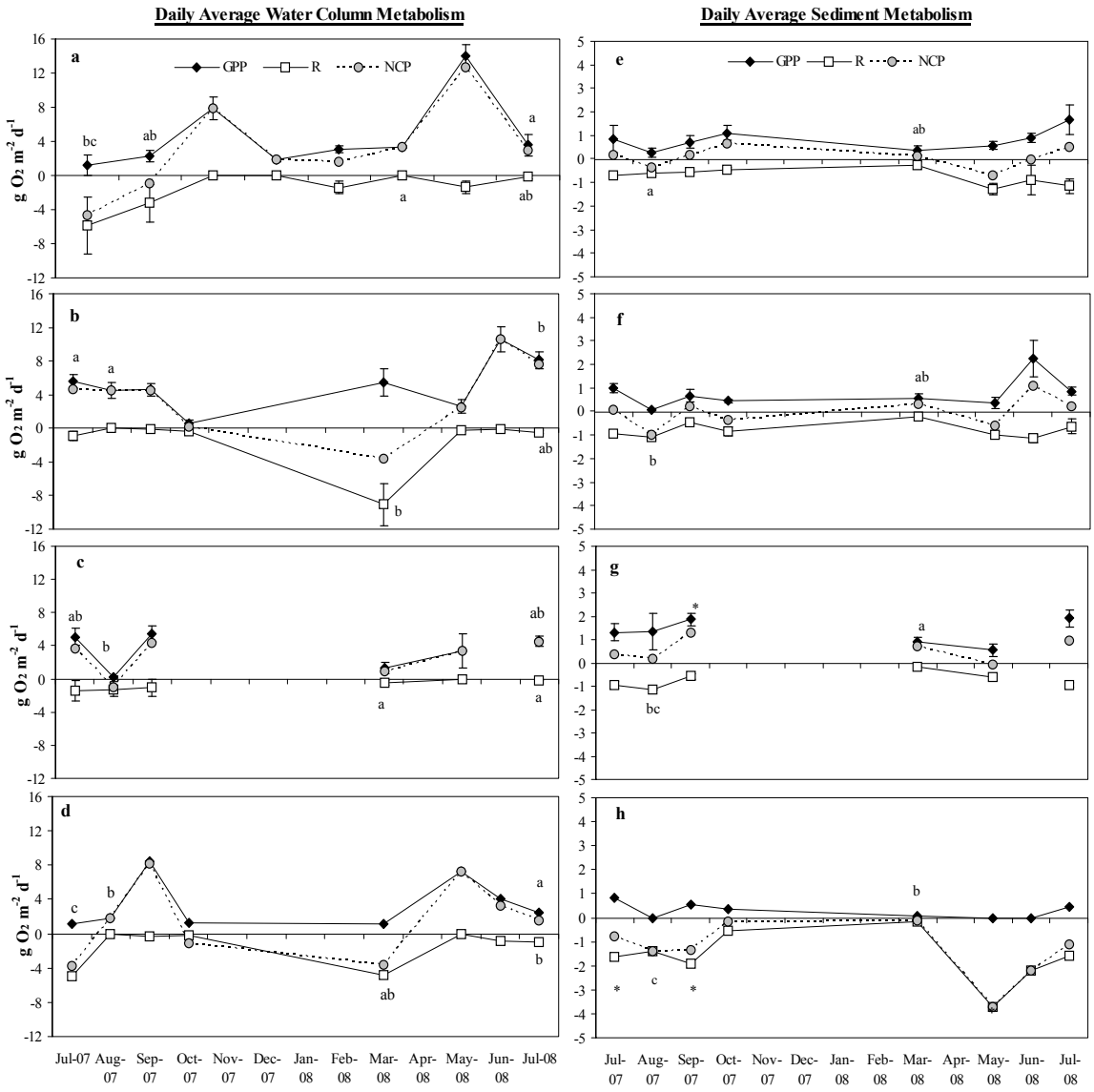

Figure 6. Measured daily water column (a-b) and sediment (e-h) GPP, net community production, and R for HIB (a,e), Burton's (b,f), IWB (c,g) and Gargathy (d,h- listed in order of increasing nutrient loading). Y-axis for water column and sediment metabolism are different scales. Error bars represent standard error (n=3; except Gargathy). Statistical significance is indicated with letters and asterisks; different letters or an asterisk indicate value(s) is/are statistically different from each other at the α=0.05 level.

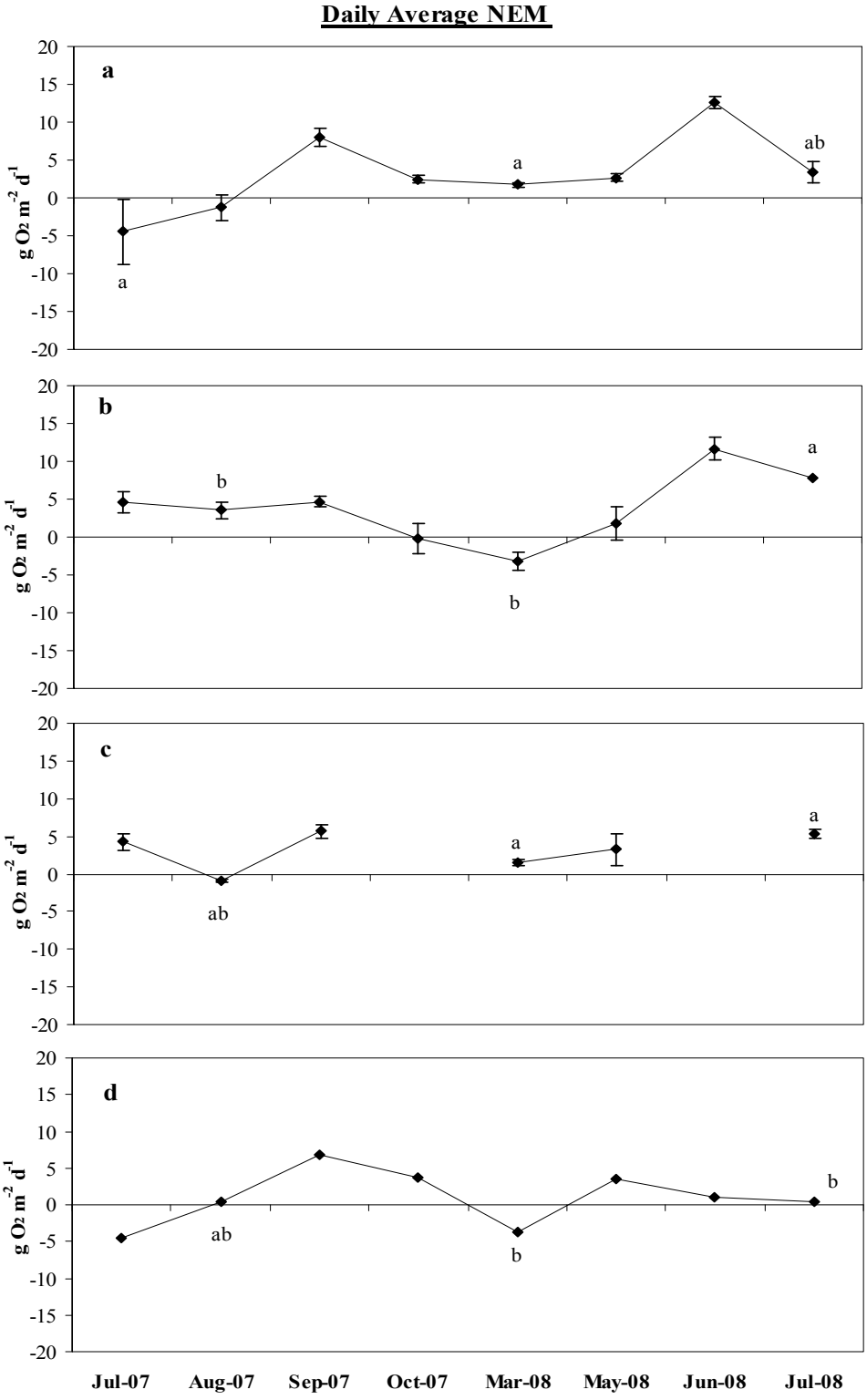

Figure 7. Daily net ecosystem metabolism of water column and sediments (macroalgal metabolism is not included) for (a) Hog Island Bay, (b) Burton's Bay, (c) Isle of Wight Bay, and (d) Gargathy Bay. Error bars represent standard error (n = 3; except GB).

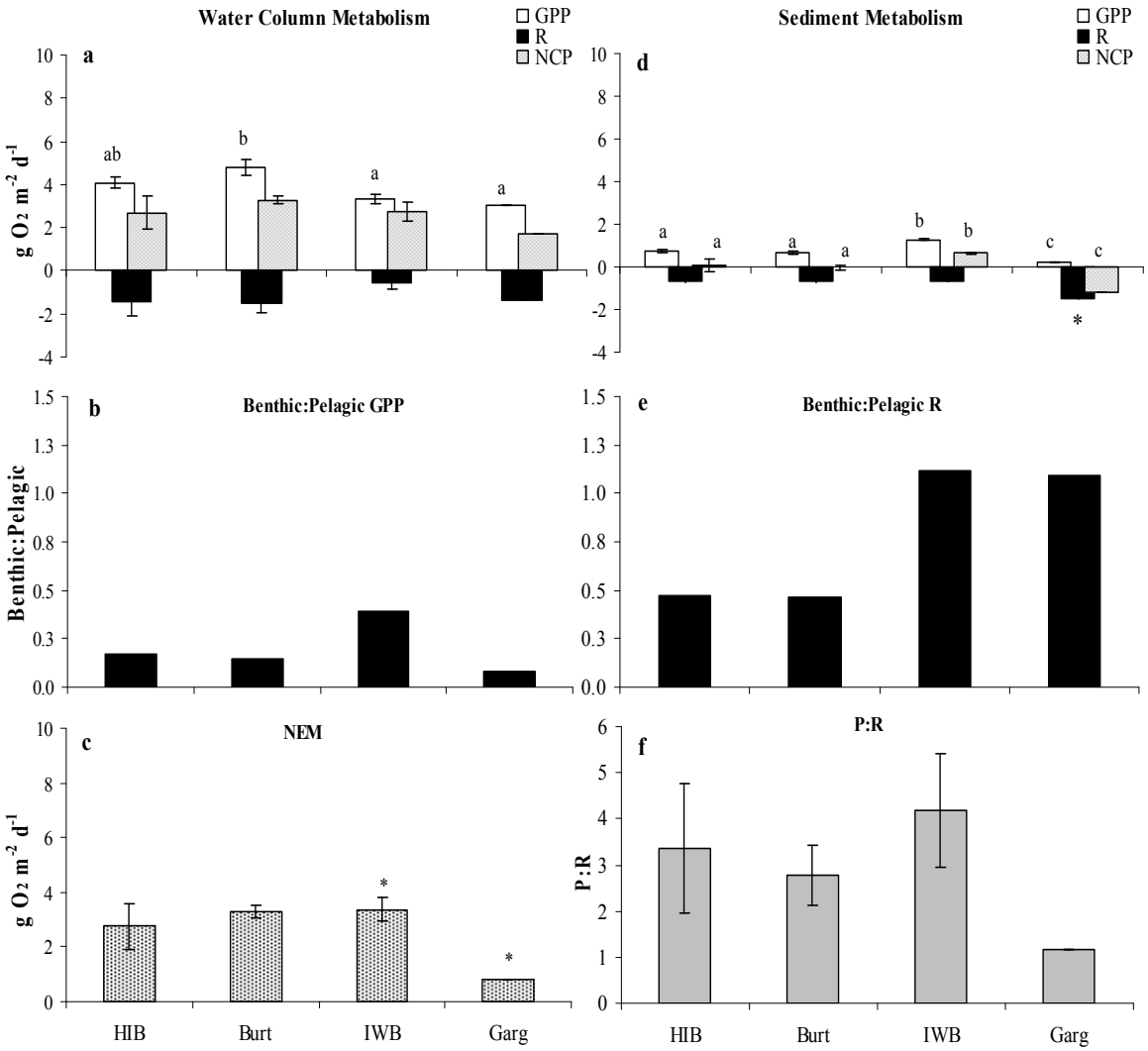

Figure 8. Daily average GPP, R and NCP for water column (a) and sediments (d), $GPP_{B:P}$ (b), and $R_{B:P}$ (e), NEM (c), and P:R (f) for the period between March through October listed in order of increasing nutrient load. Error bars represent standard error (n=3; except Gargathy).

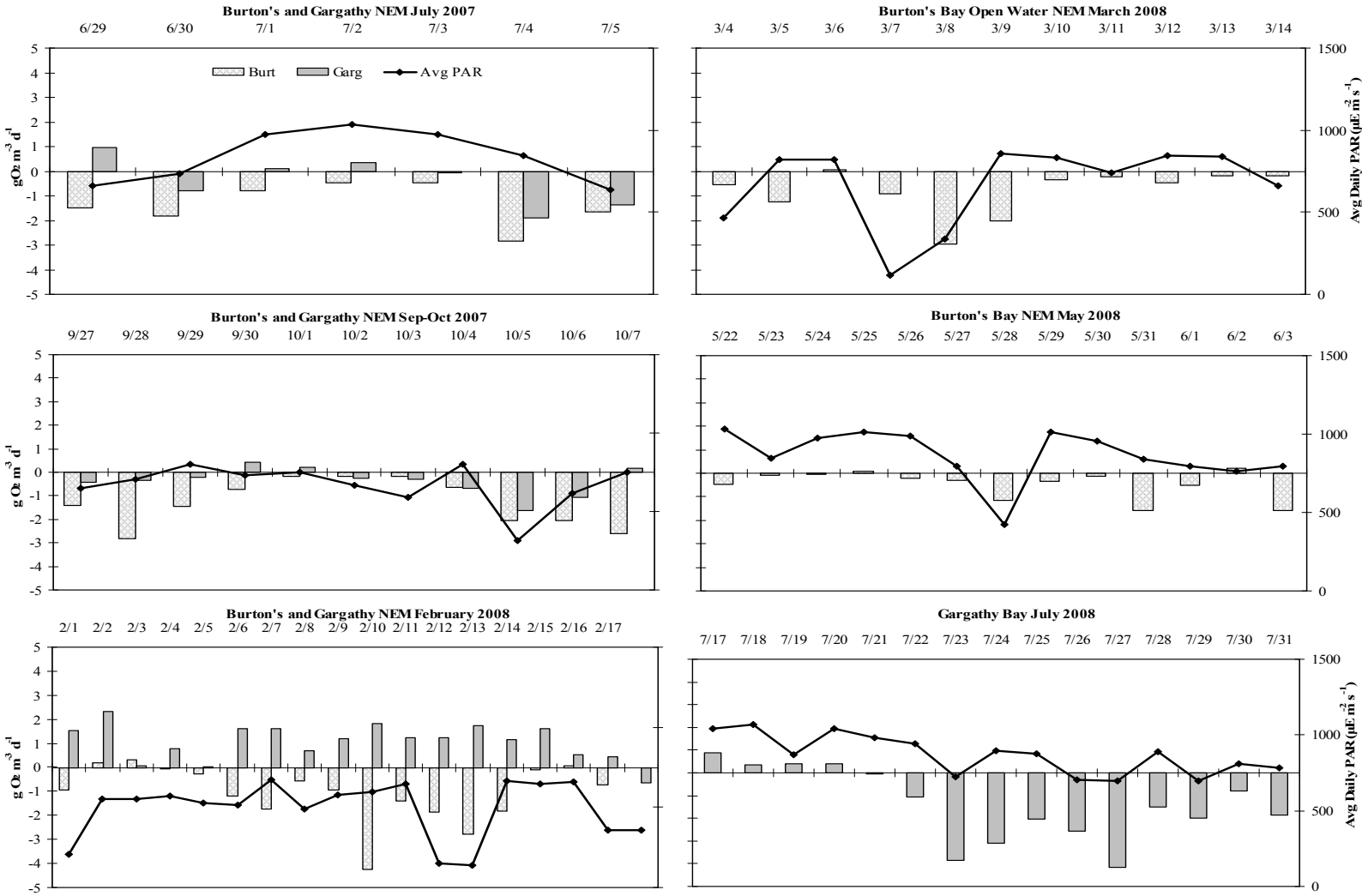

Figure 9. Open water metabolism measurements in Burton's and Gargathy Bays. Dates with measurements from both bays are displayed on the same graph. Sonde malfunction and damages in the field reduced measurements to one bay in March 2008, May 2008 and June 2008.

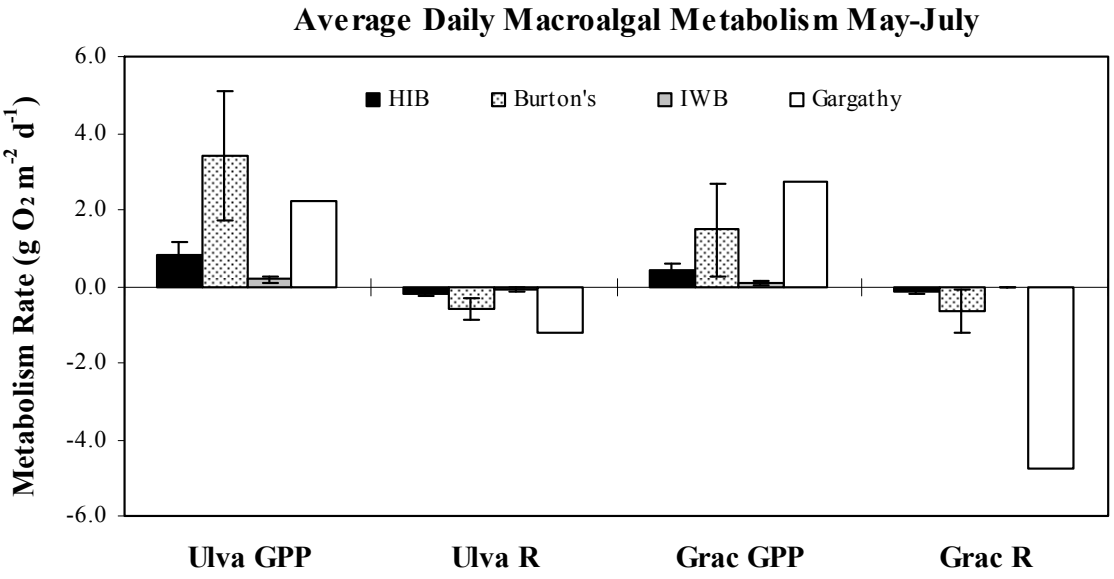

Figure 10. Average daily macroalgal metabolism for *Ulva* and *Graciliaria* for May through July 2008. Macroalgae GPP and R account for water column attenuation, self-shading within a mixed assemblage mat, and mat thickness.

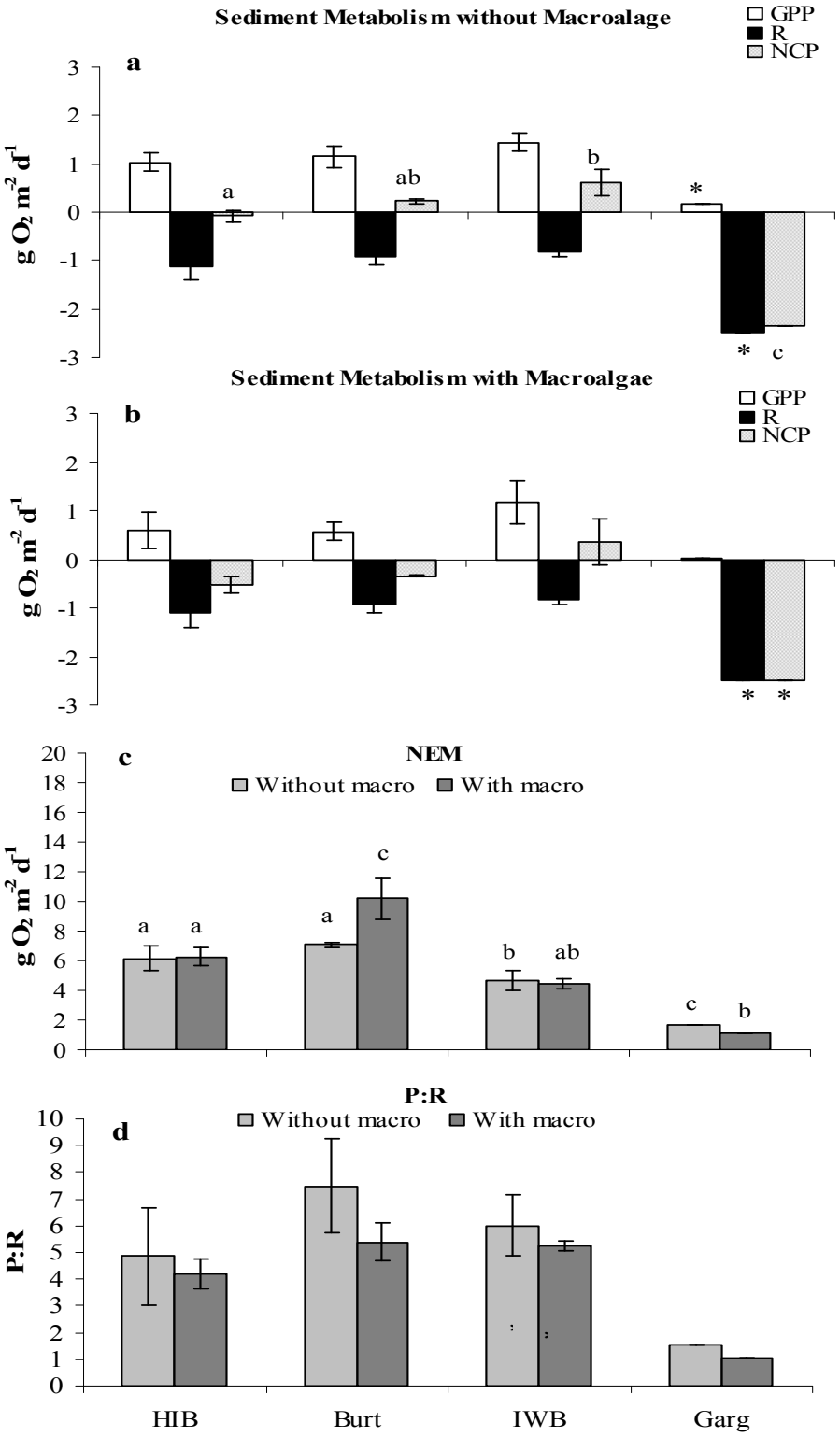

Figure 11. Average daily benthic and system metabolism for May through July 2008 (listed in order of increasing nutrient load). (a) Benthic metabolism without macroalgae; (b) benthic metabolism with macroalgae; (c) NEM; and (d) P:R. Error bars represent standard error (n=3; except Gargathy)

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CHAPTER 3: Conclusions

Land use along the Delmarva Peninsula follows a gradient from highly developed in DE to a combination of development and agriculture in MD to mainly rural agriculture and forested land in VA, resulting in variable nutrient loading rates to the adjacent coastal lagoons, although estimates are limited to only one system in VA. Using a modified watershed nutrient loading model (Valiela et *al.*, 1997; Cole, 2005), we quantified nitrogen loads to two additional VA systems to determine if the regional nutrient loading gradient extends from the upper Delmarva into VA. We adjusted the model to represent the VA watersheds we were studying, adding tomato plasticulture to the agricultural land use term and updating the crop fertilization and crop nitrogen content values. Using this model we found that despite rural land use, some VA lagoons receive annual nitrogen loads equivalent to the moderately enriched lagoons of MD and DE. Projection scenarios indicated that intensifying development within VA watersheds could result in annual nitrogen loads that would push VA lagoons towards the upper end of the Delmarva nutrient loading range.

Our study, focused on four Delmarva lagoons, found that water quality in the VA lagoons did not respond to nutrient enrichment in the same way as the MD lagoons (Boynton et *al.*, 1996). There was no evidence of increased water column chlorophyll with increasing nutrient load in the VA systems. Although we found a positive relationship between water column DIN and TDN concentrations with nutrient load, the relationship was only significant for TDN. Physical (e.g. increased flushing) or biological (e.g. elevated macroalgal or benthic microalgal biomass) factors may be responsible for the different response by the VA lagoons to nutrient enrichment.

Results of a nitrogen source tracking experiment in the four Delmarva lagoons explained more about the internal nitrogen cycling processes of the lagoons than the sources of nitrogen. Macroalgal $\delta^{15}N$ signatures in the VA lagoons were enriched relative to the potential nitrogen sources of atmospheric deposition and nitrogen fixation (~0‰), synthetic fertilizers (0-4 ‰ – Sharp, 2007), or poultry waste (~8 ‰ – Wassenaar, 1995). Because of minimal residential development and the absence of wastewater treatment plants in the VA watersheds, wastewater contributions to the annual loads were small. Thus, the enriched $\delta^{15}N$ signatures of the VA macroalgae were likely a result of the high degree of nitrogen recycling within the systems. In MD, the enriched $\delta^{15}N$ signatures (Jones et *al.*, 2004) could result from wastewater sources or recycling processes. Nitrogen source tracking confirmed the importance of coastal lagoons as transformers of anthropogenic nitrogen (Anderson et *al.*, 2001).

Water column, sediment, macroalgal, and net ecosystem metabolism (NEM) were measured in the four study lagoons using both component and open water methods to determine lagoon metabolic responses to increasing nutrient loads given the absence of clear responses by water quality parameters. Based on component method calculations, the water column was net autotrophic in all four lagoons, while the metabolic balance of the sediments differed. Sediments were slightly autotrophic to balanced in the least enriched systems, net autotrophic in the second most enriched system, and net heterotrophic in the most enriched lagoon. On a system scale, the four lagoons from March to October were net autotrophic. In the less enriched systems, there was no clear trend in NEM with nutrient load (D'Avanzo et *al.*, 1996; Caffrey, 2004), but the most enriched system demonstrated significantly reduced autotrophy. In summer 2008, the

lagoons were again net autotrophic and this is the best estimate of system metabolism as we included macroalgal metabolism in our calculations. Macroalgae did not greatly influence the metabolic balance of the lagoons, as summertime NEM was not greatly altered by the inclusion of macroalgal metabolism. However, system autotrophy increased with nutrient load, peaking at an intermediate load, then decreased in the two most enriched systems. Warmer average temperatures during the summer period relative to March to October may be driving the NEM patterns from May to July.

Though relationships between NEM and nutrient load existed, other factors, like light regime, primary producer biomass, sediment organics, and temperature complicated the relationship between NEM and nutrient load. Reduced autotrophy in the most enriched system was likely due to a combination of high vertical light attenuation, low benthic producer biomass, and high sediment organic content. Nutrient enrichment may stimulate primary production, but other physical and biological factors likely worked to mediate system response.

A comparison of open water and component methods for measuring NEM found different results with regard to the metabolic status of the lagoons, highlighting the importance of the underlying assumptions associated with each method. Net system metabolism as calculated by the open water method found mainly heterotrophy in the systems. The shallow lagoons of the VA/MD Eastern Shore are physically dynamic systems, which may have violated open-water method assumptions, biasing our *in situ* measurements of NEM. Bottle effects may have also biased component method NEM measurements, thus exacerbating the difference calculated by the two methods. Though we cannot determine the most appropriate method to use in shallow lagoon systems, we

find value in both methods as they operate on different temporal and spatial scales (Gazeau et *al.*, 2005) and contribute differently to the understanding of system metabolism.

Projections from the watershed NLM indicated that as land use shifts towards intensified development and agriculture, annual nitrogen loads to the VA lagoons will increase. Metabolic results from this study, including the influence of macroalgae, suggested that as loading increases the lagoons will become more autotrophic, but shift towards heterotrophy at high nutrient loads. Should annual nitrogen loads in VA lagoons reach or exceed that of the most enriched lagoon in our study we should expect to see reduced autotrophy and increased heterotrophy within the lagoons. Depending on the degree of heterotrophy, enriched lagoons could experience episodic hypoxia and anoxia, a change in nitrogen cycling processes and dominant primary producers, and ultimately a reduction in ecological function.

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APPENDIX I

Table 1. Nitrogen source tracking deployment locations and associated macroalgal signature. Two values in $\delta^{15}N$ column represents sample duplicate.

Bay	ID	Lat	Long	$\delta^{15}N$
Gargathy	A1	37° 46.21	75° 33.28	12.70
Gargathy	A2	37° 46.21	75° 33.28	11.49
Gargathy	B1	37° 45.91	75° 33.38	11.51
Gargathy	B2	37° 45.91	75° 33.38	11.65
Gargathy	C1	37° 46.71	75° 32.77	11.82
Gargathy	C2	37° 46.71	75° 32.77	12.54
Burton's	D1	37° 37.65	75° 40.66	12.00
Burton's	D2	37° 37.65	75° 40.66	11.86
Burton's	E1	37° 37.22	75° 40.27	12.90
Burton's	E2	37° 37.22	75° 40.27	12.52/12.39
Burton's	F1	37° 38.28	75° 39.23	13.69
Burton's	F2	37° 38.28	75° 39.23	14.59
Burton's	G1	37° 37.43	75° 38.56	13.01
Burton's	G2	37° 37.43	75° 38.56	13.24
Burton's	H1	37° 36.98	75° 37.67	13.71
Burton's	H2	37° 36.98	75° 37.67	13.56
Burton's	I1	37° 36.03	75° 38.23	Lost
Burton's	I2	37° 36.03	75° 38.23	Lost
Burton's	J1	37° 35.54	75° 37.61	13.58
Burton's	J2	37° 35.54	75° 37.61	14.71
Hog Island	K1	37° 28.75	75° 48.51	14.88
Hog Island	K2	37° 28.75	75° 48.51	12.92
Hog Island	L1	37° 28.43	75° 48.86	16.19
Hog Island	L2	37° 28.43	75° 48.86	14.88
Hog Island	M1	37° 37.73	75° 48.75	14.27
Hog Island	M2	37° 37.73	75° 48.75	13.99
Hog Island	N1	37° 27.65	75° 44.54	Lost
Hog Island	N2	37° 27.65	75° 44.54	Lost
Hog Island	O1	37° 26.23	75° 45.99	Lost
Hog Island	O2	37° 26.23	75° 45.99	Lost
Hog Island	P1	37° 23.83	75° 47.24	Lost
Hog Island	P2	37° 23.83	75° 47.24	Lost
Hog Island	Q1	37° 22.34	75° 43.83	17.02/16.92
Hog Island	Q2	37° 22.34	75° 43.83	Lost
Hog Island	R1	37° 22.32	75° 45.90	13.89
Hog Island	R2	37° 22.32	75° 45.90	11.76

Table 2. Gargathy Bay NLM sensitivity analysis- sensitivity analyses are conducted to determine changes in model results with incremental increases/decreases to various model parameters. Sensitivity analyses help identify the bias associated with parameter uncertainty.

Gargathy Bay Watershed Sensitivity Analysis

		N-Load	N-Load	N-Load	N-Load	N-Load
		5%	10%	25%	50%	100%
		Param Inc	Param Inc	Param Inc	Param Inc	Param Inc
Attenuation of Atmospheric Deposition:						
Natural vegetation attenuation	0.35	29,408	29,440	29,608	29,888	39,449
Plant attenuation, roof+driveway	0.38	29,328	29,328	29,328	29,328	29,328
Agric. plant attenuation	0.38	29404	29,480	29,709	30,090	30,851
Turf attenuation	0.38	29,330	29,332	29,337	29,345	29,362
Turf parameters:						
% lawns fertilized	0.34	29,337	29,345	29,371	29,414	29,499
Lawn fertilizer volatilization	0.39	29,322	29,317	29,301	29,273	29,219
Agricultural parameters:						
Poultry kg N per lifetime	0.054	29,328	29,328	29,328	29,328	29,328
Poultry waste % volatilization	0.50	29,328	29,328	29,328	29,328	29,328
Agric. Fertilizer volatilization	0.39	29,328	29,328	29,328	29,328	29,328
Tomato Dry:Wet Weight Ratio	0.055	29,323	29,318	29,303	29,277	29,226
Corn N content (kg N kg^{-1} dw)	0.0140	28,597	27,867	25,675	22,021	14,714
Soybean N content (kg N kg-1 dw)	0.0590	29,393	27,458	24,654	19,980	10,632
Tomato N content (kg N kg-1 dw)	0.0015	29,323	29,318	29,303	29,277	29,226
Groundwater parameters:						
ISDS leach field attenuation	0.40	29,373	29,418	29,554	29,779	30,230
Vadose zone attenuation	0.39	30,583	31,838	35,602	41,876	54,424
Aquifer attenation	0.65	30,628	31,928	35,828	42,327	55,327

Reran the param using 3,500,000 mill chicks- 32650 starting load						
Poultry kg N per lifetime	0.054	33,848	35,045	38,639	44,628	56,606
Poultry waste % volatilization	0.50	33,848	35,045	38,639	44,628	56,606

Table 3. Burton's Bay NLM sensitivity analysis

Burton's Bay Watershed Sensitivity Analysis

		N-Load 5% Param Inc	N-Load 10% Param Inc	N-Load 25% Param Inc	N-Load 50% Param Inc	N-Load 100% Param Inc
Attenuation of Atmospheric Deposition:						
Natural vegetation attenuation	0.35	81,052	81,223	81,650	82,418	83,869
Plant attenuation, roof+driveway	0.38	80,881	80,881	80,881	80,881	80,881
Agric. plant attenuation	0.38	81,010	81,138	81,524	82,102	83,322
Turf attenuation	0.38	80,888	80,895	80,916	80,947	81,013
Turf parameters:						
% lawns fertilized	0.34	80,920	80,937	81,054	81,360	81,533
Lawn fertilizer volatilization	0.39	80,860	80,839	80,774	80,668	80,465
Agricultural parameters:						
Poultry kg N per lifetime	0.054	80,881	80,881	80,881	80,881	80,881
Poultry waste % volatilization	0.50	80,881	80,881	80,881	80,881	80,881
Agric. Fertilizer volatilization	0.39	80,881	80,881	80,881	80,881	80,881
Tomato Dry:Wet Weight Ratio	0.055	80,867	80,853	80,815	80,749	80,622
Corn N content (kg N kg^{-1} dw)	0.0140	79,209	79,209	74,192	69,173	57,465
Soybean N content (kg N kg-1 dw)	0.0590	79,358	77,835	73,265	65,648	50,923
Tomato N content (kg N kg-1 dw)	0.0015	80,864	80,847	80,812	80,743	80,622
Groundwater parameters:						
ISDS leach field attenuation	0.40	80,998	81,115	81,466	82,051	83,220
Vadose zone attenuation	0.39	83,620	86,358	94,574	108,267	134,283
Aquifer attenation	0.65	83,454	86,884	94,602	109,180	136,622
Reran the param using 5,000,000 mill chicks						
Poultry kg N per lifetime	0.054	83,942	85,210	90,914	99,152	116,264
Poultry waste % volatilization	0.50	84,095	85,463	90,939	99,152	116,264

Table 4: Estimated population (0.6% annual) and housing unit increases (2% annual) and the associated potential increases in total nitrogen load, daily nitrogen load, and the contribution of wastewater to total nitrogen load.

WATERSHED POPULATION INCREASES

YEAR	POPULATION	HOUSING UNITS	LOADS (KG N Y^{-1})	DAILY N LOADING (MMOL M^{-2} D^{-1})	% WASTE-WATER NITROGEN
Burton's Bay Watershed					
2000	1874	868	80,560	0.265	2.9
2005	1,931	958	80,952	0.265	3.0
2010	1,990	1,058	81,026	0.266	3.1
2015	2,050	1,168	81,101	0.266	3.2
2020	2,112	1,290	81,178	0.266	3.3
2025	2,176	1,424	81,258	0.266	3.3
2030	2,242	1,572	81,341	0.267	3.4
Gargathy Bay Watershed					
2000	723	284	28,328	4.92	3.1
2005	747	314	29,358	4.92	3.2
2010	771	346	29,388	4.93	3.3
2015	797	382	29,420	4.93	3.4
2020	823	422	29,453	4.94	3.5
2025	850	466	29,486	4.94	3.6
2030	878	514	29,521	4.95	3.7

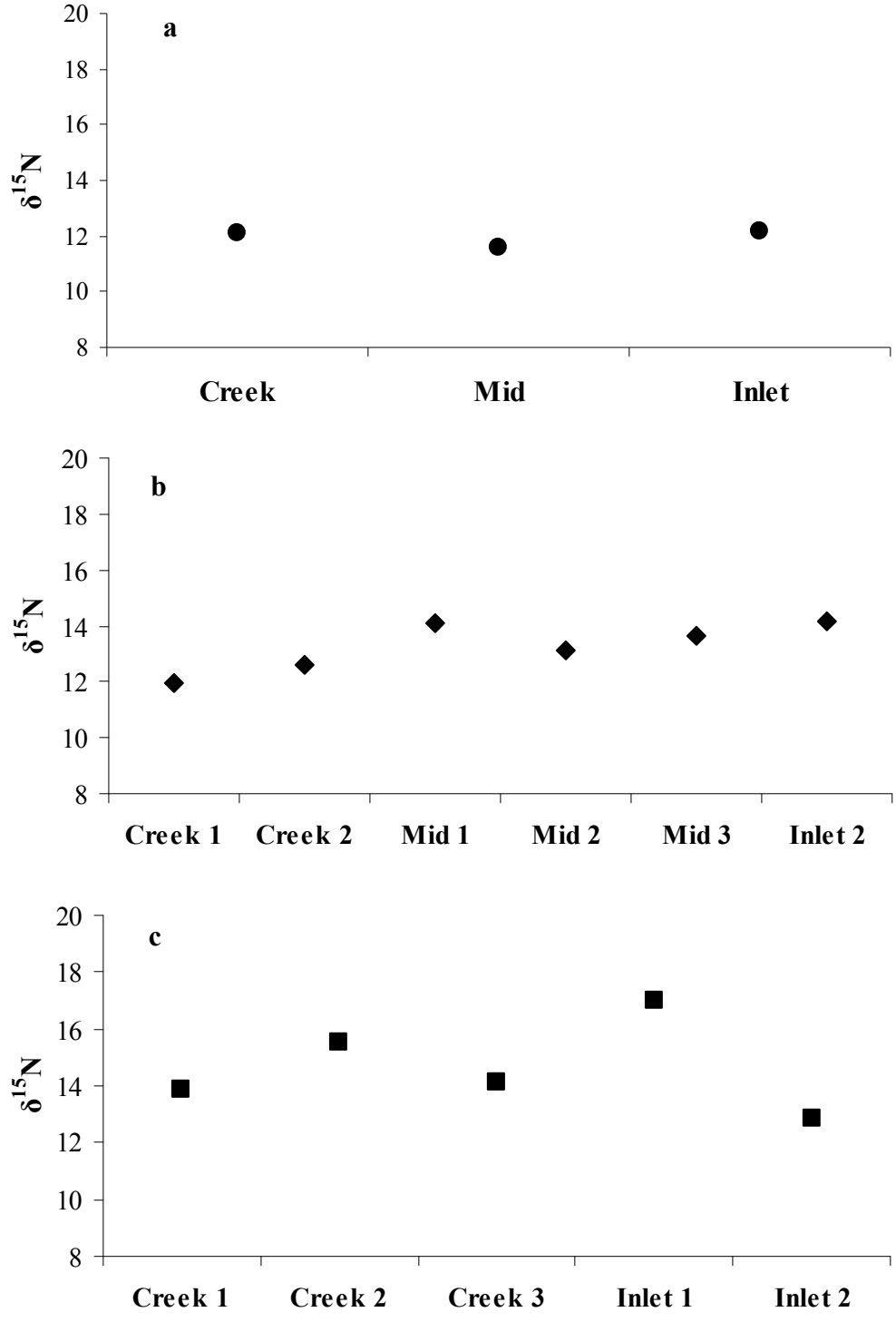

Figure 1. Macroalgal $\delta^{15}N$ values within each bay along creek to inlet transect, Gargathy (a); Burton's Bay (b)- first inlet sight samples lost; Hog Island Bay (c)- all mid-bay macroalgal samples lost. Deployments were done in duplicate and each site represents the average $\delta^{15}N$ signature.

APPENDIX II

Table 1. Location of study sites

Bay	Site	Latitude	Longitude
Hog Island Bay	Creek	37°27.81	75°48.61
Hog Island Bay	Mid	37°24.75	75°45.72
Hog Island Bay	Inlet	37°22.47	75°43.46
Isle of Wight Bay	Creek	38°23.68	75°06.85
Isle of Wight Bay	Mid	38°21.97	75°05.84
Isle of Wight Bay	Inlet	38°20.29	75°05.57
Burton's Bay	Creek	37°37.28	75°39.92
Burton's Bay	Mid	37°37.08	75°38.03
Burton's Bay	Inlet	37° 36.02	75° 37.79
Burton's Bay	YSI	37°37.16	75°38.00
Gargathy	Mid	37°46.01	75°33.55
Gargathy	YSI	37°46.24	75°33.32

Table 2. Equations defining photosynthesis-irradiance (P-I) curve models that we fit to water column and sediment production and respiration data measured in August 2007.

	Equation	Reference
1	$P = P_m\left(\frac{\alpha I}{P_m + \alpha I}\right) + R_d$	Baly (1935)
2	$P = P_m\left(\frac{e^{\alpha I(1+\varepsilon)/P_m} - 1}{e^{\alpha I(1+\varepsilon)/P_m} + \varepsilon}\right) + R_d$	Chalker et *al.* (1980)
3*	$P = P_m \tanh\left(\frac{\alpha I}{P_m}\right) + R_d$	**Jassby and Platt (1976)**
4	$P = P_m\left(\frac{I}{k_I + I}\right) + R_d$	Monod (1942)
5	$P = P_s\left(1 - e^{-\frac{\alpha I}{P_s}}\right)e^{-\frac{\beta I}{P_s}} + R_d$	Platt et *al.* (1980)
6	$P = P_m\left(\frac{\alpha I}{\sqrt{P_m^2 + (\alpha I)^2}}\right) + R_d$	Smith (1936); Talling (1957)
7	$P = \alpha I e^{-\left(\frac{\alpha I}{P_m e}\right)} + R_d$	Steel (1962)
8	$P = P_m\left(\frac{I}{\sqrt{I_k^2 + I^2}}\right) + R_d$	Tett (1989)
9	$P = P_m(1 - e^{-\left(\frac{\alpha I}{P_m}\right)}) + R_d$	Webb et *al.* (1974)
10	$P = P_m \tanh\left(\frac{\alpha(I - I_c)}{P_m}\right)$	Yoder (1979)

*Model used to estimate water column, sediment, and macroalgal metabolism.

Table 3. Information Theory Water Column PI Model Fits

Table 3a: Hog Island Bay Red Bank (Creek site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.2269	13	-39.6265	1.790863	0.408431	0.103741
Chalker et al 1980	0.1977	13	-35.846	0	1	0.253998
Jassby & Platt 1975	0.2147	13	-40.345	1.072383	0.584972	0.148582
Monod 1942	0.3056	13	-35.7556	5.661842	0.058959	0.014975
Platt et *al.* 1980	0.289	13	-30.9102	4.935787	0.084763	0.02153
Smith 1936; Talling 1957	0.219	13	-40.0872	1.330173	0.514229	0.130613
Steel 1962	0.2446	13	-38.65	2.767355	0.250655	0.063666
Tett 1989	0.219	13	-40.0872	1.330173	0.514229	0.130613
Webb et *al.* 1974	0.219	13	-40.0872	1.330173	0.514229	0.130613
Yoder 1979	0.4283	13	-31.3674	10.04995	0.006572	0.001669

Table 3b: Hog Island Bay Shoal East (Mid site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.0416	13	-61.6799	2.699312	0.259329	0.047201
Chalker et *al.* 1980	0.0338	13	-58.8077	5.571429	0.061685	0.011227
Jassby & Platt 1975	0.0346	13	-64.0751	0.304107	0.858942	0.156339
Monod 1942	0.0416	13	-61.6799	2.699312	0.259329	0.047201
Platt et *al.* 1980	0.0368	13	-57.7023	6.67691	0.035492	0.00646
Smith 1936; Talling 1957	0.0359	13	-63.5956	0.783594	0.675841	0.123012
Steel 1962	0.0368	13	-63.2737	1.105482	0.575371	0.104725
Tett 1989	0.0338	13	-64.3792	0	1	0.182013
Webb et *al.* 1974	0.0338	13	-64.3792	0	1	0.182013
Yoder 1979	0.0352	13	-63.8516	0.527609	0.768124	0.139809

Table 3c: Hog Island Bay Machipongo Inlet (Inlet site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.00308	13	-95.5211	3.739867	0.154134	0.044526
Chalker et *al.* 1980	0.00257	13	-92.303	6.957987	0.030838	0.008909
Jassby & Platt 1975	0.00257	13	-97.8744	1.386559	0.499934	0.144421
Monod 1942	0.00308	13	-95.5211	3.739867	0.154134	0.044526
Platt et *al.* 1980	0.0282	13	-61.1625	38.0984	5.33E-09	1.54E-09
Smith 1936; Talling 1957	0.0027	13	-97.2329	2.028055	0.362755	0.104793
Steel 1962	0.00231	13	-99.2609	0	1	0.28888
Tett 1989	0.0027	13	-97.2329	2.028055	0.362755	0.104793
Webb et *al.* 1974	0.00265	13	-97.4759	1.785058	0.409619	0.118331
Yoder 1979	0.00258	13	-97.8239	1.437044	0.487472	0.140821

Table 3d: Isle of Wight Bay West Cape (Creek site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.0581	13	-57.337	0	1	0.158898
Chalker et *al.* 1980	0.0561	13	-52.221	5.116041	0.077458	0.012308
Jassby & Platt 1975	0.0581	13	-57.337	0	1	0.158898

Monod 1942	0.0689	13	-55.1206	2.216377	0.330157	0.052461
Platt et *al.* 1980	0.0406	13	-56.4247	0.91226	0.633732	0.100699
Smith 1936; Talling 1957	0.0689	13	-55.1206	2.216377	0.330157	0.052461
Steel 1962	0.0689	13	-55.1206	2.216377	0.330157	0.052461
Tett 1989	0.0585	13	-57.2478	0.089194	0.956383	0.151968
Webb et *al.* 1974	0.0623	13	-56.4297	0.907345	0.635291	0.100947
Yoder 1979	0.0581	13	-57.337	0	1	0.158898

Table 3e: Isle of Wight Mid Bay (Mid site)

Model	RSS	n	AIC_c	Δi	L	w_i
Baly 1935	0.0105	13	-79.5773	2.489584	0.288001	0.03985
Chalker et *al.* 1980	0.00728	13	-78.767	3.299835	0.192066	0.026576
Jassby & Platt 1975	0.00867	13	-82.0669	0	1	0.138369
Monod 1942	0.00873	13	-81.9772	0.089656	0.956162	0.132303
Platt et *al.* 1980	0.0097	13	-75.0361	7.030771	0.029736	0.004115
Smith 1936; Talling 1957	0.00876	13	-81.9326	0.134252	0.935077	0.129386
Steel 1962	0.00872	13	-81.9921	0.074756	0.963312	0.133293
Tett 1989	0.00868	13	-82.0519	0.014986	0.992535	0.137336
Webb et *al.* 1974	0.00876	13	-81.9326	0.134252	0.935077	0.129386
Yoder 1979	0.00876	13	-81.9326	0.134252	0.935077	0.129386

Table 3f: Isle of Wight Bay Route 50-Bridge (Inlet site)

Model	RSS	n	AIC_c	Δi	L	w_i
Baly 1935	0.00824	13	-82.7282	0.400525	0.818516	0.112738
Chalker et *al.* 1980	0.0081	13	-77.3795	5.749181	0.056439	0.007774
Jassby & Platt 1975	0.00813	13	-82.9029	0.225812	0.893235	0.123029
Monod 1942	0.00824	13	-82.7282	0.400525	0.818516	0.112738
Platt et *al.* 1980	0.0184	13	-66.7132	16.41551	0.000273	$3.75 * 10^{-5}$
Smith 1936; Talling 1957	0.00799	13	-83.1287	0	1	0.137734
Steel 1962	0.00817	13	-82.8391	0.289616	0.865188	0.119166
Tett 1989	0.00799	13	-83.1287	0	1	0.137734
Webb et *al.* 1974	0.0081	13	-82.9509	0.177753	0.914959	0.126021
Yoder 1979	0.00813	13	-82.9029	0.225812	0.893235	0.123029

Table 3g: Burton's Bay Worm Flat (Creek site)

Model	RSS	n	AIC_c	Δi	L	w_i
Baly 1935	0.0265	13	-67.5423	0.914439	0.633041	0.179217
Chalker et *al.* 1980	0.0561	13	-52.221	16.23575	0.000298	$8.44 * 10^{-5}$
Jassby & Platt 1975	0.0337	13	-64.4177	4.03903	0.13272	0.037574
Monod 1942	0.0265	13	-67.5423	0.914439	0.633041	0.179217
Platt et *al.* 1980	0.0476	13	-54.3569	14.09981	0.000867	0.000246
Smith 1936; Talling 1957	0.0276	13	-67.0136	1.443163	0.485983	0.137584
Steel 1962	0.0476	13	-59.9283	8.528384	0.014063	0.003981
Tett 1989	0.0276	13	-67.0136	1.443163	0.485983	0.137584
Webb et *al.* 1974	0.0247	13	-68.4567	0	1	0.283105
Yoder 1979	0.0332	13	-64.612	3.844706	0.146262	0.041408

Table 3h: Burton's Bay Mid Bay						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.0328	13	-64.7696	13.99744	0.000913	0.000907
Chalker et *al.* 1980	0.00728	13	-78.767	0	1	0.993104
Jassby & Platt 1975	0.0338	13	-64.3792	14.38786	0.000751	0.000746
Monod 1942	0.0328	13	-64.7696	13.99744	0.000913	0.000907
Platt et *al.* 1980	0.1148	13	-42.9122	35.85479	1.64E-08	$1.63 *10^{-8}$
Smith 1936; Talling 1957	0.0313	13	-65.3781	13.38891	0.001238	0.001229
Steel 1962	0.1148	13	-48.4837	30.28336	2.65E-07	$2.64 *10^{-7}$
Tett 1989	0.0313	13	-65.3781	13.38891	0.001238	0.001229
Webb et *al.* 1974	0.0317	13	-65.213	13.55399	0.00114	0.001132
Yoder 1979	0.0338	13	-64.3792	14.38786	0.000751	0.000746

Table 3i: Burton's Bay Inlet						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.0139	13	-75.9306	12.4854	0.001945	0.00077
Chalker et *al.* 1980	0.0081	13	-77.3795	11.03651	0.004013	0.00159
Jasby & Platt 1975	0.00532	13	-88.416	0	1	0.39601
Monod 1942	0.0139	13	-75.9306	12.4854	0.001945	0.00077
Platt et *al.* 1980	0.023	13	-63.8123	24.6037	4.54E-06	0.00000
Smith 1936; Talling 1957	0.00736	13	-84.1964	4.219626	0.121261	0.04802
Steel 1962	0.023	13	-69.3837	19.03227	7.37E-05	0.00003
Tett 1989	0.00736	13	-84.1964	4.219626	0.121261	0.04802
Webb et *al.* 1974	0.00649	13	-85.8317	2.58426	0.274685	0.10878
Yoder 1979	0.00532	13	-88.416	0	1	0.39601

Table 3j: Gargathy Bay (Mid site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.0385	13	-62.6866	0	1	0.222102
Chalker et *al.* 1980	0.0384	13	-57.149	5.537618	0.062737	0.013934
Jasby & Platt 1975	0.0474	13	-59.9831	2.703532	0.258783	0.057476
Monod 1942	0.0385	13	-62.6866	0	1	0.222102
Platt et *al.* 1980	0.0413	13	-56.2025	6.484084	0.039084	0.008681
Smith 1936; Talling 1957	0.0441	13	-60.9212	1.76542	0.41366	0.091875
Steel 1962	0.0429	13	-61.2798	1.406777	0.494906	0.10992
Tett 1989	0.0441	13	-60.9212	1.76542	0.41366	0.091875
Webb et *al.* 1974	0.0423	13	-61.4629	1.223675	0.542353	0.120458
Yoder 1979	0.0469	13	-60.1209	2.565673	0.27725	0.061578

Table 4. Information Theory Sediment PI Model Fits

Table 4a: Hog Island Bay Red Bank (Creek site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	8.0467	13	2.430732	1.474998	0.478309	0.080954
Chalker et *al.* 1980	7.5657	13	5.962782	5.007048	0.081796	0.013844
Jasby & Platt 1975	7.3769	13	1.30092	0.345187	0.84148	0.142422
Monod 1942	8.0467	13	2.430732	1.474998	0.478309	0.080954
Platt et *al.* 1980	7.0053	13	4.962329	4.006596	0.13489	0.02283
Smith 1936; Talling 1957	7.6845	13	1.831994	0.876261	0.645242	0.109208
Steel 1962	7.1836	13	0.955733	0	1	0.169251
Tett 1989	7.6845	13	1.831994	0.876261	0.645242	0.109208
Webb et *al.* 1974	7.5657	13	1.629448	0.673715	0.714011	0.120847
Yoder 1979	7.3147	13	1.190843	0.23511	0.889092	0.15048

Table 4b: Hog Island Bay Shoal East (Mid site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	1.6892	13	-17.8624	0.680916	0.711444	0.105475
Chalker et *al.* 1980	1.6466	13	-13.8611	4.682197	0.096222	0.014265
Jasby & Platt 1975	1.6141	13	-18.4536	0.089708	0.956137	0.141751
Monod 1942	1.6892	13	-17.8624	0.680916	0.711444	0.105475
Platt et *al.* 1980	1.7379	13	-13.1595	5.383741	0.067754	0.010045
Smith 1936; Talling 1957	1.6333	13	-18.2998	0.243433	0.885399	0.131264
Steel 1962	1.7379	13	-17.4929	1.050408	0.591435	0.087683
Tett 1989	1.6333	13	-18.2998	0.243433	0.885399	0.131264
Webb et *al.* 1974	1.6466	13	-18.1944	0.348864	0.839934	0.124524
Yoder 1979	1.603	13	-18.5433	0	1	0.148254

Table 4c: Hog Island Bay Machipongo Inlet (Inlet site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	3.4052	13	-8.74873	0	1	0.163048
Chalker et *al.* 1980	6.5449	13	4.078578	12.82731	0.001639	0.000267
Jasby & Platt 1975	3.4052	13	-8.74873	0	1	0.163048
Monod 1942	3.4052	13	-8.74873	0	1	0.163048
Platt et *al.* 1980	3.4618	13	-4.20109	4.547638	0.102918	0.016781
Smith 1936; Talling 1957	3.4052	13	-8.74873	0	1	0.163048
Steel 1962	3.4052	13	-8.74873	0	1	0.163048
Tett 1989	3.4052	13	-8.74873	0	1	0.163048
Webb et *al.* 1974	6.5449	13	-0.25476	8.493972	0.014307	0.002333
Yoder 1979	6.5449	13	-0.25476	8.493972	0.014307	0.002333

Table 4d: Isle of Wight Bay West Cape (Creek site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	1.852	13	-16.6662	0	1	0.171974
Chalker et *al.* 1980	1.846	13	-12.3751	4.291148	0.117001	0.020121

Jasby & Platt 1975	2.0231	13	-15.5175	1.148743	0.563059	0.096831
Monod 1942	1.852	13	-16.6662	0	1	0.171974
Platt et *al.* 1980	3.2892	13	-4.86596	11.80025	0.002739	0.000471
Smith 1936; Talling 1957	1.8817	13	-16.4594	0.206823	0.901756	0.155078
Steel 1962	3.2892	13	-9.1993	7.466917	0.02391	0.004112
Tett 1989	1.8817	13	-16.4594	0.206823	0.901756	0.155078
Webb et *al.* 1974	1.9046	13	-16.3021	0.364076	0.833569	0.143352
Yoder 1979	2.0794	13	-15.1606	1.505572	0.471052	0.081009

Table 4e: Isle of Wight Bay Mid Bay

Model	RSS	n	AIC_c	Δi	L	w_i
Baly 1935	5.0113	13	-3.72564	8.443681	0.014672	0.006303
Chalker et *al.* 1980	2.1239	13	-10.552	1.617277	0.445464	0.191359
Jasby & Platt 1975	3.3358	13	-9.01641	3.152904	0.206707	0.088795
Monod 1942	5.0113	13	-3.72564	8.443681	0.014672	0.006303
Platt et *al.* 1980	2.6174	13	-7.83598	4.333333	0.114559	0.049211
Smith 1936; Talling 1957	3.8689	13	-7.08906	5.080254	0.078856	0.033874
Steel 1962	2.6174	13	-12.1693	0	1	0.429571
Tett 1989	3.8689	13	-7.08906	5.080254	0.078856	0.033874
Webb et *al.* 1974	3.9811	13	-6.71742	5.451897	0.065484	0.02813
Yoder 1979	3.1363	13	-9.81811	2.35121	0.308632	0.13258

Table 4f: Isle of Wight Bay Route 50-Bridge (Inlet site)

Model	RSS	n	AIC_c	Δi	L	w_i
Baly 1935	26.382	13	17.86719	1.643793	0.439597	0.081748
Chalker et *al.* 1980	24.2683	13	21.11488	4.891484	0.086662	0.016116
Jasby & Platt 1975	23.5063	13	16.36682	0.143418	0.930802	0.173094
Monod 1942	26.382	13	17.86719	1.643793	0.439597	0.081748
Platt et *al.*. 1980	21.6918	13	19.6558	3.432407	0.179747	0.033426
Smith 1936; Talling 1957	24.9478	13	17.14054	0.917141	0.632187	0.117563
Steel 1962	28.2749	13	18.76799	2.544596	0.280187	0.052104
Tett 1989	24.9478	13	17.14054	0.917141	0.632187	0.117563
Webb et *al.* 1974	24.2683	13	16.78155	0.558151	0.756483	0.140677
Yoder 1979	23.2484	13	16.2234	0	1	0.185962

Table 4g: Burton's Bay Worm Flat (Creek site)

Model	RSS	n	AIC_c	Δi	L	w_i
Baly 1935	0.7404	13	-28.585	3.658186	0.160559	0.025785
Chalker et *al.* 1980	0.5673	13	-27.7136	4.52959	0.103851	0.016678
Jasby & Platt 1975	0.5588	13	-32.2432	0	1	0.160594
Monod 1942	0.5685	13	-32.0195	0.223726	0.894167	0.143598
Platt et *al.* 1980	0.5807	13	-27.4101	4.833088	0.089229	0.01433
Smith 1936; Talling 1957	0.5591	13	-32.2362	0.006977	0.996517	0.160035
Steel 1962	0.5807	13	-31.7434	0.499754	0.778896	0.125086
Tett 1989	0.5591	13	-32.2362	0.006977	0.996517	0.160035
Webb et *al.* 1974	0.5673	13	-32.0469	0.196256	0.906533	0.145584

Yoder 1979	0.6723	13	-29.8393	2.40387	0.300612	0.048276

Table 4h: Burton's Bay Mid Bay						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.5663	13	-32.0699	2.677257	0.262205	0.080368
Chalker et *al.* 1980	0.5318	13	-28.5537	6.193456	0.045197	0.013853
Jasby & Platt 1975	0.5324	13	-32.8724	1.874782	0.391648	0.120043
Monod 1942	0.5446	13	-32.5778	2.169316	0.338017	0.103605
Platt et *al.* 1980	0.4609	13	-30.4138	4.333333	0.114559	0.035113
Smith 1936; Talling 1957	0.5401	13	-32.6857	2.061452	0.356748	0.109346
Steel 1962	0.4609	13	-34.7471	0	1	0.306507
Tett 1989	0.5401	13	-32.6857	2.061452	0.356748	0.109346
Webb et *al.* 1974	0.5319	13	-32.8846	1.862567	0.394048	0.120778
Yoder 1979	1.1049	13	-23.3809	11.36628	0.003403	0.001043

Table 4i: Burton's Bay Inlet						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	3.1302	13	-9.84342	3.120013	0.210135	0.060492
Chalker et *al.* 1980	2.5604	13	-8.12222	4.841212	0.088868	0.025582
Jasby & Platt 1975	2.8304	13	-11.1522	1.811188	0.404302	0.116387
Monod 1942	3.1302	13	-9.84342	3.120013	0.210135	0.060492
Platt et *al.* 1980	2.4623	13	-8.6301	4.333333	0.114559	0.032978
Smith 1936; Talling 1957	2.9345	13	-10.6827	2.280736	0.319701	0.092033
Steel 1962	2.4623	13	-12.9634	0	1	0.287871
Tett 1989	2.9345	13	-10.6827	2.280736	0.319701	0.092033
Webb et *al.* 1974	2.9194	13	-10.7498	2.213669	0.330604	0.095171
Yoder 1979	2.7604	13	-11.4778	1.485636	0.475771	0.136961

Table 4j: Gargathy Bay (Mid site)						
Model	**RSS**	**n**	**AIC_c**	**Δi**	**L**	**w_i**
Baly 1935	0.0385	13	-67.0199	0	1	0.238179
Chalker et *al.* 1980	0.7243	13	-24.5375	42.48245	$5.96*10^{-10}$	$1.42*10^{-10}$
Jasby & Platt 1975	1.0208	13	-24.41	42.60989	$5.59*10^{-10}$	$1.33*10^{-10}$
Monod 1942	0.0385	13	-67.0199	0	1	0.238179
Platt et *al.* 1980	0.0429	13	-61.2798	5.74011	0.056696	0.013504
Smith 1936; Talling 1957	0.0441	13	-65.2545	1.76542	0.41366	0.098525
Steel 1962	0.0429	13	-65.6132	1.406777	0.494906	0.117876
Tett 1989	0.0441	13	-65.2545	1.76542	0.41366	0.098525
Webb et *al.* 1974	0.0423	13	-65.7963	1.223675	0.542353	0.129177
Yoder 1979	0.0469	13	-64.4543	2.565673	0.27725	0.066035

APPENDIX III

Table 1. $\delta^{15}N$ values for deployment sites in the three VA lagoons.

Bay	Site- Cup #	$\delta^{15}N$
Gargathy	A-1	12.70
Gargathy	A-2	11.49
Gargathy	B-1	11.51
Gargathy	B-2	11.65
Gargathy	C-1	11.82
Gargathy	C-2	12.54
Burton's Bay	D-1	12.00
Burton's Bay	D-2	11.86
Burton's Bay	E-1	12.90
Burton's Bay	E-2	12.52
Burton's Bay	E-2*	12.39
Burton's Bay	F-1	13.62
Burton's Bay	F-2	14.59
Burton's Bay	G-1	13.01
Burton's Bay	G-2	13.24
Burton's Bay	H-1	13.71
Burton's Bay	H-2	13.56
Burton's Bay	I-1	Lost
Burton's Bay	I-2	Lost
Burton's Bay	J-1	13.58
Burton's Bay	J-2	14.71
Hog Island Bay	K-1	14.88
Hog Island Bay	K-2	12.92
Hog Island Bay	L-1	16.19
Hog Island Bay	L-2	14.88
Hog Island Bay	M-1	14.27
Hog Island Bay	M-2	13.99
Hog Island Bay	N-1	Lost
Hog Island Bay	N-2	Lost
Hog Island Bay	O-1	Lost
Hog Island Bay	O-2	Lost
Hog Island Bay	P-1	Lost
Hog Island Bay	P-2	Lost
Hog Island Bay	Q-1	17.02
Hog Island Bay	Q-1*	16.92
Hog Island Bay	Q-2	Lost
Hog Island Bay	R-1	13.89
Hog Island Bay	R-2	11.76

*Duplicate sample

Table 2. Nutrient loading model residential build-out scenario increasing residential populations in Burton's Bay and Gargathy Bay watersheds. Population increases based off growth estimates from Accomack County Comprehensive Plan.

	Burton's Bay Watershed		Gargathy Bay Watershed	
Year	Population	Load (mmol N m^{-2} d^{-1})	Population	Load (mmol N m^{-2} d^{-1})
2000	1874	0.264	723	0.207
2001	1885	0.264	728	0.207
2002	1897	0.264	732	0.207
2003	1908	0.264	737	0.207
2004	1919	0.264	742	0.207
2005	1931	0.264	747	0.207
2006	1942	0.264	752	0.207
2007	1954	0.264	757	0.207
2008	1966	0.265	761	0.207
2009	1978	0.265	766	0.207
2010	1990	0.265	771	0.207
2011	2001	0.265	776	0.207
2012	2013	0.265	781	0.207
2013	2026	0.265	787	0.207
2014	2038	0.265	792	0.208
2015	2050	0.265	797	0.208
2016	2062	0.265	802	0.208
2017	2075	0.265	807	0.208
2018	2087	0.265	812	0.208
2019	2100	0.265	818	0.208
2020	2112	0.265	823	0.208
2021	2125	0.265	828	0.208
2022	2138	0.265	834	0.208
2023	2150	0.265	839	0.208
2024	2163	0.265	845	0.208
2025	2176	0.265	850	0.208
2026	2189	0.265	856	0.208
2027	2202	0.265	861	0.208
2028	2216	0.266	867	0.208
2029	2229	0.266	872	0.208
2030	2242	0.266	878	0.208

Table 3. Nutrient loading model residential build-out scenarios increasing residential populations and accounting for the associated land-use changes in Burton's Bay and Gargathy Bay watersheds. Conversion scenarios high-, moderate-, low- refer to the different land-use conversions for creating residential area (i.e. converting current agriculture or natural vegetation area into residential area). Lot size refers to the area of a single residential plot used in the model to represent different development densities. Areal load is relative to water body area.

	Burton's Bay Watershed			**Gargathy Bay Watershed**		
Conversion Scenario	Lot Size (acre)	Load (kg N y^{-1})	Areal Load (kg N m^{-2} y^{-1})	Lot Size (acre)	Load (kg N y^{-1})	Areal Load (kg N m^{-2} y^{-1})
High-Impact	¼	188000	10	¼	62000	53
	½	135000	7	½	45100	39
	¾	117000	6	¾	39500	34
	1	108000	6	1	36700	31
	5	87100	5	5	29900	26
	10	84500	5	10	29100	25
Moderate-Impact	¼	148000	8	¼	61200	52
	½	109000	6	½	42200	36
	¾	95700	5	¾	35900	31
	1	89200	5	1	32700	28
	5	73400	4	5	25100	22
	10	71400	4	10	24100	21
Low-Impact	¼	124000	7	¼	48200	41
	½	79300	4	½	27100	23
	¾	64300	4	¾	20000	17
	1	56800	3	1	16500	14
	5	38800	2	5	8050	7
	10	36600	2	10	7000	6

Table 4. Nutrient loading model agricultural build-out scenario increasing chicken populations in Burton's Bay and Gargathy Bay watersheds. Number of chickens represents the number of chickens in the watershed annually. Watershed export is the amount of nitrogen exported per square meter of watershed area.

	Burton's Bay Watershed		**Gargathy Bay Watershed**	
Number of Chickens	Number of Poultry Houses	Watershed N Export (mmol m^{-2} d^{-1})	Number of Poultry Houses	Watershed N Export (mmol m^{-2} d^{-1})
3,000,000	9	*	21	0.211
3,500,000	9	*	23	0.230
4,000,000	9	*	27	0.255
4,500,000	9	*	30	0.279
5,000,000	33	0.269	33	0.303
5,500,000	37	0.280	37	0.327
6,000,000	40	0.291	40	0.351
6,500,000	43	0.303	43	0.375
7,000,000	47	0.314	47	0.399
7,500,000	50	0.325	50	0.424
8,000,000	53	0.336	53	0.448
8,500,000	57	0.348	57	0.472
9,000,000	60	0.359	60	0.496
9,500,000	63	0.370	63	0.520
10,000,000	67	0.381	67	0.544
10,500,000	70	0.392	70	0.568
11,000,000	73	0.404	73	0.593
11,500,000	77	0.415	77	0.617
12,000,000	80	0.426	80	0.641
12,500,000	83	0.437	83	0.665
13,000,000	87	0.449	87	0.689
13,500,000	90	0.460	90	0.713
14,000,000	93	0.471	93	0.737
14,500,000	97	0.482	97	0.762
15,000,000	100	0.493	100	0.786
15,500,000	103	0.505	103	0.810
16,000,000	107	0.516	107	0.834
16,500,000	110	0.527	110	0.858
17,000,000	113	0.538	113	0.882
17,500,000	117	0.550	117	0.906
18,000,000	120	0.561	120	0.931
18,500,000	123	0.572	123	0.955
19,000,000	127	0.583	127	0.979
19,500,000	130	0.594	130	1.003
20,000,000	133	0.606	133	1.027

***** Model did not detect additional nitrogen from chickens at this density of birds.

Table 5. Nutrient loading model residential build-out scenario increasing the areal extent of tomato plasticulture in Burton's Bay and Gargathy Bay watersheds.

Burton's Bay Watershed			Gargathy Bay Watershed		
Tomato Area (m-2)	Load (kg N y^{-1})	Watershed N Export (mmol m^{-2} d^{-1})	Tomato area (m^2)	Load (kg N y^{-1})	Watershed N Export (mmol m^{-2} d^{-1})
2,760,000	80600	0.264	1,100,000	29300	0.207
3,760,000	91000	0.298	1,600,000	34700	0.245
4,760,000	101400	0.333	2,100,000	39900	0.282
5,760,000	112000	0.367	2,600,000	45100	0.318
6,760,000	122000	0.401	3,100,000	50300	0.355
7,760,000	133000	0.435	3,600,000	55600	0.392
8,760,000	143000	0.470	4,100,000	60800	0.429
9,760,000	154000	0.504	4,600,000	66000	0.466
10,760,000	164000	0.538	5,100,000	71200	0.503
11,760,000	175000	0.572	5,600,000	76500	0.539
12,760,000	185000	0.607	6,100,000	81700	0.576
13,760,000	195000	0.641	6,600,000	87000	0.613
14,760,000	206000	0.675	7,100,000	92100	0.650
15,760,000	216000	0.709	7,600,000	97400	0.687
16,760,000	227000	0.744	8,100,000	103000	0.724
17,760,000	237000	0.778	8,600,000	108000	0.761
18,760,000	248000	0.813	9,100,000	113000	0.797
19,760,000	260000	0.852	9,600,000	118000	0.834
20,760,000	272000	0.892	10,100,000	123000	0.871
21,760,000	284000	0.931	10,600,000	129000	0.908
22,760,000	296000	0.970	11,100,000	134000	0.945
23,760,000	308000	1.01	11,600,000	139000	0.984
24,680,000	319000	1.05	12,100,000	145000	1.03
			12,600,000	151000	1.07
			13,100,000	157000	1.11
			13,600,000	163000	1.15
			14,100,000	169000	1.19
			14,600,000	175000	1.24
			14,800,000	177000	1.25

Table 6. Average monthly water column concentrations (mg m^{-3}) measured at each site in each bay. Values in parentheses are ± 1 standard deviation (n=3).

Bay	Site	Jul-2007	Aug-2007	Sept-2007	Oct-2007	Jan-2008	Mar-2008	May-2008	Jun-2008	Jul-2008
Hog Island Bay, VA	Creek	7.60 (0.39)	8.40 (1.27)	3.33 (0.35)	2.37 (0.24)	3.16 (0.15)	2.62 (0.05)	2.53 (0.09)	4.99 (0.20)	28.38 (2.24)
	Mid	8.19 (0.38)	27.33 (0.79)	6.76 (1.39)	2.58 (0.48)	3.98 (0.45)	3.00 (0.35)	1.84 (0.12)	7.33 (1.24)	21.60 (4.51)
	Inlet	7.06 (0.43)	9.75 (0.72)	5.70 (0.21)	3.94 (0.37)	3.80 (0.26)	3.41 (0.77)	1.98 (0.30)	7.43 (0.89)	12.80 (1.23)
Isle of Wight Bay, MD	Creek	13.87 (0.32)	15.82 (2.32)	4.41 (4.41)	---	---	3.55 (0.72)	9.57 (2.32)	---	11.26 (0.58)
	Mid	10.77 (0.75)	13.40 (2.21)	12.09 (4.38)	---	---	3.74 (0.13)	2.40 (0.07)	---	3.41 (0.39)
	Inlet	4.28 (0.33)	7.14 (4.31)	8.22 (0.76)	---	---	2.59 (0.64)	1.97 (0.22)	---	1.69 (0.21)
Burton's Bay, VA	Creek	16.98 (0.90)	32.22 (0.71)	8.81 (0.36)	2.58 (0.24)	6.04 (0.37)	17.92 (2.12)	6.39 (0.34)	11.14 (0.32)	11.46 (0.55)
	Mid	14.61 (0.95)	26.23 (0.18)	7.72 (0.13)	2.12 (0.13)	7.16 (0.24)	2.12 (0.15)	2.48 (0.24)	10.88 (0.74)	17.87 (0.90)
	Inlet	12.40 (0.51)	20.08 (1.47)	6.56 (0.30)	3.00 (0.24)	5.81 (0.18)	2.24 (0.40)	2.78 (0.06)	3.94 (0.23)	6.10 (0.42)
Gargathy Bay, VA	Mid	5.62 (0.67)	8.27 (5.59)	31.85 (3.57)	3.72 (1.29)	10.58 (0.32)	10.56 (0.88)	4.77 (0.59)	7.90 (0.37)	11.62 (0.24)

Table 7. Average monthly benthic chlorophyll concentrations (mg m^{-2}) for 0-3 mm and 3-10 mm depth segments measured at each site in each bay. Values in parentheses are ± 1 standard deviation (n=3).

Bay	Site	Depth (mm)	Jul-2007	Aug-2007	Sept-2007	Oct-2007	Jan-2008	Mar-2008	May-2008	Jun-2008	Jul-2008
Hog Island Bay, VA	Creek	0-3	10.41 (3.47)	4.63* (1.00)	19.66* (2.65)	6.94 (4.59)	16.77 (3.61)	9.08 (1.82)	10.41 (2.52)	8.21 (3.61)	71.63 (12.73)
		3-10	12.72 (5.58)	7.52* (6.09)	25.55* (10.41)	4.63 (2.65)	35.69 (1.73)	18.21 (5.12)	13.53 (2.25)	11.62 (2.57)	23.53 (9.41)
	Mid	0-3	39.03 (30.66)	27.17* (19.73)	24.86* (14.02)	45.10 (4.59)	17.34 (6.01)	21.68 (3.14)	40.70 (8.32)	34.34 (6.00)	40.99 (7.55)
		3-10	45.67 (24.05)	19.08* (15.42)	27.17* (13.02)	61.86 (7.01)	32.38 (7.01)	45.91 (2.90)	61.05 (5.72)	55.10 (5.36)	51.80 (5.56)
	Inlet	0-3	15.61 (4.59)	21.39* (10.01)	34.11* (11.02)	5.78 (2.65)	6.36 (2.65)	12.26 (4.44)	8.09 (0.99)	24.11 (10.62)	28.68 (12.42)
		3-10	23.70 (15.74)	18.50* (9.55)	33.53* (19.34)	4.34 (3.68)	8.67 (6.01)	13.82 (5.38)	16.13 (1.35)	17.17 (5.26)	23.70 (9.53_
Isle of Wight Bay, MD	Creek	0-3	40.47 (17.72)	8.09 (1.00)	72.27 (19.95)	--- ---	--- ---	64.58 (14.21)	53.02 (15.93)	--- ---	57.24 (10.39)
		3-10	56.08 (41.78)	6.36 (2.65)	93.08 (41.64)	---	---	95.05 (12.90)	86.03 (29.92)	---	93.49 (12.24)
	Mid	0-3	61.86 (20.25)	0.58 (1.00)	52.61 (14.75)	--- ---	--- ---	70.13 (7.07)	50.36 (1.84)	--- ---	92.97 (18.17)
		3-10	66.49 (25.98)	13.88 (---)	92.50 (21.96)	---	---	70.82 (10.88)	97.48 (6.76)	---	111.87 (15.84)
	Inlet	0-3	41.63 (18.11)	1.73 (2.45)	28.91 (12.31)	--- ---	--- ---	39.14 (4.77)	13.36 (0.69)	--- ---	44.11 (9.80)
		3-10	26.60 (2.65)	2.89 (2.00)	27.75 (12.14)	---	---	59.78 (8.42)	12.60 (3.49)	---	43.54 (2.45)

		0-3	4.05	3.47	5.78	2.31	13.88	47.52	7.28	14.40	25.27
Burton's Bay,	Creek		(2.65)	(1.73)	(7.01)	(1.00)	(7.56)	(12.66)	(1.21)	(8.64)	(2.12)
VA		3-10	8.09	2.31	8.09	4.05	28.91	121.70	24.72	23.82	33.19
			(4.36)	(1.00)	(5.30)	(3.61)	(15.64)	(1.91)	(5.03)	(7.66)	(3.44)
		0-3	2.31	2.89	3.47	5.20	10.98	10.93	12.37	13.41	10.41
	Mid		(1.00)	(2.00)	(2.45)	(4.91)	(5.58)	(2.70)	(0.26)	(1.87)	(1.31)
		3-10	2.89		5.20	5.78	27.17	11.39	14.16	16.88	16.07
			(2.00)		(4.59)	(4.01)	(15.55)	(7.57)	(4.56)	(8.89)	(5.78)
		0-3	22.55	4.63	12.14	8.09	2.89	9.37	11.56	14.05	12.89
	Inlet		(10.83)	(1.00)	(3.47)	(1.00)	(2.00)	(2.90)	(2.37)	(2.35)	(0.96)
		3-10	8.67	4.05	11.56	13.30	5.20	11.97	17.23	12.26	17.81
			(6.01)	(2.00)	(6.57)	(4.36)	(3.00)	(2.27)	(1.48)	(1.41)	(4.69)
		0-3	7.52	2.31	12.14	142.80	7.81	10.98	74.12	12.84	7.28
Gargathy Bay,	Mid		(4.36)	(1.00)	(4.59)	(13.13)	(3.68)	(4.20)	(48.05)	(3.91)	(1.67)
VA		3-10	14.45	1.73	12.72	150.90	14.45	12.78	71.11	36.71	8.09
			(6.57)	(---)	(5.58)	(12.51)	(2.65)	(1.74)	(21.09)	(7.11)	(2.09)

*Chlorophyll concentrations came from A. Hardison (unpublished data).

Table 8. Average monthly dissolved nitrate/nitrite (NO_x), ammonia, and organic nitrogen concentrations (μM). Single samples were taken at each site.

Bay	Site	Dissolved Nitrogen Species (μM)	Jul-2007	Aug-2007	Sept-2007	Oct-2007	Jan-2008	Mar-2008	May-2008	Jun-2008	Jul-2008
Hog Island Bay, VA	Creek	NO_x	0.801	1.35	1.95	2.97	0.291	0.655	1.93	0.370	1.94
		NH_3	0.846	2.88	4.46	8.3	0.494	1.00	5.68	0.878	3.18
		DON	---	20.8	22.9	12.4	23.6	15.5	11.5	19.8	20.4
	Mid	NO_x	0.988	0.356	1.02	2.34	0.149	0.204	2.99	2.37	0.078
		NH_3	1.344	0.286	2.12	9.7	0.191	0.612	2.68	0.396	0.570
		DON	---	21.4	24.9	11.7	23.1	15.5	16.0	9.99	17.8
	Inlet	NO_x	0.410	0.197	0.974	1.97	0.139	0.292	0.844	0.167	0.081
		NH_3	0.676	0.284	1.49	7.84	0.149	0.590	1.88	0.548	0.380
		DON	---	19.9	19.3	10.9	20.6	16.0	11.2	21.7	11..7
Isle of Wight Bay, MD	Creek	NO_x	0.283	1.03	2.08	---	---	9.73	9.60	---	0.138
		NH_3	0.456	4.00	4.28	---	---	1.34	5.84	---	0.706
		DON	---	34.7	32.9	---	---	8.71	23.7	---	39.0
	Mid	NO_x	0.401	0.251	0.273	---	---	0.472	2.14	---	0.284
		NH_3	1.344	0.246	0.302	---	---	0.512	4.52	---	3.04
		DON	---	13.1	14.5	---	---	16.4	14.3	---	17.5
	Inlet	NO_x	0.429	0.609	0.125	---	---	1.25	1.05	---	0.114
		NH_3	1.728	2.90	0.302	---	---	1.03	4.28	---	2.50
		DON	---	12.2	14.3	---	---	16.4	17.6	---	12.9
Burton's Bay, VA	Creek	NO_x	0.868	0.706	1.34	2.39	0.473	0.990	3.30	1.57	0.425
		NH_3	4.2	0.916	4.94	6.56	0.476	0.252	3.22	4.16	1.93
		DON	---	18.9	17.2	12.0	21.4	20.8	19.3	26.6	23.6
	Mid	NO_x	0.270	0.236	1.22	3.04	0.335	0.193	1.56	0.749	0.056
		NH_3	0.406	0.474	1.81	7.04	0.396	0.326	2.89	0.462	0.312
		DON	---	16.5	15.5	8.87	14.2	15.4	14.1	21.6	24.7
	Inlet	NO_x	0.449	0.264	0.422	2.60	0.214	0.171	1.82	0.269	0.048
		NH_3	0.852	0.424	1.46	8.46	0.296	0.334	3.88	1.08	0.498
		DON	---	15.0	16.4	8.13	13.1	16.0	14.8	25.2	19.4
Gargathy Bay, VA	Mid	NO_x	0.526	0.192	1.04	3.43	1.24	10.5	2.62	0.953	0.275
		NH_3	7.36	0.292	1.01	6.02	0.511	0.386	1.85	0.780	0.980
		DON	---	12.0	17.5	11.1	18.0	24.7	15.0	32.1	33.9

Table 9. Daily water column metabolism, gross primary production (GPP), respiration (R), and net community production (NCP) measured at each site in each bay (g O_2 m^{-2} h^{-1}). January values are reported, though they were not used in the final analysis. Values are relative to oxygen (positive indicates production; negative indicates respiration) and are depth integrated for a 1 meter water column. Values may not sum due to rounding.

Bay	Site	Metabolic Parameter (g O_2 m^{-2} h^{-1})	Jul-2007	Aug-2007	Sept-2007	Oct-2007	Jan-2008	Mar-2008	May-2008	Jun-2008	Jul-2008
Hog Island Bay, VA	Creek	GPP	0.001	2.93	7.92	1.70	0.867	3.53	3.47	13.4	1.62
		R	-11.4	-756	-0.001	-0.001	-2.65	-2.15	-0.001	-1.06	-0.615
		NCP	-11.4	-4.63	7.92	1.70	-1.78	1.38	3.47	12.4	1.01
	Mid	GPP	0.001	2.96	10.1	2.25	0.538	3.39	3.52	16.5	3.05
		R	-6.07	-1.68	-0.041	-0.009	-1.86	-2.22	-0.001	-2.82	-0.987
		NCP	-6.07	1.29	10.1	2.24	-1.32	1.17	3.52	13.7	2.06
	Inlet	GPP	3.53	1.00	5.53	1.58	1.76	2.32	3.11	12.0	6.03
		R	-0.022	-0.404	-0.001	-0.007	-0.088	-0.001	-0.001	-0.264	-0.240
		NCP	3.51	0.596	5.54	1.57	1.67	2.32	3.11	11.7	5.79
Isle of Wight Bay, MD	Creek	GPP	6.72	0.001	3.79	---	---	0.001	1.90	---	5.79
		R	-3.87	-2.99	-0.001	---	---	-0.322	-0.001	---	-0.264
		NCP	2.85	-2.99	3.79	---	---	-0.321	1.90	---	5.53
	Mid	GPP	3.25	0.184	7.04	---	---	2.05	0.753	---	4.14
		R	-0.488	-0.565	-3.16	---	---	-0.150	-0.001	---	-0.264
		NCP	2.76	-0.381	3.89	---	---	1.90	0.753	---	3.88
	Inlet	GPP	5.29	0.465	5.40	---	---	1.86	7.35	---	3.83
		R	-0.001	-0.197	-0.001	---	---	-0.935	-0.001	---	-0.001
		NCP	5.29	0.268	5.40	---	---	0.927	7.34	---	3.83

Burton's Bay, VA	Creek	GPP	6.46	3.25	5.59	1.54	7.69	8.47	1.18	12.3	7.54
		R	-1.06	-0.001	-0.001	-0.272	-7.95	-10.57	-0.536	-0.002	-0.438
		NCP	5.41	3.25	5.59	1.27	-0.258	-2.10	0.640	12.3	7.10
	Mid	GPP	4.01	6.35	5.09	0.000	1.09	5.12	4.00	7.65	10.1
		R	-1.79	-0.001	-0.001	-0.834	-4.09	-12.4	-0.025	-0.115	-0.178
		NCP	2.22	6.35	5.09	-0.834	-3.00	-7.31	3.96	7.50	9.93
	Inlet	GPP	6.20	3.99	3.19	0.000	7.00	2.88	2.80	11.9	6.63
		R	-0.001	-0.031	-0.462	-0.042	-4.87	-4.25	-0.001	-0.001	-0.792
		NCP	6.19	3.95	2.73	-0.042	1.22	-1.36	2.80	11.8	5.84
Gargathy Bay, VA	Mid	GPP	1.08	1.84	8.50	1.28	4.39	1.15	7.18	4.00	2.52
		R	-4.92	-0.001	-0.330	-0.176	-10.3	-4.77	-0.001	-0.792	-0.982
		NCP	-3.83	1.84	8.17	1.10	-5.89	-3.62	7.18	3.21	1.54

Table 10. Daily benthic metabolism, gross primary production (GPP), respiration (R), and net community production (NCP) measured at each site in each bay. Blank squares represent no measurement for that month. January values are reported, though they were not used in the final analysis. Values are relative to oxygen (positive indicates production; negative indicates respiration) and are assessed at a depth of 1 meter. Values may not sum due to rounding. Units are g O_2 m^{-2} h^{-1}.

Bay	Site	Metabolic Parameter (g O_2 m^{-2} h^{-1})	Jul-2007	Aug-2007	Sept-2007	Oct-2007	Jan-2008	Mar-2008	May-2008	Jun-2008	Jul-2008
Hog Island Bay, VA	Creek	GPP	0.124	0.658	0.269	0.815	0.297	0.091	0.397	0.888	2.89
		R	-0.673	-0.677	-0.551	-0.565	-0.505	-0.297	-1.13	-2.16	-1.77
		NCP	-0.549	-0.019	-0.282	0.249	-0.209	-0.206	-0.734	-1.27	1.12
	Mid	GPP	2.01	0.025	0.713	1.74	0.003	0.701	0.894	0.522	0.933
		R	-0.561	-0.729	-0.428	-0.477	-0.185	-0.009	-0.971	-0.048	-0.995
		NCP	1.45	-0.704	0.285	1.26	-0.182	0.693	-0.077	0.474	-0.062
	Inlet	GPP	0.445	0.105	1.17	0.757	0.127	0.316	0.404	1.25	1.13
		R	-0.832	-0.472	-0.647	-0.327	-0.088	-0.503	-1.75	-0.498	-0.701
		NCP	-0.386	-0.367	0.527	0.431	0.039	-0.187	-1.34	0.755	0.430
Isle of Wight Bay, MD	Creek	GPP	0.642	2.81	1.51	---	---	1.28	0.083	---	2.04
		R	-0.833	-1.11	-0.499	---	---	-0.185	-0.667	---	-1.12
		NCP	-0.191	1.70	1.01	---	---	1.10	-0.584	---	0.918
	Mid	GPP	1.37	0.968	1.66	---	---	0.662	0.583	---	2.45
		R	-1.21	-1.16	-0.803	---	---	-0.192	-0.343	---	-0.848
		NCP	0.161	-0.191	0.855	---	---	0.471	0.240	---	1.60
	Inlet	GPP	1.92	0.209	2.42	---	---	0.727	0.958	---	1.23
		R	-0.809	-1.15	-0.415	---	---	-0.190	-0.826	---	-0.857
		NCP	1.11	-0.945	2.00	---	---	0.537	0.132	---	0.374

Burton's Bay, VA	Creek	GPP	0.966	0.002	0.320	0.327	0.458	0.939	0.141	3.75	0.902
		R	-0.884	-1.25	-0.510	-0.807	-0.578	-0.267	-1.13	-1.36	-1.23
		NCP	0.082	-1.25	-0.189	-0.481	-0.120	0.671	-0.984	2.39	-0.332
	Mid	GPP	0.664	0.037	0.492	0.543	0.005	0.318	0.856	1.16	1.14
		R	-0.988	-0.897	-0.408	-1.17	-0.298	-0.280	-1.18	-1.28	-0.184
		NCP	-0.324	-0.860	0.084	-0.626	-0.292	0.037	-0.328	-0.119	0.952
	Inlet	GPP	1.33	0.151	1.20	0.457	0.337	0.415	0.115	1.83	0.535
		R	-0.917	-1.08	-0.478	-0.508	-0.354	-0.127	-0.659	-0.799	-0.471
		NCP	0.411	-0.927	0.722	-0.051	-0.017	0.288	-0.545	1.03	0.064
Gargathy Bay, VA	Mid	GPP	0.853	0.001	0.557	0.368	0.245	0.064	0.000	0.000	0.456
		R	-1.64	-1.40	-1.90	-0.525	-0.748	-0.168	-3.70	-2.23	-1.57
		NCP	-0.783	-1.40	-1.34	-0.157	-0.503	-0.104	-3.70	-2.23	-1.12

Table 11. Daily net ecosystem metabolism. Blank squares represent no measurement for that month. January values are reported, though they were not used in the final analysis. Values are relative to oxygen (positive indicates production; negative indicates respiration). Units are g O_2 m^{-2} h^{-1}.

Bay	Site	Metabolic Parameter (g O_2 m^{-2} h^{-1})	Jul-2007	Aug-2007	Sept-2007	Oct-2007	Jan-2008	Mar-2008	May-2008	Jun-2008	Jul-2008
Hog Island Bay, VA	Creek	NEM	-11.987	-4.648	7.636	1.946	-1.990	1.172	2.732	11.115	2.125
	Mid	NEM	-4.621	0.584	10.391	3.503	-1.502	1.866	3.446	14.201	1.996
	Inlet	NEM	3.126	0.229	6.063	2.003	1.709	2.134	1.765	12.464	6.221
Isle of Wight Bay, MD	Creek	NEM	2.654	-1.286	4.801	---	---	0.775	1.315	---	6.447
	Mid	NEM	2.922	-0.572	4.742	---	---	2.366	0.993	---	5.477
	Inlet	NEM	6.396	-0.677	7.400	---	---	1.464	7.477	---	4.204
Burton's Bay, VA	Creek	NEM	5.490	1.998	5.400	0.792	-0.379	-1.427	-0.344	14.727	6.769
	Mid	NEM	1.891	5.487	5.172	-1.460	-3.292	-7.270	3.628	7.378	10.882
	Inlet	NEM	6.606	3.027	3.448	-0.093	1.212	-1.072	2.254	12.880	5.903
Gargathy Bay, VA	Mid	NEM	-4.615	0.441	6.824	0.944	-6.395	-3.728	3.475	0.979	0.427

Table 12. Burton's Bay open water net ecosystem metabolism measurements. Day column refers to the numerical day of the deployment. Units of NEM are g O_2 m^{-3} d^{-1}. Values have been corrected for air-sea exchange.

Burton's Bay Open Water NEM					
Day	**July 2007**	**Sept-Oct 2007**	**Feb 2008**	**Mar 2008**	**May 2008**
1	-2.93	-1.39	-0.947	-0.557	-0.469
2	-3.62	-2.83	0.189	-1.23	-0.073
3	-2.11	-1.47	0.300	0.073	-0.049
4	-0.973	-0.737	-0.072	-0.908	0.090
5	-0.897	-0.175	-0.266	-2.95	-0.211
6	-5.24	-0.168	-1.21	-2.02	-0.281
7	-3.23	-0.180	-1.74	-0.348	-1.17
8	-1.67	-0.639	-0.568	-0.224	-0.329
9		-2.06	-0.923	-0.461	-0.13
10		-2.07	-4.25	-0.165	-1.58
11		-2.60	-1.38	-0.184	-0.528
12			-1.86	-0.882	0.192
13			-2.77	-0.595	-1.57
14			-1.84	-0.041	-1.33
15			-0.085	0.009	-0.526
16			0.063	-0.869	-0.523
17			-0.721	-2.82	-1.28
18				-0.706	-1.46
19					-1.18
20					-1.14

Table 13. Burton's Bay open water net ecosystem metabolism measurements. Day column refers to the numerical day of the deployment. Units of metabolism are g O_2 m^{-3} d^{-1}. Values have been corrected for air-sea exchange.

Gargathy Bay Open Water NEM				
Day	**July 2007**	**Sept-Oct 2007**	**Feb 2008**	**Jul-Aug 2008**
1	0.956	-0.447	1.52	0.870
2	-0.788	-0.350	2.30	0.349
3	0.112	-0.223	0.080	0.402
4	0.344	0.435	0.791	0.384
5	-0.045	0.219	0.037	-0.051
6	-1.92	-0.248	1.62	-1.08
7	-1.37	-0.317	1.62	-3.84
8		-0.705	0.695	-3.10
9		-1.62	1.17	-2.02
10		-1.07	1.81	-2.55
11		0.181	1.23	-4.16
12			1.21	-1.51
13			1.74	-1.99
14			1.13	-0.776
15			1.62	-1.85
16			0.514	-1.02
17			0.436	-0.821
18			-0.654	

Table 14. March to October average daily water column and sediment gross primary production (GPP), respiration (R), and net community production (NCP); net ecosystem metabolism (NEM), production to respiration ratio (P:R), benthic to pelagic ratio of GPP and R. Extrapolated metabolic values were calculated by weighting measured daily rates for the number days in the month.

Bay	Site	Metabolic Parameter ($g\ O_2\ m^{-2}\ h^{-1}$)	Water Column	Sediments	NEM	P:R	Benthic:Pelagic GPP	Benthic:Pelagic R
Hog Island Bay, VA	Creek	GPP	3.81	0.684				
		R	-2.56	-0.869				
		NCP	1.25	-0.184	1.07	1.31	0.180	0.339
	Mid	GPP	4.61	0.842				
		R	-1.54	-0.472				
		NCP	3.06	0.370	3.43	2.71	0.183	0.306
	Inlet	GPP	3.88	0.619				
		R	-0.104	-0.639				
		NCP	3.77	-0.020	3.75	6.05	0.160	6.132
Isle of Wight Bay, MD	Creek	GPP	3.086	1.33				
		R	-0.865	-0.672				
		NCP	2.22	0.654	2.88	2.87	0.430	0.777
	Mid	GPP	3.173	1.31				
		R	-0.782	-0.691				
		NCP	2.39	0.619	3.01	3.04	0.413	0.884
	Inlet	GPP	3.720	1.24				
		R	-0.127	-0.616				
		NCP	3.59	0.619	4.21	6.67	0.332	4.843

Burton's Bay, VA	Creek	GPP	6.23	0.810				
		R	-3.37	-0.828				
		NCP	2.86	-0.018	2.84	1.68	0.130	0.245
	Mid	GPP	5.62	0.578				
		R	-3.44	-0.711				
		NCP	2.18	-0.133	2.05	1.49	0.103	0.207
	Inlet	GPP	5.03	0.666				
		R	-1.40	-0.561				
		NCP	3.63	0.105	3.73	2.90	0.132	0.399
Gargathy Bay, VA	Mid	GPP	4.14	0.256				
		R	-2.13	-1.46				
		NCP	2.04	-1.20	0.811	1.23	0.062	0.685

Table 15. May to July average daily macroalgal gross primary production (GPP), respiration (R), and net production (NP). Rates are normalized to biomass measured in the field.

Bay	Site	Metabolic Parameter ($g\ O_2\ m^{-2}\ h^{-1}$)	Ulva metabolism	Gracilaria metabolism
Hog Island Bay, VA	Creek	GPP	0.016	0.121
		R	-0.002	-0.023
		NP	0.013	0.098
	Mid	GPP	1.21	0.700
		R	-0.240	-0.240
		NP	0.968	0.450
	Inlet	GPP	1.15	0.420
		R	-0.280	-0.160
		NP	0.870	0.260
Isle of Wight Bay, MD	Creek	GPP	0.260	0.130
		R	-0.040	-0.030
		NP	0.220	0.100
	Mid	GPP		
		R	No algae found at this site	No algae found at this site
		NP		
	Inlet	GPP	0.100	
		R	-0.120	
		NP	-0.020	
Burton's Bay, VA	Creek	GPP	1.31	0.560
		R	-0.290	-0.150
		NP	1.02	0.410
	Mid	GPP	6.79	
		R	-1.14	No Gracilaria found at this site
		NP	5.66	
	Inlet	GPP	2.11	3.88
		R	-0.290	-1.77
		NP	1.82	2.12
Gargathy Bay, VA	Mid	GPP	2.21	2.73
		R	-1.21	-4.74
		NP	1.00	-2.01

Table 16. May to July average daily sediment gross primary production (GPP), sediment respiration (R), sediment net production (NP), net ecosystem metabolism (NEM), and production to respiration ratio (P:R). All parameters presented with and without the influence of macroalgae during May to July. Given the spatial variability of macroalgae, these rates represent the areas in which we sampled and are not representative of the entire bay.

Bay	Site	Metabolic Parameter ($g\ O_2\ m^{-2}\ h^{-1}$)	Sediments without macroalgae	Sediments with macroalgae	NEM without macroalgae	NEM with macroalgae	P:R without macroalgae	P:R with macroalgae
Hog Island Bay, VA	Creek	GPP	1.40	1.35				
		R	-1.68	-1.68				
		NCP	-0.284	-0.333	5.261	5.458	0.180	0.339
	Mid	GPP	0.786	0.292				
		R	-0.678	-0.678				
		NCP	0.108	-0.386	6.465	7.393	0.183	0.306
	Inlet	GPP	0.926	0.150				
		R	-0.987	-0.987				
		NCP	-0.061	-0.837	6.756	5.980	0.160	6.132
Isle of Wight Bay, MD	Creek	GPP	1.38	1.367				
		R	-0.970	-0.970				
		NCP	0.412	0.397	4.788	5.026	0.430	0.777
	Mid	GPP	1.82	1.82				
		R	-0.678	-0.678				
		NCP	1.14	1.14	3.966	3.966	0.413	0.884
	Inlet	GPP	1.14	0.336				
		R	-0.846	-0.846				
		NCP	0.293	-0.510	5.308	4.315	0.332	4.843

Burton's Bay, VA	Creek	GPP	1.57	0.923				
		R	-1.24	-1.24				
		NCP	0.337	-0.314	6.967	7.742	0.130	0.245
	Mid	GPP	1.05	0.496				
		R	-0.877	-0.877				
		NCP	0.171	-0.381	7.295	12.404	0.103	0.207
	Inlet	GPP	0.815	0.302				
		R	-0.641	-0.641				
		NCP	0.174	-0.339	6.949	10.379	0.132	0.399
Gargathy Bay, VA	Mid	GPP	0.154	-0.015				
		R	-2.50	-2.50				
		NCP	-2.35	-2.49	1.634	1.070	0.062	0.685

Table 17. Measured light attenuation at each site during each sampling month. Units are m^{-1}.

	Hog Island Bay K_d (m^{-1})			Isle of Wight Bay K_d (m^{-1})			Burton's Bay K_d (m^{-1})			Gargathy Bay K_d (m^{-1})
	Creek	Mid	Inlet	Creek	Mid	Inlet	Creek	Mid	Inlet	Mid
Jul-07	3.81	1.57	1.74	2.21	1.61	0.937	1.55 (0.16)	2.03 (0.44)	1.38 (0.10)	2.03 (0.94)
Aug-07	2.55 (0.21)	5.07 (2.3)	2.36 (0.02)	0.771 (0.09)	2.12 (0.17)	4.96 (0.27)	6.77 (1.58)	3.87 (0.49)	3.12 (0.22)	5.29 (1.23)
Sep-07	3.26 (0.15)	2.65 (0.17)	1.11 (0.47)	1.00 (0.29)	1.03 (0.42)	0.490 (0.62)	2.87*	1.88*	1.66*	2.92*
Oct-07	2.13 (0.16)	0.97 (0.08)	1.76 (0.09)				1.42 (0.06)	1.03 (0.02)	1.26 (0.04)	1.83 (0.03)
Jan-08	1.07 (0.22)	6.14 (0.22)	1.94 (0.16)				1.35 (0.13)	2.02 (0.08)	1.20 (0.04)	1.72 (0.03)
Mar-08	1.11 (0.23)	1.20 (0.02)	1.04 (0.01)	1.38 (0.00)	1.44 (0.18)	0.559 (0.04)	0.904**	1.16 (0.14)	0.61 (0.14)	3.48 (4.27)
May-08	2.14 (1.6)	3.28 (0.36)	1.97 (0.02)	4.39 (2.39)	2.94 (1.18)	1.09 (0.01	4.42 (0.13)	1.46 (0.04)	3.75 (0.21)	2.92*
Jun-08	3.00 (0.09)	3.00 (0.29)	2.31 (0.02)				2.34 (0.23)	1.38 (0.05)	1.30 (0.23)	3.19 (0.17)
Jul-08	2.14 (0.09)	2.56 (0.04)	1.44 (0.08)	0.847 (0.08)	0.686 (0.49)	1.38 (0.05)	2.87*	1.88*	1.66*	2.92*

* Average light attenuation value for all sampling months; used average value when in field measurements were not viable due to equipment malfunction or incorrect readings.
** Depth was very shallow (< 0.1 m).

Table 18. Sediment organic content measured at each site in the lagoon. Organic content values are percentages. Values in parentheses are ± 1 standard deviation (n=3).

	Hog Island Bay Sediment Organic Content (%)			Isle of Wight Bay Sediment Organic Content (%)			Burton's Bay Sediment Organic Content (%)			Gargathy Bay Sediment Organic Content (%)
	Creek	Mid	Inlet	Creek	Mid	Inlet	Creek	Mid	Inlet	Mid
Jul-07	3.83 (0.46)	0.794 (0.10)	3.55 (4.34)	0.992 (0.12)	0.764 (0.05)	0.850 (0.24)	3.30 (0.58)	1.92 (0.26)	1.31 (0.12)	3.72 (0.12)
Aug-07	2.23 (0.18)	1.99 (0.19)	1.09 (0.52)	0.737 (0.10	0.774 (0.06)	0.96 (0.06)	4.80 (0.35)	2.92 (0.18)	1.71 (0.11)	4.07 (0.94)
Sep-07	1.34 (0.07)	1.10 (0.11)	2.00 (0.09)	1.23 (0.05)		0.68 (0.10)	3.14 (0.48)	3.97 (0.09)	2.83 (0.19)	1.66 (0.39)
Oct-07	1.53 (0.15)	0.992 (0.18)	2.17 (0.28)				1.52 (0.28)	2.59 (0.55)	4.34 (0.60)	3.98 (0.51)
Mar-08	3.75 (0.26)	0.930 (0.08)	1.26 (0.27)	0.955 (0.05)	0.774 (0.09)	1.18 (0.29)	1.36 (0.40)	3.04 (0.05)	1.62 (0.21)	4.12 (0.25)
May-08	2.23 (0.60)	1.01 (0.23)	1.49 (0.69)	0.926 (0.26)	1.00 (0.46)	0.455 (0.02)	4.87 (2.41)	1.85 (0.28)	0.883 (0.25)	9.51 (0.30)
Jun-08	1.80 (0.60)	0.788 (0.08)	0.937 (0.03)				3.34 (0.33)	1.63 (0.22)	1.21 (0.04)	5.08 (0.20)
Jul-08	1.00 (0.42)	0.653 (0.02)	0.710 (0.04)	1.15 (0.12)	1.56 (0.22)	3.83 (1.10)	3.99 (0.48)	0.92 (0.05)	3.26 (0.28)	1.21 (0.2)

VITA

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On March 6th, 1983, Juliette was born on Camp Pendleton Marine Corps Base, California and was raised as a military brat, graduating overseas from Patch American High School in Stuttgart, Germany in 2001. She attended Virginia Polytechnic Institute and State University, graduating with a B.S. in Animal and Poultry Science in 2005. She then enrolled at the College of William and Mary under the concurrent M.P.P – M.S. degree program beginning her M.P.P. in the Thomas Jefferson Public Policy Program in 2005 and her M.S. at the Virginia Institute of Marine Science in 2006.