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INVESTIGATIONS OF PHYTOPLANKTON DIVERSITY IN CHESAPEAKE BAY

by

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A Thesis Submitted to the Faculty of
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ABSTRACT

INVESTIGATIONS OF PHYTOPLANKTON DIVERSITY IN CHESAPEAKE BAY

Todd Arthur Egerton
Old Dominion University, 2013
Director: Dr. Harold G. Marshall

Characterizing the diversity of a community in relation to environmental conditions and ecosystem functions are core concepts in ecology. While decades of research have led to a growing comprehension of diversity in many ecosystems, our understanding in aquatic habitats and microbial organisms remains relatively limited. Phytoplankton represent a diverse and important group that contribute approximately half of global primary productivity and are intrinsically connected to changing environmental conditions, especially in systems as dynamic as estuaries. To better understand the ecological processes governing phytoplankton composition and diversity, spatial and temporal patterns of environmental parameters and their relation to the algal community of Chesapeake Bay were analyzed using data collected over a 25 year period (1985-2009).

The phytoplankton community of Chesapeake Bay, containing 1480 taxa was characterized as one of high richness and low evenness, with a single species accounting for at least half of the biomass in almost one third of all samples examined. High gamma-diversity was attributed to seasonal succession of dominant flora and spatial heterogeneity along the estuarine gradient with high species turnover between salinity regions. Alpha-diversity was greatest in freshwater and polyhaline regions, and minimal

in lower mesohaline waters. Multivariate ordination analysis identified regional differences corresponded to salinity, turbidity, and nutrient gradients, with lowest richness in regions of intermediate salinity, total nitrogen and phosphorus concentrations and highest dissolved organic nitrogen. Temporal factors included negative impacts of streamflow related nutrient increases leading to greater algal abundance and lower diversity particularly within the polyhaline Bay. Results indicate that greater algal biomass was associated with higher richness and lower evenness, and may be associated with lower ecosystem stability, with greater variance in inter-annual phytoplankton biomass.

To address short-term environmental variability including nutrient loading, daily sampling of the Lafayette River, was conducted in spring 2006. During consecutive blooms of *Cryptomonas* sp. and *Gymnodinium instriatum* up to 99% of total biomass was due to the individual bloom species, although species richness was not significantly reduced. Time lag correlations indicated that the *Cryptomonas* sp. bloom was related to precipitation related increases in dissolved inorganic nitrogen concentrations, while the *G. instriatum* bloom followed periods of reduced nitrogen concentrations that were accompanied by an algal community of high richness and low evenness. Based on its connectivity to both environmental and biological variables, phytoplankton diversity is recognized as a significant indicator of ecosystem condition, with high species richness and evenness as potential goals for restoration efforts.

This thesis is dedicated to my family

Jessica, Evan and Anna Egerton.

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INTRODUCTION TO BIODIVERSITY AND CHESAPEAKE BAY

Biological diversity is a cornerstone concept in ecological science, with research focused on examining linkages between the variety of organisms and the environment. With estimates of over 10 million species living on Earth inhabiting almost every combination of environmental gradients, this is a formidable endeavor. By building an understanding of where differing levels of diversity exist we can develop a better model of the role the environment plays on shaping the biological community. It is increasingly vital to identify diversity patterns and their drivers in order to attempt and uncover the causes and potential effects of declines of biodiversity such as those being observed globally.

At its most fundamental level, diversity is simply a description of the variety of items within some given unit. Although there are an incredibly large number of definitions, sub-divisions, and levels in the examination of diversity, they all share two basic characteristics. These are the number of different types of items, referred to in the literature as richness, and the relative amount of each type, or evenness. It is the different interpretations and combinations of these two qualities regarding the description of biological organisms which represent the vast body of research in biodiversity.

Diversity metrics

Species richness can be used as a measure of diversity, and is the easiest to determine, most widely used metric, and may describe the same patterns as other more complicated indices (Pianka 1966). However it can also be affected by the presence of rarities due to sampling bias, in which rare species may be missed during a survey (Hubálek 2000). Multiple communities may have the same number of species, with one

community dominated by a small number of species, and the other community being more homogenous. A measurement of species richness alone would not differentiate between the two; therefore the calculation of evenness is often vital. Conversely, in a case where two communities with identical diversity indices, but one with a high richness and a low evenness, and the other with low richness but high evenness, would best be differentiated using richness (Hubálek 2000). Species evenness however can be calculated in different ways, and it is usually the case that diversity is presented as an index using a calculation which combines richness with evenness (Huston 1994).

There are a number of indices that been developed which attempt to describe diversity as a measure of richness and evenness since the mid-20th century (i.e. Shannon and Weaver 1949, Margalef 1958, Menhinick 1964, Routledge 1979, Izsak and Papp 2000). There has been considerable debate in the literature over which index to use depending on the situation. An evaluation of diversity measurements by Hubálek (2000) tested 24 different indices using real data and simulated models. The most used index (besides richness alone) is the Shannon index, represented as H' (Shannon and Weaver, 1949):$H' = -\sum(p_i * logp_i)$ with p_i the proportion of the total sample which is composed of species i (Huston 1994). I have chosen to examine phytoplankton species richness and the Shannon index H'. These have been chosen primarily because they are both commonly used indices in the majority of ecological papers, including phytoplankton studies (e.g. Huang et al. 2004, Irigoien et al. 2004, Ptacnik et al. 2008, Witman et al. 2008, Chalar 2009). The use of these indices is also supported by their ability to perform well in comparative analyses (Hubálek 2000). While consistent methodology throughout the study should limit potential effects of differing sampling

techniques, species richness alone may potentially overestimate the diversity in phytoplankton communities such as those found in Chesapeake Bay. These communities are often dominated by relatively few species with abundances several orders of magnitude higher than other species present (Marshall and Alden 1990, Marshall and Nesius 1996).

Thus far, the different descriptions of diversity, including all of the above indices have been discussed in terms of what is known as alpha diversity. This refers to within-habitat diversity; in terms of species diversity this would be the number and distribution of species in a habitat (Magurran 1998). In terms of phytoplankton research, this may be the diversity of algal species in a pond, or at a specific station in a larger body of water. These species are involved in interactions within a community and coexist with each other in competition for similar resources (Tilman 1977). Diversity between habitats is termed beta diversity and can be seen as the ways that organisms relate to a heterogeneous environment (Huston 1994). Examinations of diversity trends over environmental gradients are often actually comparisons of alpha diversity at each individual location. An examination of beta diversity usually contains both a comparison of alpha diversity as well as a measurement of similarity (Huston 1994). For these studies, it is not only important how many species are present, but which species are present, especially the changes in species composition between areas of different environmental characteristics. In terms of phytoplankton research, an area such as a river, with high beta diversity would represent a large difference in algal communities at different environments within the river, due for example to differences in salinity. Moving up to larger spatial coverage, gamma diversity, is defined similarly to alpha

diversity but at a regional scale (Shmida and Wilson 1985). This can be described as the number of species in a region that includes a variety of environmental conditions. Other researchers have also used gamma diversity to represent beta diversity on a regional scale (Noss 1983).

The last several decades of ecological research concerning biodiversity has led to a staggering breadth of concepts that must be addressed when deciding to examine the diversity of a system. As far as a working definition of species, I believe that in terms of phycology and most current systematic work, we are operating under the framework of the phylogenetic species concept. While the actual identification of phytoplankton species in this research is carried out based on morphological characteristics, the current system of algal taxonomy is based on phylogenetic systematics (Marshall et al. 2005). Some species which previously had been identified as closely related based on similar morphology, have been re-instated to other taxonomic levels based on molecular analysis and ultrastructure microscopy (e.g. Marshall et al. 2006, Tang et al. 2008). The understanding is that taxonomic groupings to the species level should represent the actual natural path of evolution whenever possible. This is the hierarchal taxonomic structure that is employed by the Old Dominion University Phytoplankton Analysis Laboratory, with major taxonomic groupings representative of shared ancestral lineage (Marshall et al. 2005, Marshall et al. 2006b).

Drivers of diversity

The level of biodiversity observed in a particular habitat is generally influenced by both the degree of isolation and the quality of the environment available (Pianka 1966, MacArthur and Wilson 1967, Interlandi and Kilham 2001). These two forces work at

different scales, and involve numerous interactions over time (Sommer et al. 1993). The degree of isolation largely acts on an evolutionary timeline where generations of mutations and selective pressures in an area sufficiently removed from an influx of outside genetic information allows for the divergence of organisms into a variety of forms (Falkowski et al. 2004). The historic distribution of taxa therefore may have a large effect on the current distribution and diversity if there is a limited ability to migrate or be distributed elsewhere (Gómez 2006). Conversely, in situations where populations are not limited in their ability to be distributed, isolation forces will be relatively less important in determining the level of diversity than the current environmental conditions and subsequent biological interactions.

Microbial organisms are often considered to have a ubiquitous distribution, with Beijerinck (1913) and Baas Becking (1934) famously stating "everything is everywhere, but the environment selects." This concept is generally thought to describe that theoretically all microbial cells are able to be transported globally, but local environmental conditions will limit or favor particular taxa contributing to the community composition and diversity that is observed at a given habitat (Martiny et al. 2006). Due to their small size and apparent ease of transport by air and water currents, the diversity of phytoplankton taxa has generally been considered to be most affected by current environmental conditions (Finlay and Clarke 1999). While examinations of diatom populations suggest that historical distributions and isolation forces may significantly affect diversity patterns on a global scale (Vyverman et al. 2007), studies at local and regional scales as well the majority of global scale analyses illustrate changes in

diversity corresponding to environmental gradients (e.g. Carrick et al. 1988, Estrada et al. 2006, Kerswell 2006).

Describing patterns of diversity along environmental gradients and understanding the causative forces that shape these patterns have long been goals of ecologists (e.g. Dobzhansky 1950, Pianka 1966). Rarely are these patterns consistent across all studies or habitats, with exceptions found in most cases; however certain factors have been shown to be significant across a number of investigations. One of the first and most often identified spatial patterns is latitude, with generally reduced diversity observed in most terrestrial organisms and many aquatic systems at higher latitudes (Gaston 2000, Willig et al. 2003, Barton et al. 2010). Diversity patterns have also been observed in relationship to other abiotic variables including altitude (Rahbek 1997), depth (Smith and Brown 2002) and salinity (Remane 1934).

While these examples illustrate numerous spatial patterns of biodiversity of larger organisms, and the various linkages to environmental gradients, there is considerably less information on the diversity patterns of microbial taxa including prokaryotic and eukaryotic phytoplankton species (Green and Bohannan 2006). This can largely be attributed to both the relative difficulty in describing microbial diversity, as well as the long held paradigm that microbial taxa had cosmopolitan distributions (Green and Bohannan 2006). There have a growing number of studies exploring spatial and to a lesser degree temporal patterns of algal diversity (Platt et al. 1970, Moss 1973, Harris and Trimbee 1986, Nogueira 2000, Interlandi and Kilham 2001, Barton et al. 2010). A key significant finding has been declines in algal diversity related to anthropogenic

disturbances (Passy and Blanchet 2007, Ptacnik et al. 2008).

Phytoplankton diversity

Phytoplankton can serve as a model for examining the drivers and effects of diversity for several reasons. Being microscopic, algal cells are easily dispersed and capable of being transported over a wide range of habitats (Boo et al. 2010). This, more cosmopolitan distribution means that biogeographic constraints, experienced by other, less ubiquitous organisms are to a large degree not a factor in determining the range and growth of algal species (Dodge and Marshall 1994, Finlay et al. 2006). The presence or absence of a given species in a certain habitat can be attributed to conditions that are present at that location to a much larger degree than in other systems (Prescott 1968, Dolan 2005). Estuarine phytoplankton have relatively fast population growth rates as well (doubling time often ~1day or less) (Alpine and Cloern 1988). This means when conditions are ideal for a species, populations may grow rapidly, outcompete others, and have a measurably higher abundance (Tilman 1977). With different algal types having different physiologies and life histories, the "ideal" conditions for growth will vary depending on the algae (Tilman 1977). Some algae species are associated with characteristics ranging from reducing dissolved oxygen to toxin production (Hallegraeff 1993). When these species respond to a set of environmental conditions and becomes abundant it is often referred to as a harmful algal bloom (HAB). Through careful monitoring of algal populations, including background populations and bloom conditions, one can begin to identify how environmental variables affect different algal species and subsequently the diversity of the plankton community (Interlandi and Kilhman 2001, Marshall et al. 2006b, Costa et al. 2009, Stomp et al. 2011).

There are numerous investigations of phytoplankton community composition in estuaries, but few that focus on diversity distribution along the entire salinity gradient (Muylaert et al. 2009). Often, studies rely on meta-analysis of multiple data from different sources to develop a framework to examine diversity patterns and environmental linkages (i.e. Telesh et al. 2001). Conversely, studies may rely on a single transect or otherwise temporally limited dataset to describe the environment, making descriptions of seasonal and inter-annual variability in these patterns problematic (i.e. Muylaert et al. 2009). This study examines the diversity of phytoplankton in relation to environmental parameters and ecosystem functions in a large tidal estuary.

Chesapeake Bay

Chesapeake Bay is the largest estuary in the United States with a surface area of 11,600 km^2 (Chehata et al. 2007). More than 150 rivers and streams drain into the Bay with nearly half of freshwater input coming from the Susquehanna River (Dauer et al. 2000, Kemp et al. 2005). Salinity varies from 0 at the mouth of the Susquehanna River to 25-30, ca. 300 km to the south where the Bay empties into the Atlantic Ocean. A considerable number of investigations of phytoplankton have been conducted in the Chesapeake Bay, with a large focus on the effects of nutrient eutrophication (e.g. Harding and Perry 1997, Kemp et al. 2005, Dauer et al. 2009, Marshall et al. 2009b). Phytoplankton growth in the upper Bay is considered light limited at certain points in the year by high turbidity, the lower Bay is generally nitrogen limited, with the mid Bay varying seasonally between nitrogen and phosphorus limitations (Kemp et al. 2005). While these studies show that there are spatial and seasonal variations in the limitations of phytoplankton growth, there is little indication as to the patterns and controlling factors

of phytoplankton diversity. In comparison to studies relying on pigment concentrations as a proxy for phytoplankton abundance (e.g. Roman et al. 2005, Adolf et al. 2006, Werdell et al. 2009), there are relatively fewer examinations of the effects of these environmental conditions on the composition of the phytoplankton community (e.g. Marshall and Nesius 1996, Marshall and Alden 1997, Marshall et al. 2009), fewer still that specifically address the level of diversity (Dauer et al. 2009) and to my knowledge none that explicitly examine algal species diversity across the entire salinity gradient of Chesapeake Bay.

Research questions

This dissertation addresses the many aspects of phytoplankton diversity within Chesapeake Bay through a series of examinations. Each study, while focusing on specific components and utilizing different data subsets adds to the understanding of the causative forces of species diversity and the associated ecosystem functions. A large portion of these studies make use of data gathered through the Chesapeake Bay Monitoring Program (CBMP), a vast collection of long term (25 years) water quality and living resource data. Depending on the nature of the specific questions being addressed, and to maintain consistency in data comparability, it was necessary to limit the data to certain temporal and spatial boundaries. Whenever possible, the largest most complete dataset was used with some analyses taking advantage of over 20 years of monitoring data, and even the most modest analysis including ten years of data. In all cases, quality control practices were implemented to maintain consistency in the dataset (Egerton et al. 2006), particularly concerning data originating from different sources, including the construction of a species list that is consistent across all collections so that accurate

diversity measures could be calculated. The specifics of the following questions and analyses are laid out as such.

The first step to a better understanding of the diversity of a system, particularly one as large and complex as Chesapeake Bay is through a description of the spatial distributions. The second chapter describes the spatial patterns of phytoplankton diversity and composition in relation to the environmental conditions. An important aspect to this component is to characterize the relationship between species diversity and environmental parameters across the entire spectrum of the estuarine salinity gradient within the Bay. Fortuitously, phytoplankton populations have been monitored within the estuary at stations with average salinities ranging from fresh to polyhaline conditions from 1985 to the present day (2012). Unfortunately, phytoplankton collections of the sole freshwater station (CB1.1) were discontinued in 1996, and the oligo- (CB2.2) and mesohaline stations (CB3.3C, CB4.3C, CB5.2) were halted in 2010. It was decided that to maximize the utility of the phytoplankton data, records from 1985-2009 would be included for this component. These data include information on the phytoplankton community from the entire estuary for 11 years (1985-1995) and for eight of the nine stations for 25 years.

While Chapter 2 concentrates on spatial patterns and linkages to environmental parameters, Chapter 3 address temporal changes in phytoplankton diversity. This chapter looks at how phytoplankton richness and evenness fluctuates both seasonally as well as inter-annually. One of the goals of this chapter is to examine the effect of streamflow on the water quality of the Bay and the phytoplankton community. For this study, water quality and phytoplankton records from 1985-2009 were utilized in conjunction with

monthly and annual measurements of streamflow from the major tributaries into Chesapeake Bay. To focus the examination on the seasonality of multiple environmental and biological variables, including algal diversity, the spatial component was condensed to averages within the four salinity zones present in the estuary. This approach allows for a comparison of temporal patterns within different regions, taking account for the spatial patterns observed in Chapter 2.

Chapter 4 addresses the potential ecosystem impacts of varying phytoplankton diversity by utilizing additional sources of data. One of the most recognized ecosystem functions that has been related to biodiversity is productivity. Productivity can be measured multiple ways including biomass and productivity rates. These characteristics are monitored as part of the CBMP with primary productivity measurements recorded between 1989-2009. For this aspect of the chapter, analyses utilize data within this time period. An investigation of temporal stability is also conducted as an analysis of the inter-annual variance in algal biomass. The effect of diversity of one trophic level to that of another trophic level is another important ecosystem function parameter. Along with the phytoplankton monitoring data, zooplankton community data was collected within Chesapeake Bay between 1985 and 2001. Analyses of these data occur during this time period.

Chapters 2 through 4 examine phytoplankton communities across large temporal and spatial scales to address the large scale processes that influence the diversity of these taxa within a large tidal estuary. However phytoplankton are effected by a wide range of scales, both spatially and temporally. Chapter 5 looks at daily fluctuations in water quality parameters at one location in relation to phytoplankton composition and diversity.

By examining the relationship between algal diversity and the environment on a small scale, and comparing that to the patterns observed on a larger scale, the hope is to obtain a more complete understanding of the overall processes. Furthermore, this component was conducted at an urban eutrophic site, the Lafayette River which may serve as a potential model for how a larger system such as the Chesapeake Bay as a whole might respond to increased eutrophic conditions in terms of biodiversity and ecosystem function.

SPATIAL PATTERNS OF PHYTOPLANKTON DIVERSITY AND COMPOSITION IN CHESAPEAKE BAY

Introduction

Species diversity is a core concept in ecology; however the drivers regulating diversity in many systems are not fully understood. Describing the spatial distribution of organisms is often the first step in understanding the ecology of a species. In the same manner that species distributions are non-random, with patterns related to evolutionary history and environmental conditions, species diversity patterns are also heterogeneous. It is increasingly important to develop assessments of biological diversity and relate them to environmental conditions to gauge current and future changes to biodiversity (Butchart et al. 2010). Identification of these patterns and recognition of significant drivers of diversity is complicated by the complexity of multiple environmental gradients and biological interactions seen in natural systems.

Species richness and evenness are fundamental to assessing biodiversity. Comparing levels of species richness between sites with different environmental features is an important first step to identifying possible drivers of diversity that are influencing a particular ecosystem. While the number of species at a particular site is termed alpha diversity, the total number of species in different environments within a particular region is known as gamma diversity (Magurran 2004). Gamma diversity can also serve as a measure of the diversity present on a temporal scale, such as the total number of species observed at a location over an extended period of time (Arscott et al. 2003, Stegen et al. 2012). The measurement of how diversity and community composition changes between environments within these regional scales, or time periods is referred to as beta diversity

(Whittaker 1960, Harrison et al. 1992). Beta diversity can be used to measure change over spatial and temporal periods (Zamora et al. 2007). By looking at not only the level of species richness, but also the makeup of the community as it transitions along various environmental gradients, a better understanding of the potential effect of these variables can be determined (Nabout et al. 2007). This also adds to the understanding of how heterogeneity in the habitat, or region, both spatially and temporally, due to differences in environmental factors, may allow for the coexistence of multiple species and contribute to the overall diversity (Hutchinson 1961).

Ecological research has identified numerous such environmental features as significant to shaping the spatial variability in species diversity including latitude, altitude, water and nutrient availability (Huston 1994). In estuarine habitats, one of the most significant features is the salinity gradient formed from the continuum of riverine input to marine waters. Described by Remane (1934), the diversity of brackish water organisms is greatest in freshwater and marine waters and reduced in intermediate salinities (Fig. 1A). This view of minimal diversity at intermediate salinities is generally referred to as the artenminimum model. The underlying concept behind the model is that freshwater species have evolved and become adapted to low salinities, marine species are adapted to high salinities, and relatively few species are adapted to be tolerant enough to exist in the transitional area between the two.

This model was first used to describe the spatial distribution of benthic invertebrate diversity in the Baltic Sea, and has subsequently been used to describe the diversity of

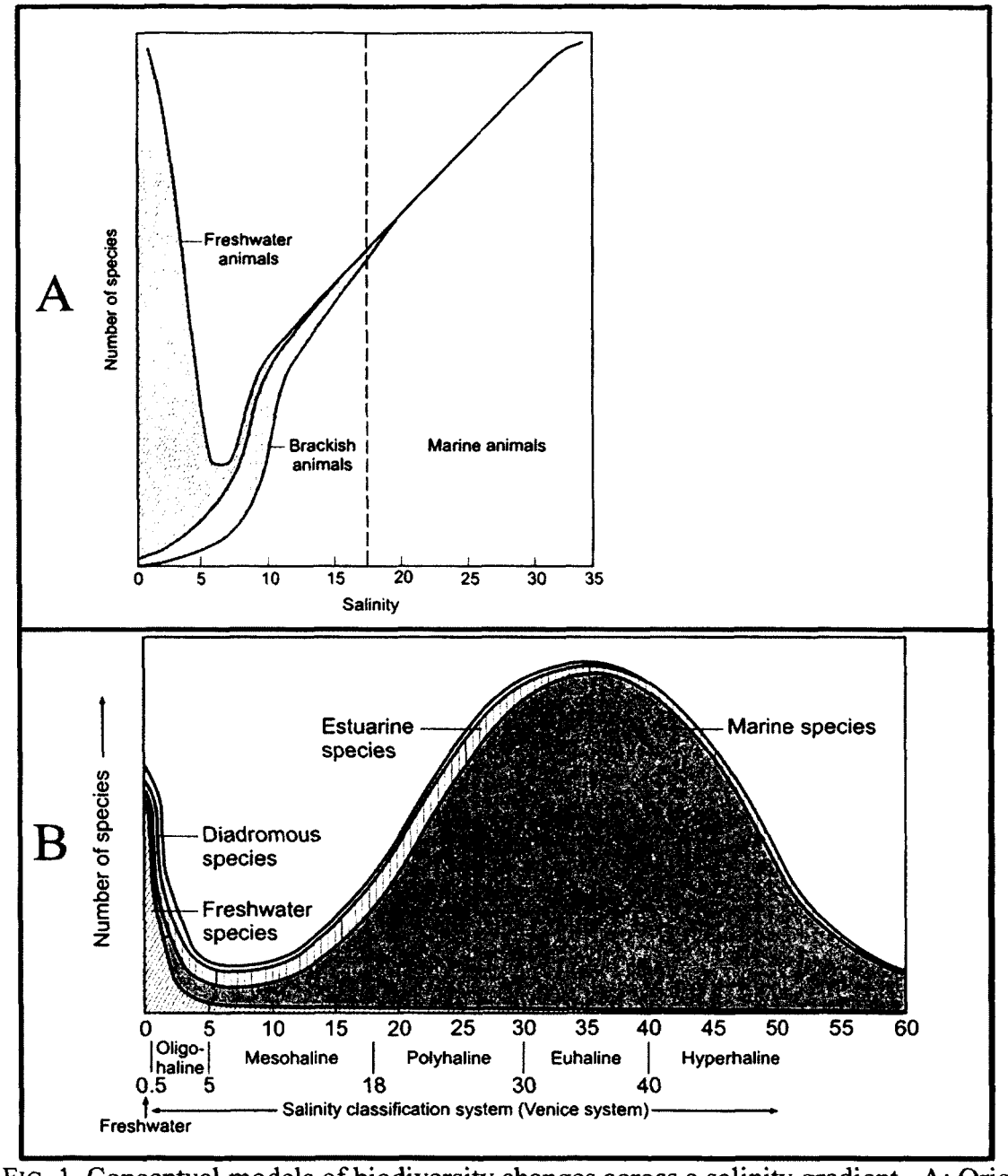

FIG. 1. Conceptual models of biodiversity changes across a salinity gradient. A: Original diagram of Remane (1934) B: Refined model of Whitfield al. (2012) incorporating salinity classification system, euhaline and hyperhaline conditions

various groups of organisms in numerous transitional saline waters globally including estuaries (e.g. Wagner 1999, Martino and Able 2003, Lercari and Defeo 2006). Thus, the model has become a standard component in textbooks regarding species diversity in estuaries (McLusky and Elliott 2004, Whitfield 2012). Through decades of research, there have also been brackish water systems found that demonstrate differing patterns of diversity, as well as different causative forces proposed and several revisions have been made to the artenminimum model (Fig. 1B; Whitfield 2012). In general, studies have shown reduced species richness in low intermediate salinities, generally 5-10 continues to be observed in most systems, with debate over the causative forces responsible. One proposed model to explain this pattern involves the observation that in tidal waters, the variation in salinity is highest at locations with intermediate mean salinity values. Attrill (2002) argues that the cause of low diversity in estuaries in these regions is the stress exerted by variable salinity rather than its absolute value.

The artenminimum model has also been challenged in its applicability to describing diversity within planktonic communities. Planktonic organisms are suspended within the water and should therefore not be as affected by salinity fluctuations as are benthic organisms (Telesh et al. 2011). In contrast to Remane's artenminimum model, Telesh et al. (2011) present data illustrating highest planktonic diversity in transitional salinities. These results have subsequently been challenged as artifacts of the statistical analysis conducted (Ptacnik et al. 2011). Additionally, there are numerous other parameters that co-vary with salinity along the estuarine gradient, and which may also affect species diversity.

Phytoplankton can serve as a model for examining the drivers and effects of diversity for several reasons. Being microscopic, algal cells are easily dispersed and capable of being transported over a wide range of habitats (Boo et al. 2010). This, more cosmopolitan distribution means that biogeographic constraints, experienced by other, less ubiquitous organisms are to a large degree not a factor in determining the range and growth of algal species (Dodge and Marshall 1994, Finlay et al. 2006). The presence or absence of a given species in a certain habitat can be attributed to environmental factors such as salinity and water quality conditions that are present at that location to a much larger degree than in other systems (Prescott 1968, Dolan 2005). Phytoplankton have relatively fast population growth rates as well (Alpine and Cloern 1988). This means when conditions are ideal for a species, its population may grow rapidly, outcompete others, and have a measurably higher abundance (Tilman 1977). With different algal types having different physiologies and life histories, the "ideal" conditions for growth will vary depending on the algae (Tilman 1977). Some algae species are associated with characteristics ranging from reducing dissolved oxygen to toxin production (Hallegraeff 1993). When these species respond to a set of environmental conditions and becomes abundant it is often referred to as a harmful algal bloom (HAB). Through careful monitoring of algal populations, including background populations and bloom conditions, one can begin to identify how environmental variables, including salinity affect different algal species and subsequently the diversity of the plankton community.

There are numerous investigations of phytoplankton community composition in estuaries, but few that focus on changes in diversity along the entire salinity gradient (Muylaert et al. 2009). Often, studies rely on meta-analysis of multiple data from

different sources to develop a framework to examine diversity patterns and environmental linkages (i.e. Telesh et al. 2001). Conversely, many studies rely on a single survey transect or are otherwise temporally limited, making descriptions of seasonal and inter-annual variability in these patterns problematic (i.e. Muylaert et al. 2009). In the present study, I have examined the diversity and composition of the phytoplankton community along the salinity gradient of Chesapeake Bay using data collected monthly as part of a long-term monitoring program of this estuary.

Study site

Chesapeake Bay is the largest estuary in the United States with a surface area of 11,600 km^2 (Fig. 2; Chehata et al. 2007). More than 150 rivers and streams drain into the Bay with nearly half of freshwater input coming from the Susquehanna River (Dauer et al. 2000, Kemp et al. 2005). Salinity varies from 0 at the mouth of the Susquehanna River to 25-30, ca. 300 km to the south where the Bay discharges into the Atlantic Ocean. A considerable number of investigations of phytoplankton have been conducted in the Chesapeake Bay, with a large focus on the effects of nutrient eutrophication on primary production and algal abundance (e.g. Harding and Perry 1997, Kemp et al. 2005, Dauer et al. 2009, Marshall et al. 2009). Phytoplankton growth in the upper Bay is considered light limited at certain points in the year due to high turbidity, the more saline lower Bay is generally thought to be nitrogen limited, with the mid-Bay varying seasonally between nitrogen and phosphorus limitations (Kemp et al. 2005).

While these studies show that there are spatial and seasonal variations in what limits phytoplankton growth, factors controlling phytoplankton diversity have not been examined. In comparison to studies relying on pigment concentrations as a proxy for

phytoplankton abundance (e.g. Roman et al. 2005, Adolf et al. 2006, Werdell et al. 2009), there are relatively fewer examinations of the effects of these environmental conditions on the composition of the phytoplankton community (e.g. Marshall and Nesius 1996, Marshall and Alden 1997, Marshall et al. 2009), fewer still that specifically address the level of diversity (Dauer et al. 2009) and to my knowledge none that explicitly examine algal species diversity across the entire salinity gradient of Chesapeake Bay.

Methods

Since 1984, the interagency Chesapeake Bay Monitoring Program has overseen a network of stations within the Bay and its tributaries that are monitored for a wide suite of water quality parameters and living resources. Within this network, a subset of stations, including 9 within the mainstem of the Bay were monitored monthly (twice monthly 1985-1989) to characterize phytoplankton abundance and composition (Fig. 2; Marshall et al. 2005). For these stations, above pycnocline depth composite whole water samples (0.5-1L) were collected in polycarbonate bottles and immediately fixed with Lugol's solution. Following a settling procedure, a fraction of the sample was examined using inverted light microscopy with all phytoplankton cells identified to the lowest taxonomic unit and abundances recorded as cells L^{-1} (Marshall et al. 2005). Seasonal phytoplankton diversity was evaluated as species richness defined here as the number of unique algal taxa enumerated whitin individual monthly samples (alpha diversity). For months where two collections were made, the average richness for the month was used in the analyses. Diversity was also measured using the Shannon index (H') which is a measure of the relative abundance of each species within a sample and therefore is

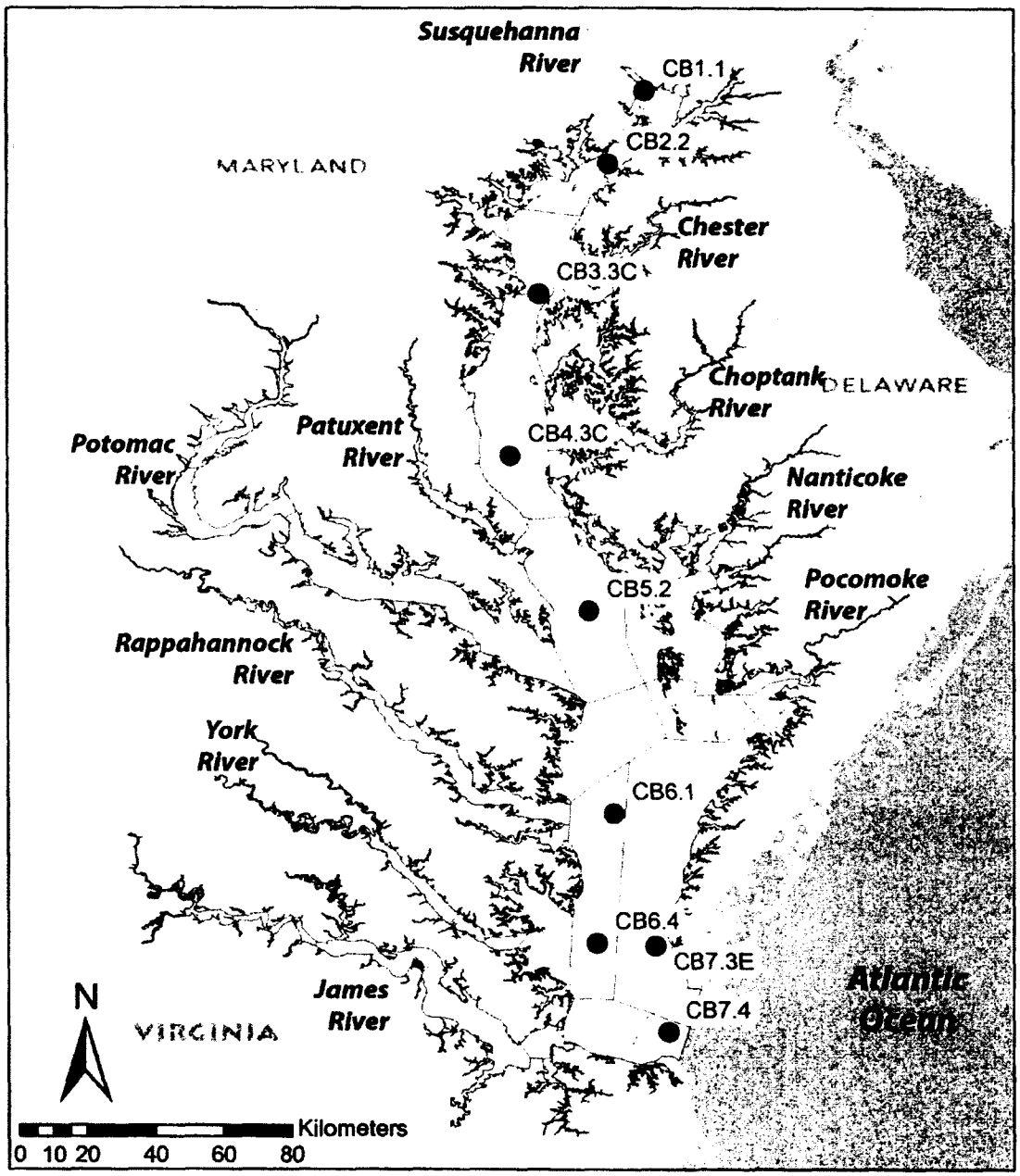

FIG. 2. Map of Chesapeake Bay and its major tributaries as well as the plankton monitoring stations sampled by the Chesapeake Bay Monitoring Program 1985-2009.

commonly used as a measure of species evenness (Shannon and Weaver 1949): $H' = -\sum(p_i \log p_i)$ where p_i is the proportion of the total algal biomass of species *i*. Higher values of *H'* indicate a greater species diversity, and generally indicate a greater level of species evenness, with a more widely distributed range of biomass attributed to a larger number of species.

Phytoplankton composition data has been collected at these stations from 1985-2009, with the exception of CB1.1, which was discontinued in 1996 (Fig. 2). Algal primary productivity was measured at these stations as the rate of ^{14}C bicarbonate incorporation reported as $\mu gC\ L^{-1}h^{-1}$ (Nesius et al. 2007). Sampling also included measurements of water temperature, salinity, chlorophyll *a*, secchi depth, dissolved oxygen (DO), silica, total suspended solids (TSS), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), particulate nitrogen (PN), total nitrogen (TN), orthophosphate (PO_4^{3-}), particulate phosphorus (PP) and total phosphorus (TP), which were collected bi-weekly to monthly from 1985 to the present (Dauer et al. 2009). These data were used to relate phytoplankton diversity indices to environmental drivers.

Data analyses

To examine the distribution of alpha diversity along the salinity gradient, phytoplankton species richness and *H'* were plotted against salinity following Telesh et al. (2011). To avoid the possible statistical artifact suggested by Ptacnik et al. (2011), salinity values were plotted directly instead of binning them into categories. Paired diversity and salinity data were plotted for all collections (1985-2009). Separate plots were generated for each season, (Winter: December-February; Spring: March-May; Summer: June-August; Autumn: September-November) to investigate potential seasonal

differences in this relationship. Additionally, mean salinity, species richness and *H'* were calculated for each station, to identify spatial variability. To investigate whether phytoplankton diversity was affected not by absolute salinity values but salinity variation as per the results of Attrill (2002), species richness was compared to the annual range of salinity recorded for all station/year combinations using analysis of variance of linear and polynomial (quadratic) regression models conducted on the entire dataset. A significance of 0.05 was used for all analyses. If both models were significant, partial *F* tests were used to determine whether the polynomial model better fit the data than the linear model (Quinn and Keough 2002, Witman et al. 2008).

Spatial gamma diversity (γ_S) was calculated as the total number of species identified within the Bay mainstem at a given time, in this case one month. As the number of species identified is dependent by the area sampled (number of stations sampled) (Harrison et al. 1992), months when all 9 stations were not sampled were excluded from this analysis. Phytoplankton monitoring at the northernmost station (CB1.1) was discontinued in 1996, therefore the Bay-wide gamma diversity only used data collected between 1985-1995. 99 months of data were included in this analysis as a result. Seasonal means of monthly γ_s were compared using ANOVA. Temporal gamma diversity (γ_T) was calculated as the total number of species identified at each individual site over a year (Arscott et al. 2003). Temporal beta diversity (β_T) can be used as an indication of species turnover through time (Shurin et al. 2010). β_T was calculated as Whitaker's (1960) γ/α-1 to relate the proportion of total richness observed over a year to the richness present at a single period of time (one month) following Arscott et al. (2003).

To evaluate the effect of the salinity gradient on these parameters, analysis of variance of linear and quadratic regression models of γ_T and β_T with salinity were conducted.

In order to identify the degree to which environmental and biological factors varied and co-varied with salinity along the estuarine gradient, linear and quadratic regression analyses were conducted using the physical and chemical data collected at the same time as the phytoplankton collections, and the distance of each station downstream from the mouth of the Susquehanna River at the uppermost section of the Bay. ANOVA was also used to evaluate significant differences between stations. These analyses included the 13 measured environmental variables listed above as well as the TN:TP ratio.

Finally, to explore the linkages between environmental variables and phytoplankton species composition (spatial beta diversity), a nonmetric multidimensional scaling (NMDS) ordination analysis was used (Rothenberger et al. 2009). Initial analyses utilizing the full water quality and phytoplankton dataset comprising 2117 collections contained too much noise to discern trends and therefore indicated data reduction was necessary to observe spatial patterns. As the focus of the study was on spatial and seasonal variability, average species compositions and environmental parameters were calculated for each station (n=9)/ month (n=12) combination for a total of 108 collections. Species abundances in cells L^{-1} were $\log_{10}$ transformed after adding 1 to each value, and species that were present in less than 5% of collections were removed from analyses (Rothenberger et al. 2009). The four seasonal environmental distance matrices were made up of 27 collections and the 14 environmental parameters listed above in addition to the biological parameters of species richness, chlorophyll, primary productivity and total phytoplankton cell abundance. The number of species included in

the analyses varied by season resulting in four matrices; Winter with 317 species columns, Spring with 334, Summer with 373 and Fall with 362 species, all with 27 collection rows. NMDS analysis was conducted for each season based on the Sørensen distance measure of the phytoplankton composition data, using PC-ORD 5.10 for Windows (MjM Software, Gleneden Beach, OR) (Rothenberger et al. 2009). Joint plots were generated based on the ordination distance matrices and overlaid with environmental vectors that were correlated with R^2 value of 0.3 or higher. IBM SPSS Statistics 20 (IBM) was used for all other statistical analyses.

Results

Environmental parameters

There was a high degree of spatial heterogeneity in physical and chemical characteristics within the Chesapeake Bay mainstem (Table 1), with ANOVA detecting significant differences between stations of all measured parameters ($p<0.0001$) with the exception of water temperature ($p=0.989$) over the ca. 300 km distance along the Bay. While the most apparent constituent of the estuarine gradient in Chesapeake Bay is the salinity increase downstream (as indicated by the significant positive linear regression with distance $p<0.000$, $R^2=0.862$), other parameters displayed a variety of spatial patterns, both linear and non-linear. Secchi depth also generally increased linearly downstream ($p<0.0001$, $R^2= 0.361$), with the highest water clarity at the baymouth. A number of environmental parameters declined with distance downstream in a relatively linear fashion, including DIN ($p<0.0001$, $R^2=0.615$), PP ($p<0.0001$, $R^2=0.267$), silica ($p<0.0001$, $R^2=0.558$), TN ($p<0.0001$, $R^2=0.721$) and TP ($p<0.0001$, $R^2=0.270$). These parameters all had highest average values in the upper Bay with lower values

TABLE 1. Physical and chemical parameters of Chesapeake Bay (CB) mainstem stations as well as their distance downstream from the mouth of the Susquehanna River for each season. Values are long term station averages (1985-2009) Abbreviation for parameters defined within text.

CB	km	Salinity ppt	Secchi m	DO mg L^{-1}	TSS mg L^{-1}	SIF mg L^{-1}	Temp C	DIN mg L^{-1}	DON mg L^{-1}	PN mg L^{-1}	TN mg L^{-1}	PO_4F mg L^{-1}	PP mg L^{-1}	TP mg L^{-1}	TN:TP
	0	0.00	0.93	9.3	9.9	1.28	17.7	1.149	0.242	0.142	1.528	0.008	0.027	0.043	39.71
1.1		(0.02)	(0.28)	(2.3)	(10.7)	(0.63)	(8.4)	(0.33)	(0.09)	(0.05)	(0.32)	(0.006)	(0.013)	(0.018)	(13.7)
	29	2.32	0.69	8.8	16.8	1.35	16.9	0.896	0.260	0.152	1.307	0.016	0.030	0.053	25.80
2.2		(2.17)	(0.29)	(2.2)	(9.5)	(0.63)	(8.3)	(0.37)	(0.07)	(0.08)	(0.35)	(0.008)	(0.014)	(0.015)	(8.1)
3.3	71	9.65	1.10	9.4	7.7	1.09	17.3	0.395	0.273	0.253	0.901	0.008	0.025	0.043	23.33
C		(3.35)	(0.37)	(2.2)	(3.3)	(0.42)	(8.4)	(0.33)	(0.05)	(0.10)	(0.28)	(0.006)	(0.010)	(0.014)	(11.3)
4.3	120	12.68	1.76	8.9	5.1	0.66	16.7	0.240	0.303	0.185	0.721	0.005	0.015	0.028	29.00
C		(3.09)	(0.47)	(2.2)	(1.3)	(0.38)	(8.2)	(0.23)	(0.05)	(0.05)	(0.22)	(0.004)	(0.005)	(0.009)	(14.9)
	170	14.59	1.87	9.0	5.3	0.40	17.0	0.146	0.316	0.184	0.643	0.003	0.013	0.025	29.65
5.2		(2.90)	(0.58)	(2.1)	(1.4)	(0.33)	(8.3)	(0.16)	(0.05)	(0.06)	(0.16)	(0.002)	(0.005)	(0.008)	(15.1)
	231	17.21	1.84	9.7	9.6	0.33	15.9	0.079	0.272	0.156	0.506	0.003	0.015	0.024	24.31
6.1		(2.93)	(0.61)	(2.0)	(6.5)	(0.28)	(8.3)	(0.10)	(0.07)	(0.07)	(0.13)	(0.003)	(0.007)	(0.010)	(11.0)
	270	20.19	1.71	9.4	9.3	0.25	15.7	0.050	0.229	0.139	0.418	0.005	0.015	0.025	18.98
6.4		(2.98)	(0.58)	(1.9)	(6.6)	(0.22)	(8.2)	(0.07)	(0.05)	(0.06)	(0.10)	(0.004)	(0.006)	(0.010)	(8.7)
	276	22.49	1.91	9.3	9.0	0.20	16.0	0.038	0.215	0.125	0.376	0.006	0.014	0.025	17.17
7.3E		(2.68)	(0.64)	(1.8)	(6.7)	(0.17)	(8.0)	(0.05)	(0.05)	(0.05)	(0.09)	(0.005)	(0.006)	(0.012)	(7.19)
	302	25.68	2.16	8.9	9.5	0.17	15.8	0.030	0.191	0.107	0.326	0.008	0.012	0.025	14.44
7.4		(3.18)	(0.85)	(1.6)	(8.2)	(0.15)	(7.3)	(0.03)	(0.06)	(0.04)	(0.09)	(0.006)	(0.005)	(0.010)	(5.56)

downstream. Other parameters were non-linear with downstream distance, and were better explained by quadratic regression models. For instance orthophosphate ($p<0.000$, $R^2=0.262$) and TSS ($p<0.0001$, $R^2=0.074$) both had a U-shaped distribution, with lowest concentrations in the mid Bay and higher values in the upper and lower regions. Conversely, average DO ($p=0.003$, $R^2=0.013$), DON ($p<0.0001$, $R^2=0.316$) and PN ($p<0.0001$, $R^2=0.128$) levels were highest in the mid Bay and lower in the upper and lower Bay stations, illustrated as an inverse U or hump shaped relationship with downstream distance.

Biological parameters

Phytoplankton abundance, productivity and composition also differed along the Chesapeake Bay transect (Table 2). ANOVA indicating significant differences between stations of total phytoplankton abundance (chlorophyll, productivity rate, cell densities) and composition (relative abundance of major groups). These biological parameters had varying spatial distributions within the Bay, with some explained by significant linear regression models with downstream distance, and others by quadratic polynomial models. Regression analysis indicated a weak, but significant negative linear relationship between total phytoplankton abundance and distance ($p<0.000$, $R^2=0.050$), with a lower average cell density downstream compared to upper Bay stations. Both chlorophyll concentrations and primary productivity rates were highest within the mid Bay, displaying a unimodal relationship better explained by significant quadratic regression models (chlorophyll $p<0.0001$, $R^2=0.024$, productivity $p<0.0001$, $R^2=0.182$).

The phytoplankton community of Chesapeake Bay contains species belonging to 13 major taxonomic groups spanning two domains, however between 97.1-99.3% of all

TABLE 2. Biological parameters of Chesapeake Bay (CB) mainstem phytoplankton stations. Values are long term station averages (CB1.1: 1985-1995, all other stations 1985-2009).

CB	Chlorophyll ($\mu g\ L^{-1}$)	Productivity rate ($\mu gC\ L^{-1}\ H^{-1}$)	Total phytoplankton abundance ($cells\ L^{-1}$)	Diatoms (percent abundance)	Dinoflagellates (percent abundance)	Cyanobacteria (percent abundance)	Chlorophytes (percent abundance)	Cryptomonads (percent abundance)	Others (percent abundance)
1.1	8.5	41.9	20,438,140	44.2%	0.7%	33.3%	16.0%	4.9%	1.0%
2.2	6.7	30.4	9,495,147	45.8%	6.4%	27.3%	5.4%	13.9%	1.3%
3.3C	13.5	59.3	17,227,386	39.9%	16.6%	21.2%	1.4%	18.0%	2.9%
4.3C	9.2	45.9	18,504,615	41.9%	9.8%	25.9%	1.8%	18.2%	2.4%
5.2	8.9	40.8	20,075,635	45.3%	6.0%	26.6%	1.7%	17.8%	2.5%
6.1	9.3	29.4	7,686,584	60.9%	5.9%	8.8%	1.0%	22.8%	0.7%
6.4	8.2	34.9	7,511,324	61.0%	6.6%	5.5%	1.3%	24.6%	1.1%
7.3E	6.8	25.3	5,976,787	62.7%	5.7%	7.0%	0.9%	23.0%	0.8%
7.4	5.3	23.1	5,477,952	65.8%	4.7%	6.6%	0.6%	21.6%	0.8%

algal cells identified belong to five groups. These include the prokaryotic cyanobacteria, and the eukaryotic chlorophytes, cryptomonads, diatoms and dinoflagellates. Diatoms were the most abundant phytoplankton group within all regions of Chesapeake Bay, making up between 39.9-65.8% of the average algal community (Table 2). Relative diatom abundance increased with proximity to the baymouth ($p<0.0001$, $R^2=0.102$). The percentage of cryptomonads also increased significantly in a linear fashion with downstream distance ($p<0.0001$, $R^2=0.110$), and represented approximately 20% of total cell abundance in all areas but the upper Bay. Conversely, the proportion of cyanobacteria ($p<0.0001$, $R^2=0.205$) and chlorophytes ($p<0.0001$, $R^2=0.179$) significantly declined from the upper to lower Bay stations. Cyanobacteria abundance was highest in the upper Bay, with moderate relative abundances in the mid Bay, and extremely low abundances in the lower Bay. The abundance of chlorophytes declined more rapidly with downstream distance, and were largely absent within the Bay except for the uppermost stations. Dinoflagellates made up a higher percentage of the phytoplankton within the mid Bay, with reduced representation in the upper and lower Bay regions, having a unimodal distribution better explained by a significant quadratic regression with distance ($p<0.0001$, $R^2=0.063$). The remaining taxa not belonging to these five categories were grouped into an others category, which had no significant ($p>0.05$) linear or quadratic relationship with distance.

Phytoplankton diversity

A total of 1480 phytoplankton taxa were identified within the Chesapeake Bay and its tidal tributaries over the course of over 25 years of monitoring (Table 3-Appendix). Diatoms contained the highest richness with 687 taxa belonging to 110

genera. Chlorophytes were represented by 279 taxa (71 genera) followed by dinoflagellates with 199 taxa (37 genera) A total of 125 cyanobacteria taxa were identified from 40 genera. Of the other taxa, these were 63 euglenophytes, 39 chrysophytes, 25 xanthophytes, 19 cryptophytes, 16 coccolithophores, 12 prasinophytes, six raphidophytes, five silicoflagellates, and five prymnesiphytes. Following the conventions of Reichert et al. (2010), 1297 taxa were considered rare (present in less than 1% of the total collections). There were 118 taxa considered intermediate (between 1% and 10%), and 65 common taxa (present in 10% or more of the collections). The most ubiquitous taxa included the diatoms *Skeletonema costatum*, *Chaetoceros* sp., *Thalassionema nitzschioides*, *Dactyliosolen fragilissimus*, *Cylindrotheca closterium*, *Ceratuaulina pelagica*. The dinoflagellates *Gymnodinium* sp., *Prorocentrum minimum, Heterocapsa rotundata*, and *Prorocentrum micans*, and the cryptomonad *Crytomonas* sp. also made up the most frequently observed taxa.

Alpha diversity, mesaured as species richness, varied by an order of magnitude, ranging from 6-76 phytoplankton taxa per sample, with a mean of 34.5. While characterized by relatively high species richness, the phytoplankton community generally had low species evenness. That is there was a large disparity between abundances of dominant and background taxa, such that 64% of samples had at least half of the total algal biomass due to one of the aforementioned algal groups. These collections were most often dominated by diatoms (24%), cryptomonads (18%), or dinoflagellates (16%). In 29% of the samples, a single species accounted for at least half of the total biomass. These samples were most often dominated by diatom species (20%), with *Ceratulina pelagica* and *Skeletonema costatum* being the most frequent dominant taxa.

A significant effect of salinity on alpha species richness was found, with significant regressions observed in each season (Fig. 3). The polynomial (quadratic) model better described the U-shaped relationship between the two variables more so than the linear model due to the high diversity at the freshwater station (CB1.1). Variability in salinity accounted for between 34 and 46% of the variability in phytoplankton species richness (Fig. 3). There was also a significant non-linear relationship between salinity and *H'*, however there was much greater variability, with the variability in salinity only explaining between 2 and 9% of the variability in *H'* depending on the season. There were also no significant linear ($p=0.578$) or quadratic ($p=0.710$) relationships between the salinity range experienced at a station and phytoplankton species richness (data not shown). The relationship between species richness and salinity was apparent in both the entire dataset (1985-2009) as well as the data from 1985-1995. Average station species richness values differed between 0.19% and 7.72% between the two datasets, compared to the up to 211% differences between different stations along the gradient. With the focus of this analysis on the spatial differences along the Bay transect, and due to the similarity in results, I have chosen to include the 1985-2009 data except where noted.

In all seasons, species richness was generally higher at the freshwater site and declined with increased salinity to a minimum in the 5-10 range and then increased with salinity to what were often the maximum levels at the highest salinities. Winter samples had the lowest average species richness at the freshwater station (CB1.1), while still having high diversity in the more saline sites leading to the most linear relationship with salinity (Fig. 3A). Winter collections also had higher variability in richness at many of the more saline locations, including particularly high values in the upper meshohaline/

lower polyhaline region (15-20) and lower values in the upper polyhaline locations (>25). Spring collections were the most variable, including both high and low richness in the oligohaline and lower mesohaline, resulting in the lowest R^2 values (Fig. 3B). Spring collections also included samples with the highest species richness, originating from the freshwater site. Summer and fall collections were the most bimodal, with high species richness in freshwater and polyhaline waters and low diversity in meso- and oligohaline locations, resulting in U-shaped distributions with the steepest slopes (Fig. 3C,D). Diversity as measured by *H'* was much more variable, with less apparent relationship with salinity or seasonal patterns (Fig. 4). In contrast to species richness, which was minimal at lower mesohaline salinities, *H'* although variable, was often lowest at higher salinities, generally near 12-15. This trend was most apparent in the spring, with average *H'* values below 2.5 at meso and polyhaline stations.

The level of spatial gamma diversity varied greatly, ranging between 72-184 different algal taxa observed within the Chesapeake Bay (1985-1995) during a one month time period, and between 257-383 taxa within a calendar year. Spatial gamma diversity was significantly different between seasons ($p<0.0001$) (Fig. 5). The highest average total number of phytoplankton taxa (115.4) was observed in the autumn. Samples collected during spring had the lowest average gamma diversity (91.8), significantly lower than summer (102.8) and autumn, but not significantly different than average winter values (101.9). Temporal gamma diversity at each station was also highly variable, ranging from 52-168 unique algal taxa observed during a year at an individual station. Temporal gamma diversity was related to salinity in much the same way as alpha diversity (Fig. 6), being best described by a significant U-shaped quadratic regression

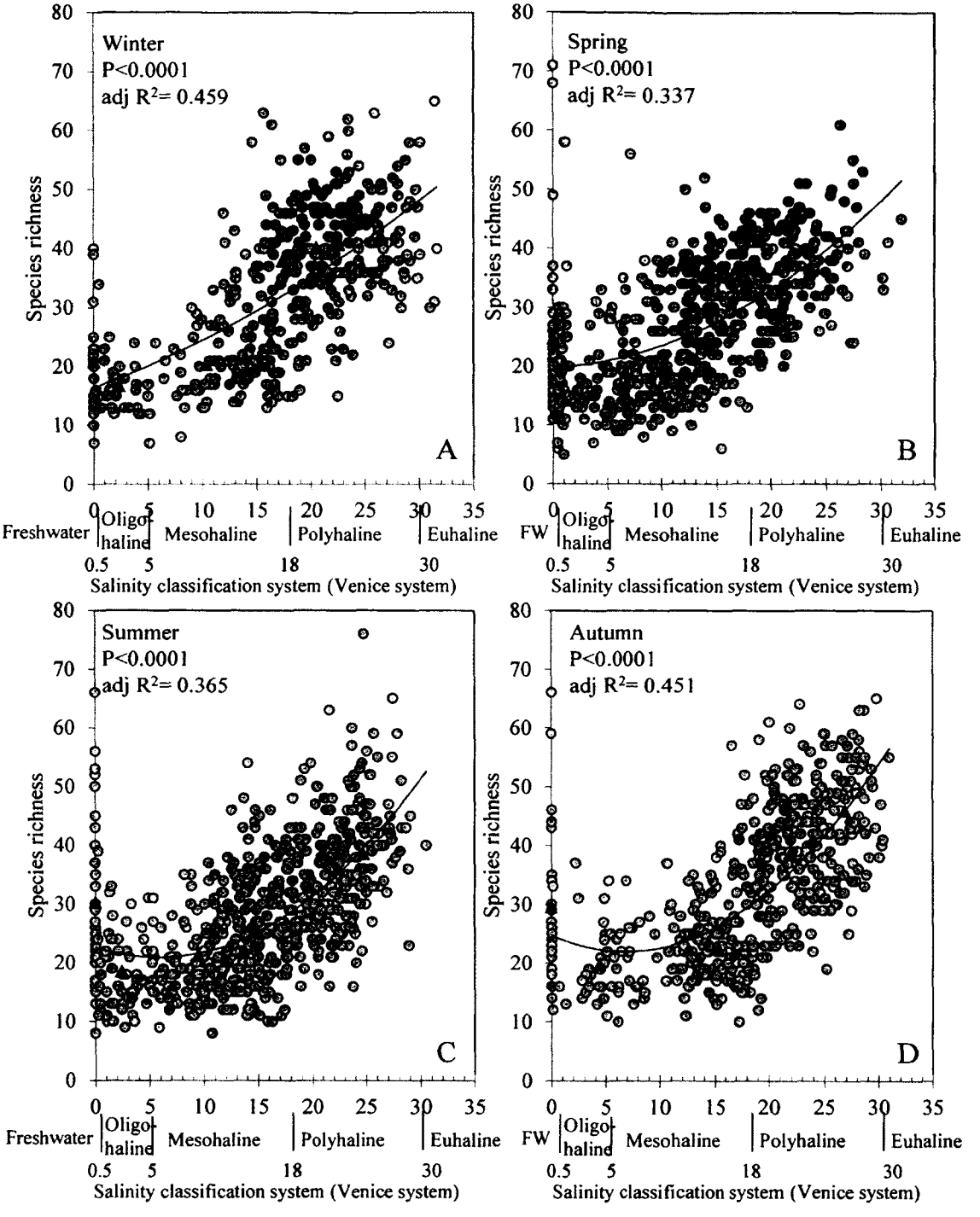

FIG. 3: Seasonal phytoplankton species richness and salinity values collected within Chesapeake Bay in (1985-2009). All collection data shown illustrated as circles, with triangles representing mean values for the nine sampling stations. Trendlines illustrate significant non-linear (quadratic) regressions between richness and salinity.

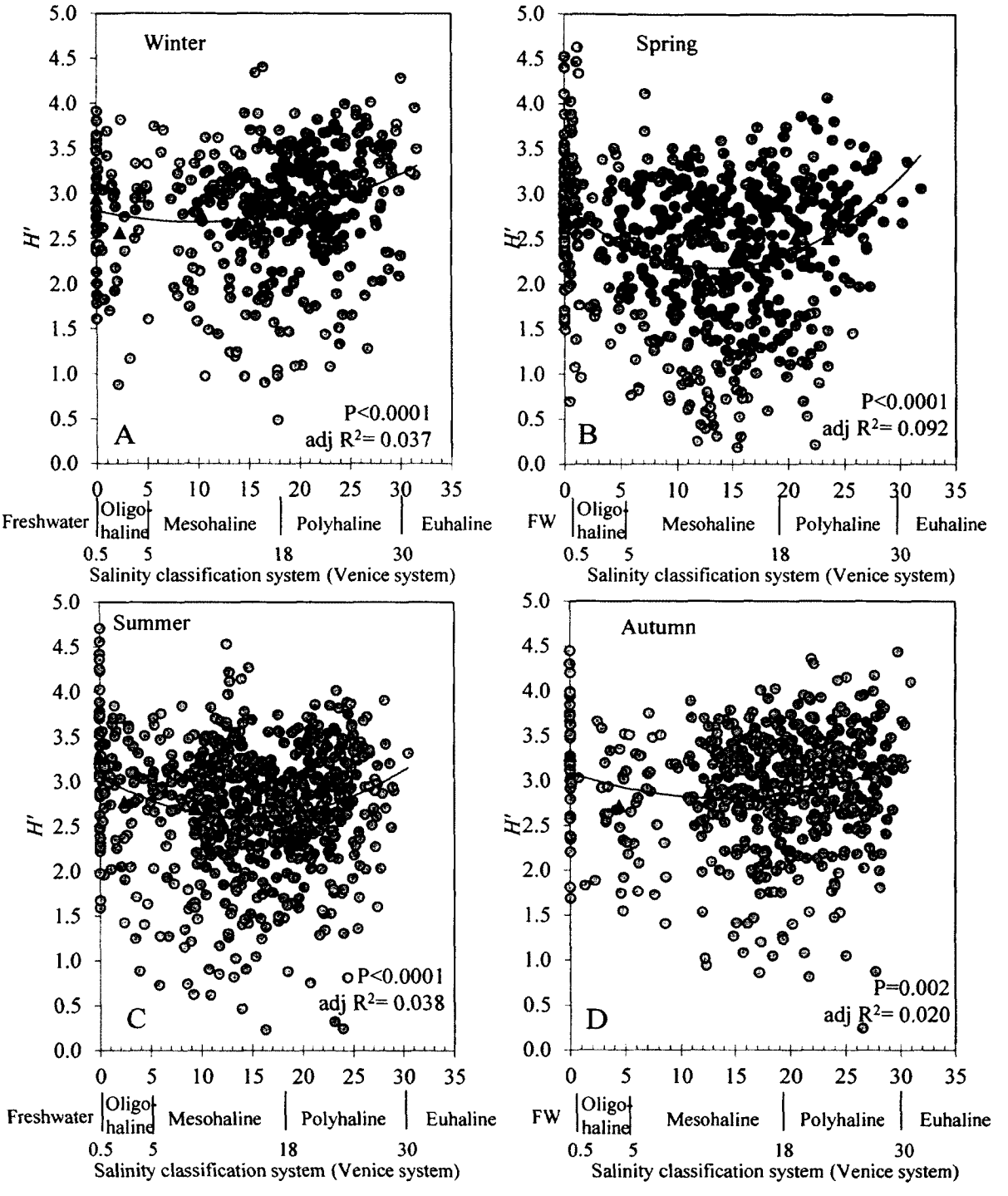

FIG. 4: Seasonal phytoplankton diversity (Shannon index *H'*) and salinity values collected within Chesapeake Bay in (1985-2009). All collection data shown illustrated as circles, with triangles representing mean values for the nine sampling stations. Trendlines illustrate significant non-linear (quadratic) regressions between richness and salinity.

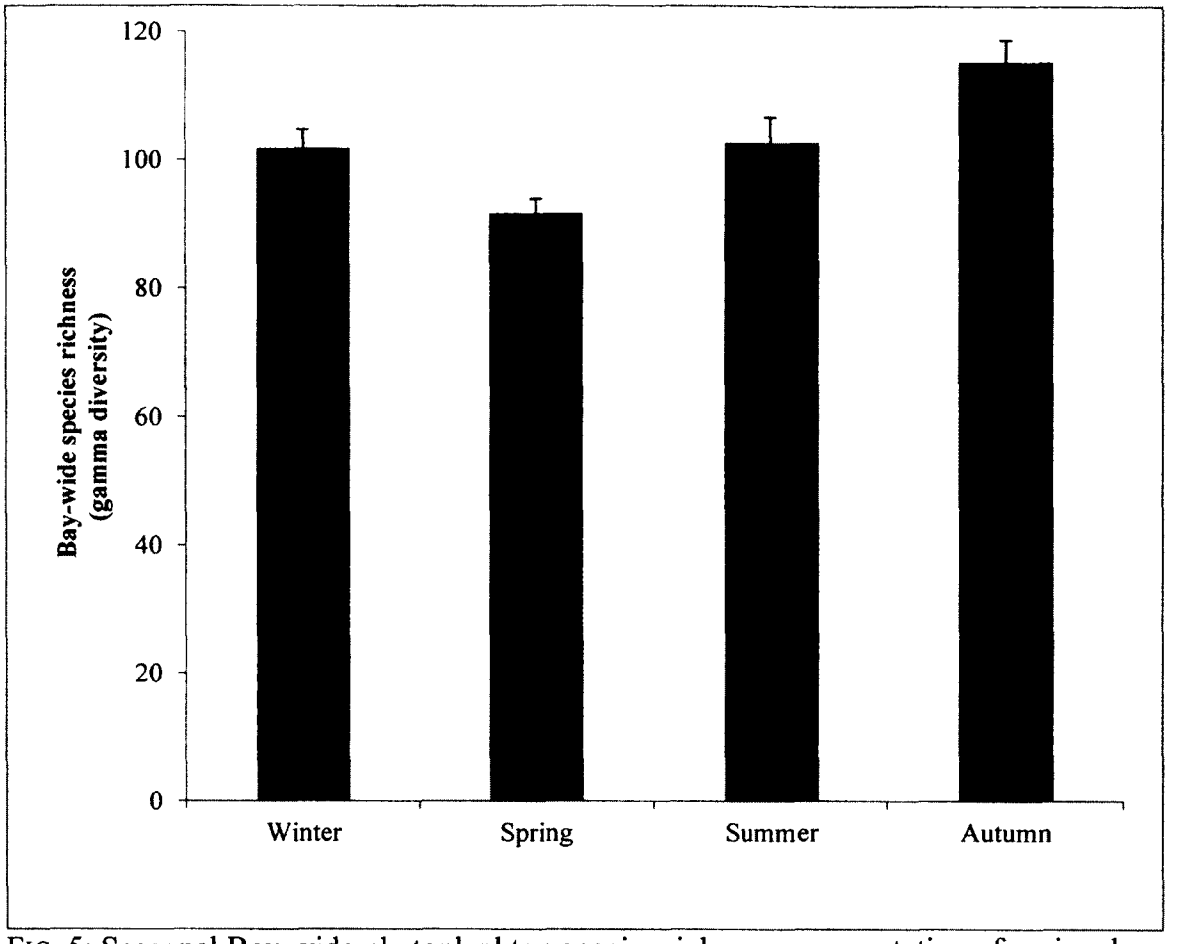

FIG. 5: Seasonal Bay-wide phytoplankton species richness representative of regional (gamma) diversity (1985-1995). ANOVA indicates significant differences in richness between seasons ($p<0.000$). Groups with the same letter are not significantly different than each other.

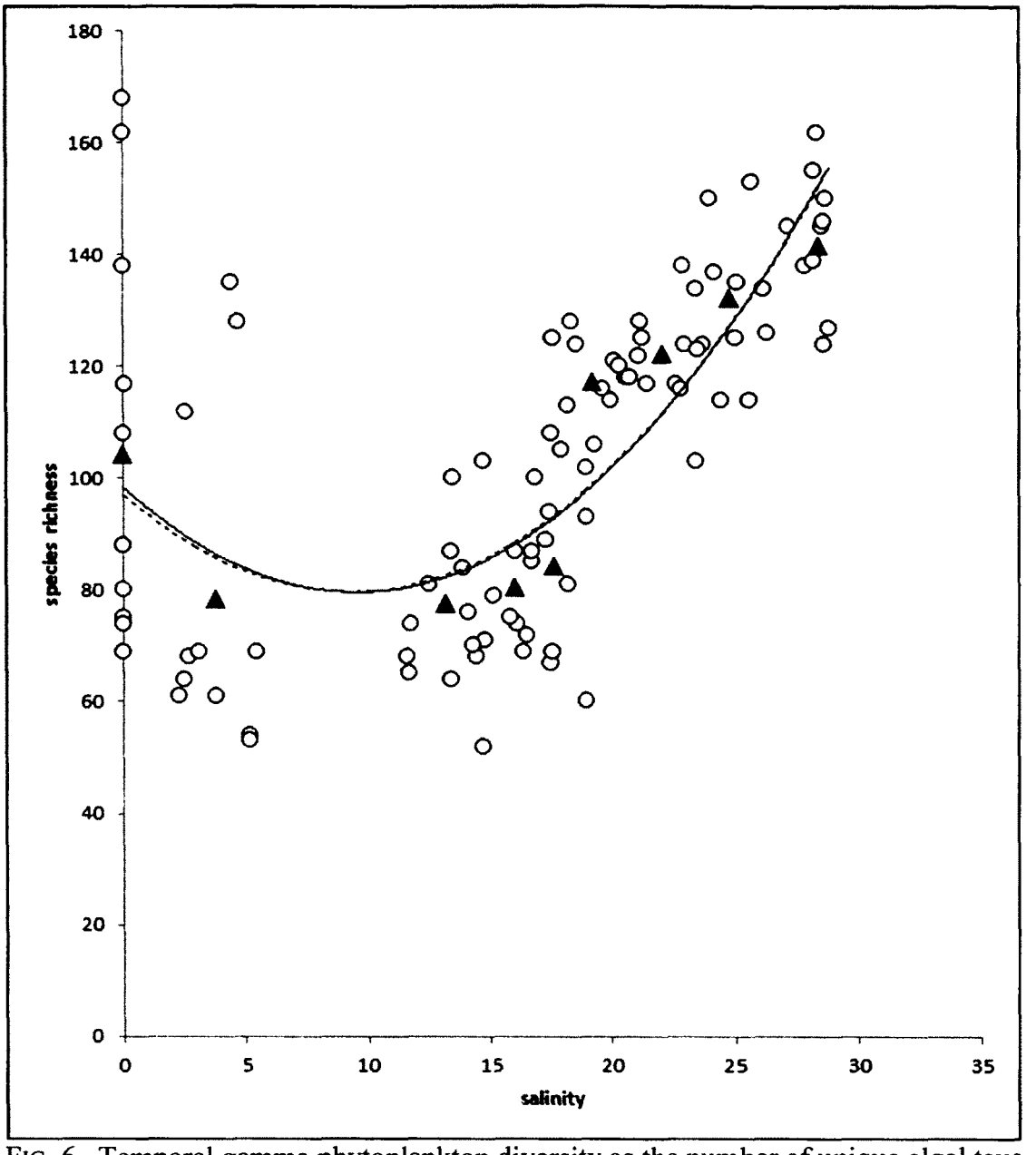

FIG. 6. Temporal gamma phytoplankton diversity as the number of unique algal taxa observed at a station (n=9) each year (n=11) plotted against the annual average salinity at that station (1985-1995). Long-term station averages are displayed as triangles. Trendline indicates a significant U-shaped quadratic regression between salinity and gamma species richness ($p<0.000$, $R^2=0.501$)

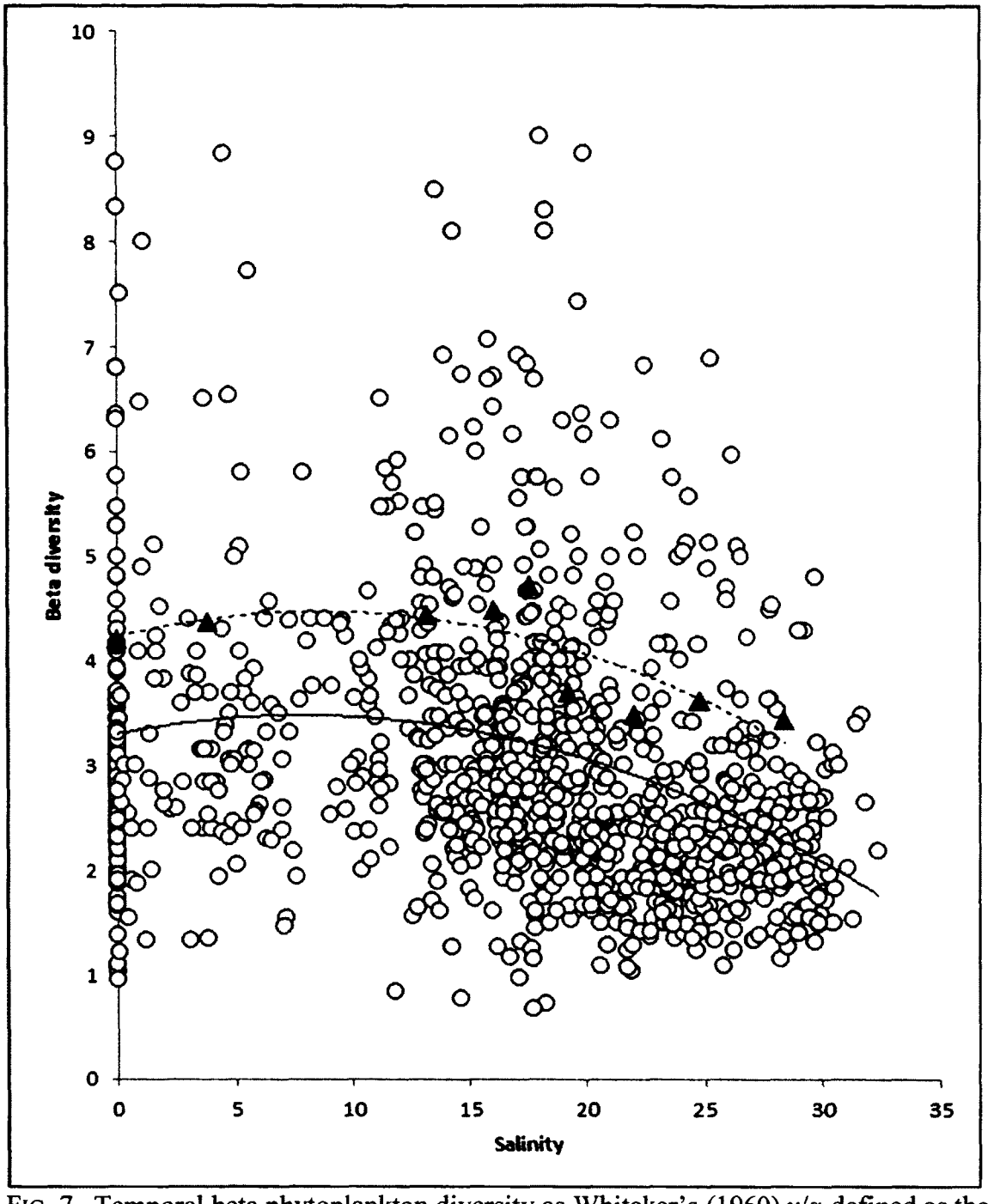

FIG. 7. Temporal beta phytoplankton diversity as Whitaker's (1960) γ/α defined as the yearly species richness of a station divided by the monthly richness observed, plotted against the monthly salinity values (1985-1995). Long-term station averages are displayed as triangles. Trendline indicates a significant unimodal quadratic regression between salinity and gamma species richness ($p<0.000$, $R^2=0.083$)

model ($p<0.0001$, $R^2 = 0.501$). While there was a greater degree of variability, particularly in the oligohaline region, the trend was similar with reduced diversity at intermediate salinities, with greater values at the upper and lower reaches of the estuary. Temporal beta diversity also varied with salinity, with significant negative linear ($p<0.000$, $R^2=0.055$) and hump shaped quadratic ($p<0.0001$, $R^2=0.083$) regressions, although with a much weaker signal than the other diversity metrics (Fig. 7). While weak, the trend was for a greater degree of temporal beta diversity in the mesohaline region, and lower salinities in general in relation to the polyhaline samples. Stations with higher temporal beta diversity experienced a greater degree of variation in average monthly species richness in relation to the total diversity present at the station during the year, and therefore had a higher degree of difference in species present throughout the year (Arscott et al. 2003). Stations with lower beta diversity, such as the polyhaline had less variation in species richness, with a lower variability of species present over time.

Phytoplankton composition

The NMDS ordination analyses of phytoplankton species abundances illustrated that community composition varied greatly within the Bay throughout the four seasons (Figs. 8-11). The ordination plots show how similar the phytoplankton communities are based on their distance to each other. Points which are close to each other represent similar species composition while those that are further away are less similar. These metrics incorporate both the presence/absence of individual species and the abundances of those species. The points are coded by station, with each point representing the average monthly phytoplankton composition for that station, based on the long-term average of individual species abundances (1985-2009). Again, separate NMDS analyses

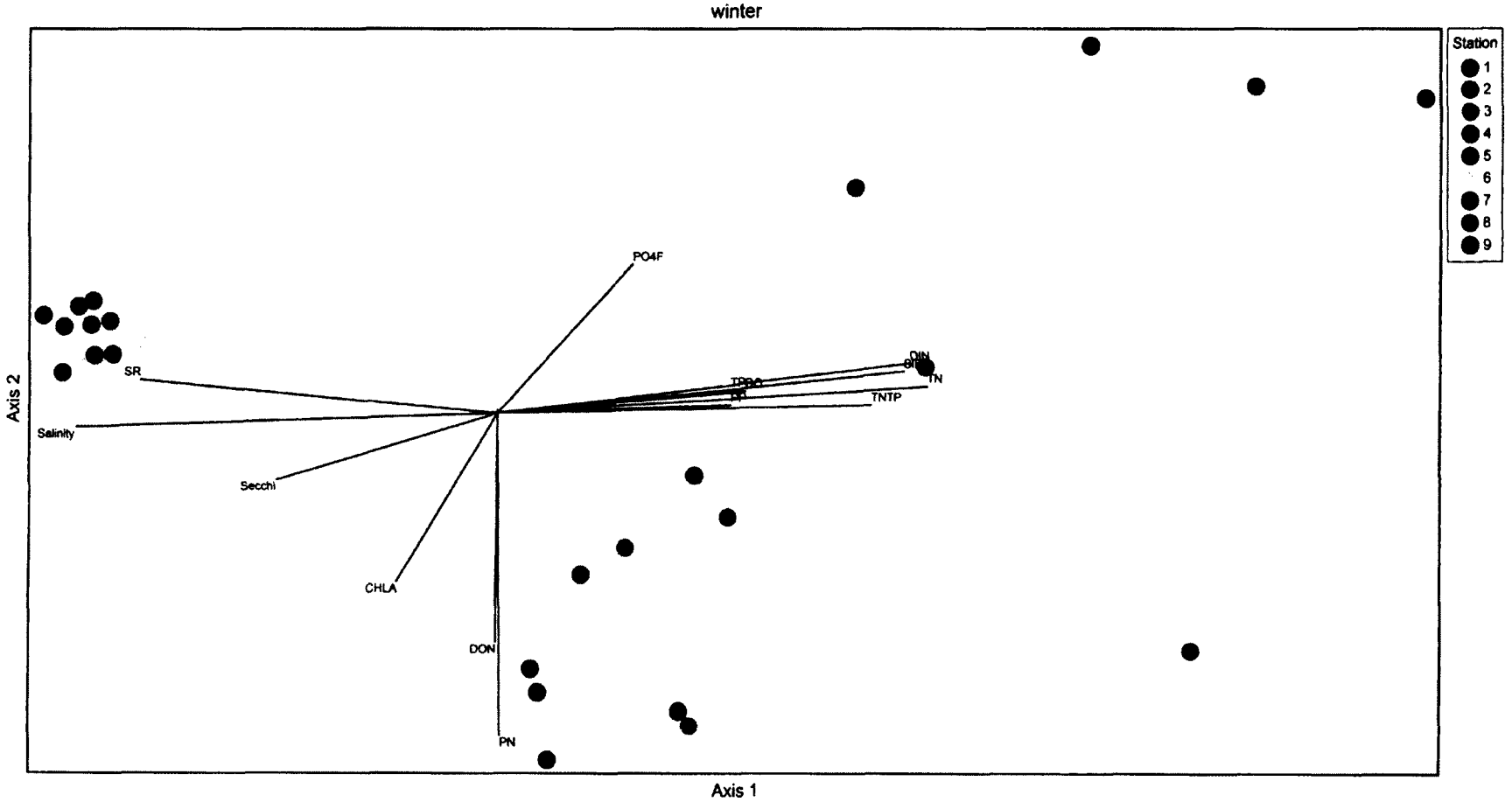

FIG. 8: NMDS Ordination by phytoplankton data of winter collections, showing spatial differences in environmental factors and algal species composition. Each point represents the mean abundance of phytoplankton species for a given station and month (CB6.1: 1985-1995, all other stations 1985-2009). Similarity in species composition between is represented by distance between points. Vectors indicate correlation with environmental and biologic variables and species composition, with length representative of strength of relationship (r^2). Vectors with r^2 of 0.3 and higher shown.

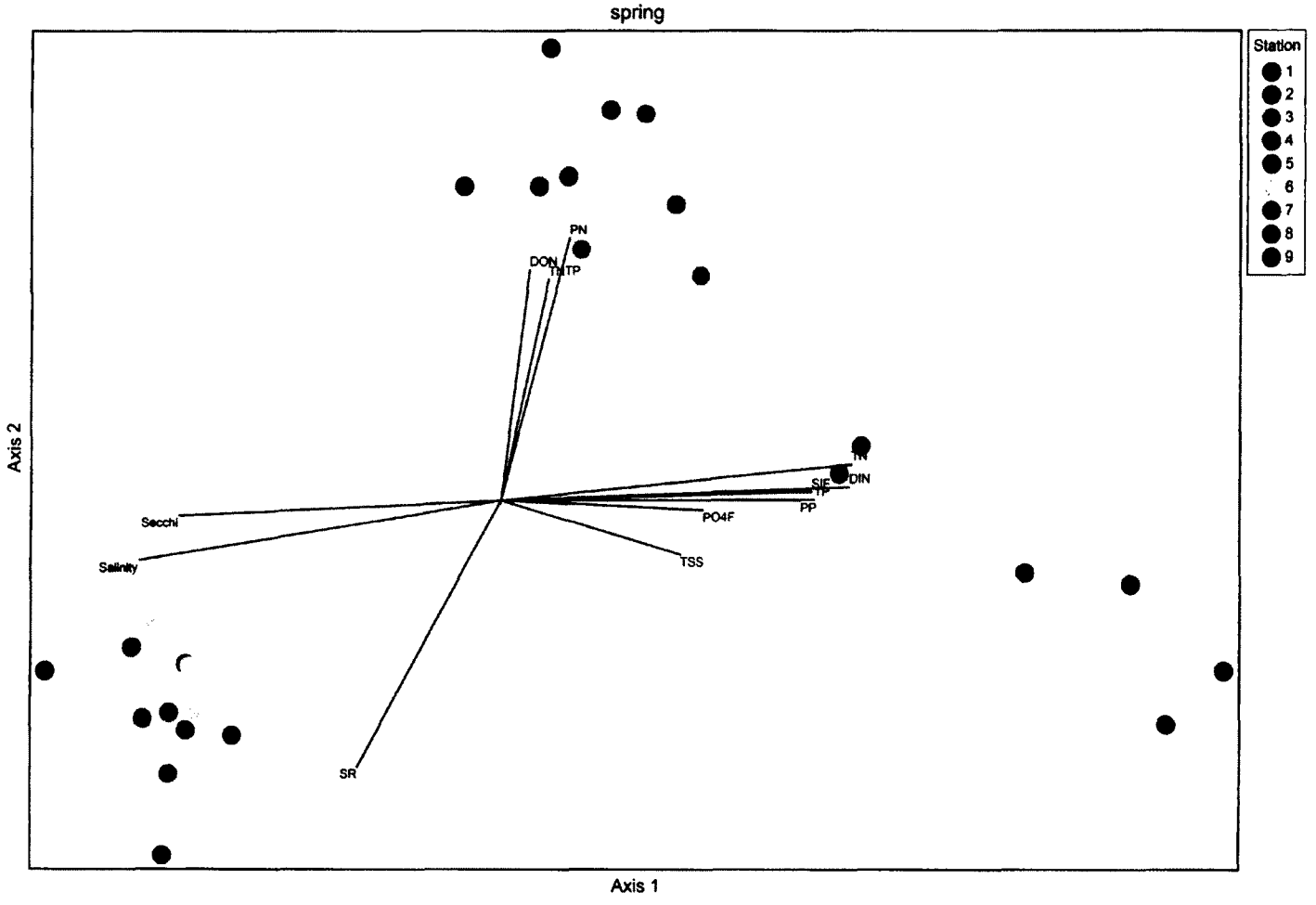

FIG. 9: NMDS Ordination by phytoplankton data of spring collections, showing spatial differences in environmental factors and algal species composition. Each point represents the mean abundance of phytoplankton species for a given station and month (CB6.1: 1985-1995, all other stations 1985-2009). Similarity in species composition between is represented by distance between points. Vectors indicate correlation with environmental and biologic variables and species composition, with length representative of strength of relationship (r^2). Vectors with r^2 of 0.3 and higher shown.

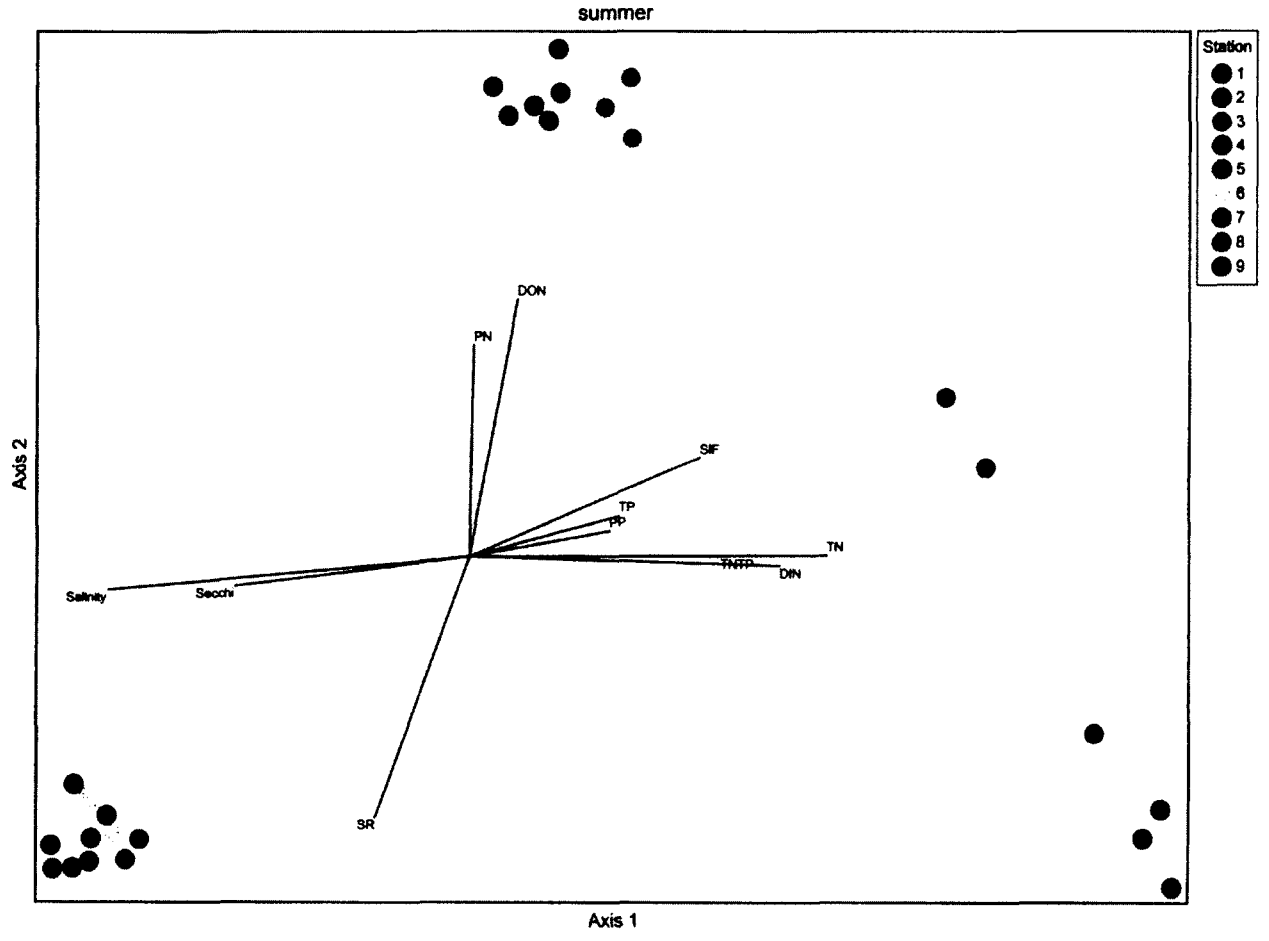

FIG. 10: NMDS Ordination by phytoplankton data of summer collections, showing spatial differences in environmental factors and algal species composition. Each point represents the mean abundance of phytoplankton species for a given station and month (CB6.1: 1985-1995, all other stations 1985-2009). Similarity in species composition between is represented by distance between points. Vectors indicate correlation with environmental and biologic variables and species composition, with length representative of strength of relationship (r^2). Vectors with r^2 of 0.3 and higher shown.

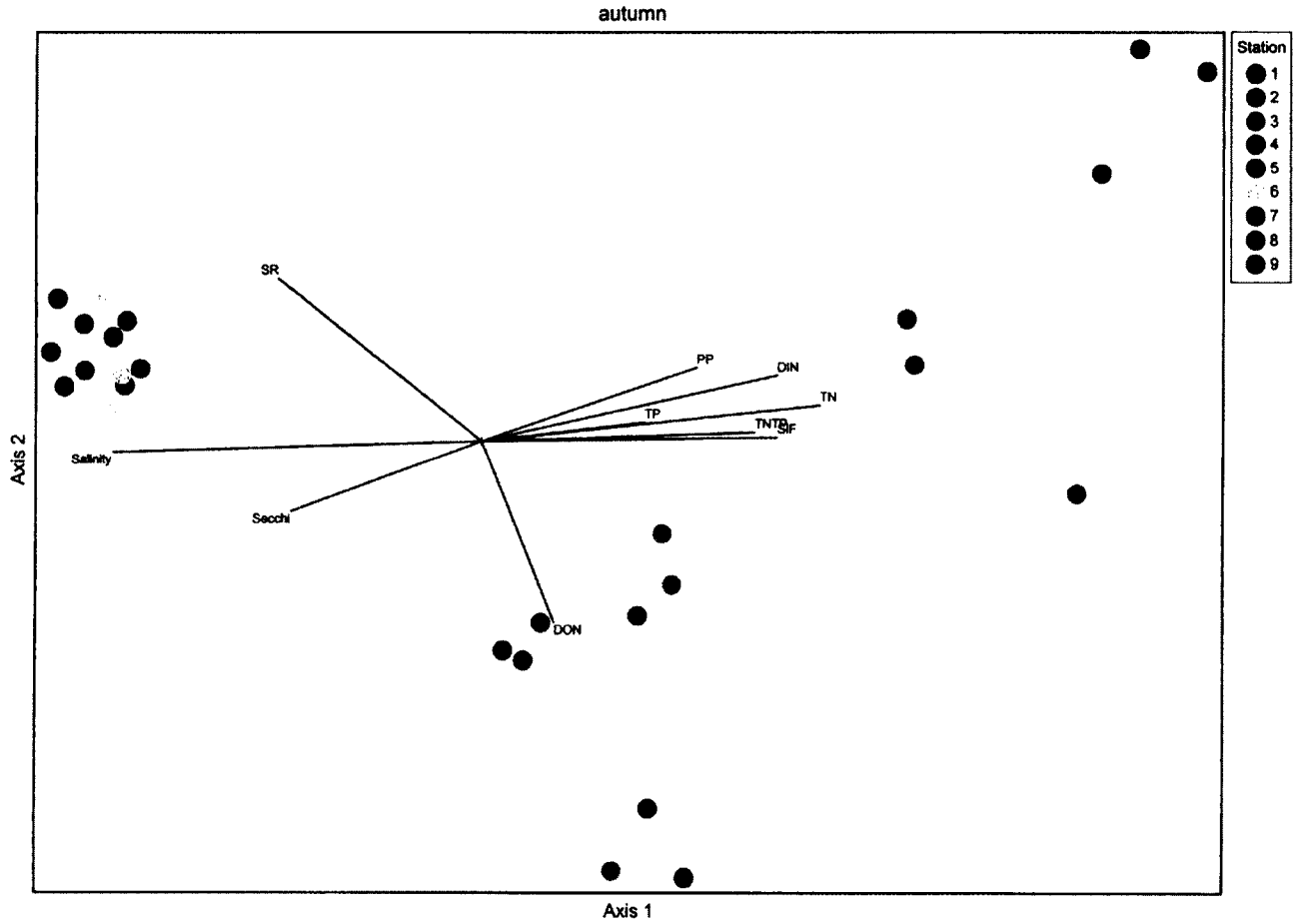

FIG. 11: NMDS Ordination by phytoplankton data of autumn collections, showing spatial differences in environmental factors and algal species composition. Each point represents the mean abundance of phytoplankton species for a given station and month (CB6.1: 1985-1995, all other stations 1985-2009). Similarity in species composition between is represented by distance between points. Vectors indicate correlation with environmental and biologic variables and species composition, with length representative of strength of relationship (r^2). Vectors with r^2 of 0.3 and higher shown.

were conducted utilizing only the 1985-1995 data, which produced comparable results to the full dataset, including the same spatial and seasonal patterns of composition, as well as relationships with environmental factors, and did not offer any additional insights or contradictory results to those using the full dataset. Therefore only the results of the NMDS analysis on the complete 1985-2009 data are presented. The NMDS ordinations also contain vectors which represent the correlation between the environmental variables and the distribution of species compositions. These describe both direction and strength, as the bearing of the line is towards increasing higher values and the length of the line indicates the R^2 value of the parameter. Only those variables with a correlation coefficient of 0.3 or higher are shown on the plots. Species richness, chlorophyll, total cell abundance and primary productivity rates are also included as vectors, to further illustrate the relationship between alpha diversity, the environmental variables, and the phytoplankton species composition and abundance. The vector data are also based on the long-term monthly averages for each station. This approach captured the vast majority of the variability of the dataset, with the seasonal biplots accounting for between 91-97% of the variance in the distance matrix within the two plotted axes.

Phytoplankton composition varied both spatially (between stations) and temporally (both between and within seasons). While there were differences in each season, the ordination bi-plots (Figs. 8-11) indicate several patterns and groupings of similarity in species composition that are consistent with the spatial distribution of the sampling sites. Samples from the four polyhaline stations (CB6.1, CB6.4, CB7.3E and CB7.4) form a distinct assemblage in the left half of each seasonal plot, indicating a very similar composition within this region, relative to the rest of the Bay. Diatoms, including

Skeletonema costatum, Ceratulina pelagica and *Dactyliosolen fragilissimus* dominated this region year-round along with the flagellate *Cryptomonas* sp. Species composition in the mesohaline stations (CB3.3C, CB4.3C and CB5.2) were similar to each other, with points from these stations concentrated in the center of the joint plots. This grouping is tighter in the analysis of the summer months (Fig. 10) indicating similar composition between stations at this time of the year, with less similarity in other seasons, particularly in the winter (Fig. 8). This region contained a variety of algal taxa of varying abundances depending on the season. Winter algal composition was dominated by diatoms, including *S. costatum* and *Chateoceros* spp., with spring samples containing a larger fraction of cyanobacteria and dinoflagellate taxa including the bloom forming taxa *Microcystis* spp. and *Prorocentrum minimum.* Cell abundance was greatest in the mesohaline Bay during the summer season and strongly dominated by cyanobacteria including *Microcystis* and *Merismopedia* species, with lesser densities during autumn. Collections from the oligohaline (CB2.2) and freshwater (CB1.1) stations were generally more distantly related to other species compositions, located to the right on the ordination plots (Fig. 8-11). The composition within the freshwater collections were the most dissimilar to the other sites, and could be described as forming its own grouping, particularly in the autumn (Fig. 11). The freshwater region was seasonally dominated by a variety of cyanobacteria with *Microcystis*, *Merismopedia* and *Oscillatoria* species being the most dominant, particularly during summer. This station also contained a much higher number of chlorophyte taxa than other regions in the Bay, with *Scenedesmus quadricauda* being the most abundant. Composition within the oligohaline station was intermediate between the freshwater and mesohaline collections, and was more similar to one group,

or the other depending on the season. In the spring the composition of the oligohaline and freshwater stations were more similar, with high concentrations of small diatoms including *Cyclotella* species, and filamentous cyanobacteria such as *Oscillatoria* (Fig. 9).

The 1st axis of the ordination plots describes much of the overall estuarine gradient present, both in terms of the location of the phytoplankton stations and the environmental parameters that are associated with those stations (Table 3). In general the horizontal axis of the plot describes the spatial distribution and condition along the length of the Chesapeake Bay from north to south (Figs. 8-11). The composition of the collections made closest to the baymouth are located to the left of the plots, with increasingly upstream collections shown further to the right. The overlaid vectors also describe the changing environmental variables along this gradient, with salinity, secchi depth and generally nutrient concentrations (particularly nitrogen and especially DIN) all strongly correlated with the 1st axis (Table 3). The 2nd axis (vertical) is most correlated with DON and PN, and much less so by salinity (Table 3).

Species richness, chlorophyll, productivity and abundance are correlated in very different ways with the species composition patterns and environmental factors (Table 4). Species richness is correlated with both axes, especially in the winter and autumn seasons, while the other biological metrics are generally only correlated with one axes, and largely to a much lower degree (Table 3). There are differences in some parameters seasonally, but the lower-Bay collections to the left of the plots are associated with higher salinity and water clarity, and lower nutrient concentrations, particularly both the organic and inorganic forms of nitrogen as well as silica and to a lesser degree phosphorus. The mid Bay collections (those points marked in the central portion of the ordinations) are

TABLE 3: Pearson correlations between environmental and biological variables and ordination axes of NMDS similarity matrix ordination plots of Chesapeake Bay phytoplankton species composition for each season. Winter: Dec-Feb, Spring: Mar-May, Summer: Jun-Aug, Autumn: Sep-Nov.

	Winter		Spring		Summer		Autumn	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Salinity	0.871	0.028	0.877	0.142	0.921	0.084	0.911	0.027
Secchi	0.458	0.134	0.783	0.037	0.597	0.073	0.473	0.170
DO	0.514	0.045	0.001	0.000	0.137	0.048	0.040	0.004
TSS	0.003	0.123	0.464	0.129	0.004	0.140	0.003	0.153
SIF	0.842	0.085	0.756	0.020	0.590	0.247	0.732	0.011
Temperature	0.297	0.001	0.001	0.007	0.025	0.005	0.035	0.019
DIN	0.855	0.102	0.848	0.034	0.794	0.024	0.731	0.160
DON	0.003	0.463	0.071	0.547	0.125	0.638	0.181	0.438
PN	0.007	0.650	0.166	0.620	0.012	0.524	0.098	0.098
TN	0.890	0.055	0.851	0.085	0.913	0.004	0.838	0.088
PO_4F	0.281	0.302	0.491	0.024	0.131	0.002	0.180	0.059
PP	0.483	0.019	0.729	0.000	0.358	0.063	0.534	0.177
TP	0.484	0.047	0.762	0.003	0.382	0.102	0.403	0.046
TN:TP	0.774	0.017	0.115	0.522	0.643	0.001	0.676	0.022
Chlorophyll	0.209	0.068	0.010	0.239	0.125	0.240	0.022	0.000
Productivity	0.027	0.284	0.221	0.077	0.582	0.612	0.253	0.378
Cell abundance	0.090	0.347	0.174	0.267	0.265	0.008	0.285	0.005
Species richness	0.738	0.068	0.350	0.629	0.241	0.645	0.507	0.391

related with intermediate values of salinity and secchi depth, and intermediate concentrations of inorganic and total nitrogen. These assemblages, are most related with increased levels of organic and particulate nitrogen year round, and elevated TN:TP ratios in spring (Figs. 8-11). The groupings of the oligohaline, and to a greater degree the freshwater collections are associated with low salinity and water clarity, and highest concentrations of nutrients, especially inorganic nitrogen. The position of the CB1.1 and polyhaline samples in the opposite half of the plots as the DON and PN vectors also illustrates that these sites are connected with reduced levels of organic and particulate nitrogen, particularly in the summer (Fig. 10).

Discussion

Estuaries represent complex transitional habitats of multiple environmental gradients including the continuum from marine to freshwater. In Chesapeake Bay, there is a multifaceted gradient of highly correlated variables that influence phytoplankton growth and composition, including salinity, nutrient concentrations and light availability (Table 1). The ordination analyses (Figs. 8-11) illustrate the strong interconnectedness of environmental parameters over the length of the estuary. While the physical and chemical features within the Bay do transition over the 302 km between the Susquehanna River and the Atlantic Ocean, not all do so in a continually directional fashion that is often implied in estuary gradients. The resulting combination of linear and non-linear gradients leads to a spatially heterogeneous environment capable of supporting a large and diverse biological overall community (gamma diversity), made up of multiple dissimilar community assemblages.

Alpha species richness was highly correlated with salinity more consistently with the Artenminimum model of Remane (1934) than that proposed by Telesh et al. (2011), with minimal algal species generally found in regions with salinities of 5-10 (Fig. 3). The Artenminimum model does a much better job describing species richness patterns than diversity as *H'* along a salinity gradient (Fig. 4). These results are consistent with the majority of examinations of species richness of organisms within estuaries (Whitfield et al. 2012), including within tributaries of Chesapeake Bay (Wagner 1999). In contrast to the results of Attrill (2002), this relationship is linked to the salinity value itself, or another correlated variable (such as secchi or TN) and not the variation in salinity, as there was no significant relationship between salinity range at a site and species richness. The model proposed by Attrill (2002) may better describe the degree of stress on species richness due to salinity fluctuations exerted on benthic organisms such as those on which it is based rather than plankton. Additionally, the range in salinity examined by Attrill (2002) in the Thames estuary (0-35) exceeds that observed in this study (0-27), with the upper polyhaline samples having minimal salinity fluctuations in the Thames. Therefore it is possible that an extended transect of data collections from the baymouth into the higher salinities of the Atlantic might reveal species richness patterns more indicative of the Attrill (2002) model.

Phytoplankton spatial distributions within estuaries in general and Chesapeake Bay in particular are complex and have been recognized as heterogeneous by multiple investigators (eg. Marshall and Nesius 1996, Kemp et al. 2005, Roman et al. 2005, Lacouture et al. 2006, Adolf et al. 2006). Even with a high degree of seasonal variability, the assemblages of phytoplankton composition illustrated by the NMDS ordination

analyses generally align to unique habitats along the length of the Bay. While these habitats can be defined by multiple environmental and biological traits, they can be described for convenience using the construct of the salinity boundaries known as the Venice System, defined in short as freshwater/limnetic zone 0-0.5, oligohaline zone 0.5-5, mesohaline zone 5-18, polyhaline zone 18-30, and euhaline zone >30 (Oertli 1964, Bleich et al. 2011). There is growing evidence that these zonations, particularly the separation between oligohaline and lower mesohaline waters (5-10) constitute more of a biologic boundary (ecocline) than a steady transition between the two (ecotone) (Attrill and Rundle 2002). The relative similarity of species composition within these zones and dissimilarity between zones indicates a strong effect of the salinity gradient on the plankton community structure. High species turnover (beta diversity) near the meso/polyhaline transition has also been observed in the Schelde estuary of Belgium and the Netherlands, where it represented the transition between riverine and coastal phytoplankton communities (Muylaert et al. 2009). This relationship with salinity also appears to have a temporal component, with the stations located in the mesohaline, generally having higher average temporal beta diversity values than stations at higher and lower salinities (Fig. 7).

The freshwater community of Chesapeake Bay collected at the mouth of the Susquehanna River typically contained a greater abundance of cyanobacteria species including colonial and filamentous bloom forming species typical of eutrophic freshwater systems (Steinberg and Hartmann 1988). These populations included the toxin producing species *Microcystis aeruginosa* and *Aphanizomenon flos-aquae,* plus representatives from other genera which contain potentially toxic species including *Anabaena* (Marshall

et al. 2008). Along with the lowest salinity, this community was associated with the highest nitrogen concentrations in the Bay, particularly the level of DIN which was as much as two orders of magnitude higher than other regions. There was considerable inter- and intra-annual variability, but average (α) and annual (γ_T) species richness was generally high (Fig. 3) along with a relatively high degree of temporal beta diversity (Fig. 7) indicating a more variable species composition throughout the year.

Environmental conditions were highly variable at the station CB2.2, with average salinity fluctuating seasonally within the oligohaline zone. During the spring when salinities at the station were lowest, the phytoplankton composition was most representative of freshwater conditions including the same cyanobacteria observed upstream, and least so in autumn, with a greater abundance of diatoms and flagellates particularly the bloom forming *Heterocapsa rotundata*. Water clarity was lowest in this region with the highest levels of TSS (Table 1). These conditions contribute to light limitation (Kemp et al. 2005) and reduced phytoplankton abundance, biomass and productivity (Table 2). The oligohaline also has some of the lowest levels of algal diversity observed, both at the α level (Fig. 3) and at the γ_T level (Fig. 6), further illustrated by the separation of the species richness vector and the composition of collections from this region especially during the winter (Fig. 8). This region had a variable inter-annual species composition indicated by the elevated average β_T values (Fig. 7).

The mesohaline zone, located within the mid Bay, while having intermediate values of most environmental parameters (Table 1) (particularly salinity and nitrogen concentrations), have the highest levels of phytoplankton biomass and productivity

(Table 2). The mid Bay is also deeper than the upper and lower Bay, with a greater residence time (Roman et al. 2005), and consequently the site of the highest degree of hypoxia and anoxia ("deadzones") within the Bay (Cerco and Cole 1993, Kemp et al. 2005). This region contains a number of HAB taxa including the previously mentioned cyanobacteria and the bloom forming dinoflagellate *Prorocentrum minimum*. *P. minimum* blooms, commonly known as mahogany tides, are prevalent in this region and have been associated with finfish and shellfish mortality and loss of submerged aquatic vegetation habitat (Tango et al. 2005). While containing intermediate values of TN and DIN, this zone had the highest concentrations of DON and PN in the Bay (Table 1, Figs. 8-11). Elevated DON has been linked to cyanobacteria and dinoflagellate blooms (Glibert et al. 2001, Glibert et al. 2004). Average and annual phytoplankton species richness was generally low, with stations CB3.3C at the mouth of the Chester River (just below Baltimore, MD) and CB4.3C at the mouth of the Choptank River regularly having the lowest diversity in the Bay, often with only half the number of taxa observed compared to the upper and lower Bay stations. While α and γ diversities were low, this area had the highest average values of β_T diversity, indicating the greatest level of intra-annual species turnover (Fig. 7; Shurin et al. 2010).

Higher salinities and lower nutrient concentrations (particularly nitrogen) were observed within the polyhaline Bay (Table 1). Water clarity was highest in this region along with the lowest average levels of phytoplankton abundance and productivity (Table 2). These conditions were associated with a diverse number of algal species including a dominance of centric chain forming diatoms, particularly the ubiquitous taxa *S. costatum*, *D. fragillissimus* and *C. pelagica*. A higher percentage of centric diatoms relative to

pennate forms is often linked to eutrophication (Cooper 1995). However, this group is also much more associated with more saline waters than are pennate diatoms (Guillard and Kilham 1977), so the linkage along this gradient is confounded and potentially spurious. Cryptomonads as a group increased within the Bay with salinity and were most abundant in the polyhaline zone, making up a significant portion of the phytoplankton community throughout the year (Table 2). Alpha and gamma species richness was generally high within the polyhaline, with the highest levels observed at the baymouth (station CB7.4). This station often contained not only a diverse mixture of taxa observed throughout the rest of the Bay, but also numerous oceanic species rarely encountered at other sites, including large pelagic diatoms such as *Odontella sinensis* and oceanic associated dinoflagellates including *Dinophysis caudata*. There was a much lower degree of seasonal species turnover in the polyhaline, with average beta diversity values lower than the rest of the Bay (Fig. 7). The relative stability of environmental factors compared to upstream habitats was reflected in a lower degree of variability in species composition and variation in species richness over time.

While there has been considerable debate regarding the issue, there is a growing consensus of evidence that higher biological diversity is associated with greater ecosystem stability (Tilman et al. 1998, McCann 2000, Cadotte et al. 2012). One of the proposed pathways of this relationship is that more diverse communities exhibit greater resistance and resilience to environmental stressors and biological invasions (Alison 2004, Britton-Simmons 2006). Both low alpha diversity (Paavola et al. 2005) and high beta diversity (Steiner and Leibold 2004) have been linked to greater susceptibility to biological invasions. HABs have been characterized as biological invasions and linked to

periods of low stability in freshwater habitats in which there was higher probability of *M. aeruginosa* blooms following the beginning of a decline in algal species diversity (Chalar 2009). There have been other attempts to utilize phytoplankton diversity as a metric of ecosystem health, with lower diversity generally related to degraded conditions (Revelante and Gilmartin 1980, Danilov and Ekelund 1999, Ptacnik et al. 2008). The spatial patterns of algal diversity within the Chesapeake Bay estuary may be seen as consistent with these predictions, in that regions with lower species richness and evenness (mid-Bay) have higher biomass and are more prone to algal blooms and reduced dissolved oxygen. However, caution must be taken in drawing conclusions from these correlations, as the salinity zone and physical characteristics of the mid-Bay and brackish waters in general also contribute significantly to these traits (Paavola et al. 2005).

Conclusions

Chesapeake Bay supports a diverse phytoplankton community comprised of multiple assemblages of algal taxa associated with spatially heterogeneous environmental conditions along the length of the estuary. The community can be characterized as one of high richness and low evenness, with a small number of dominant taxa and a larger number of less abundant background species. While there is considerable overlap in the distribution of certain taxa within the Bay such as *Ceratulina pelagica* and *Skeletonema costatum*, the dissimilarity of these algal assemblages between salinity zones suggests that the ecosystem is better described as a series of ecological boundaries, with high beta diversity occurring at these ecoclines, particularly between polyhaline and mesohaline waters and mesohaline and freshwaters. The manner in which alpha species richness

changes along this salinity gradient is consistent with the artenminimum model of Remane (1934), and challenges the generality of the findings of Telesh et al. (2011) regarding estuarine plankton diversity patterns. While the artenminimum model presents a simplified model of changing diversity within and estuary, the complexity of multiple environmental gradients and changing species composition is illustrated through the ordination analyses. Species richness patterns were not correlated with environmental parameters in the same way as algal productivity and biomass, indicating that management practices aimed at affecting one may have varying or negligible results on the other. Highest regional diversity was observed during periods of increased patchiness both in environmental conditions and phytoplankton composition, when the distinction between salinity zones was greatest. Areas that contained lower levels of alpha and gamma diversity generally had higher levels of productivity and experienced higher rates of species turnover, observations which may have additional implications due to potential higher susceptibly of biological invasions including HABs.

SEASONAL PATTERNS OF WATER QUALITY, PHYTOPLANKTON ABUNDANCE, COMPOSITION AND DIVERSITY AND THE EFFECTS OF STREAMFLOW IN CHESAPEAKE BAY.

Introduction:

Phytoplankton populations are known to be associated with specific environmental conditions and habitats (Smayda 1958, Paerl 1988, Bustillos-Guzmán et al. 1995, Marshall et al. 2006b). Included in the array of variables influencing phytoplankton presence and abundance in estuaries are water temperatures, salinity, nutrient concentrations and their ratios to each other, and water flow. Changes among these variables often occur seasonally in a predictable resulting in an environment that is more or less favorable to the development of certain species within the regional phytoplankton community, corresponding to relatively consistent patterns in phytoplankton abundance and community composition (Reynolds 1989, Lehman and Smith 1991, Figueredo and Giani 2001). These seasonal patterns often represent a continuum of successional stages of dominant phytoplankton populations throughout the year, such as that observed in estuaries and coastal systems including Chesapeake Bay (e.g. Marshall 1980, Mallin et al. 1991, Harding 1994).

Chesapeake Bay is the largest estuary in the United States, with a basin of ca. 11,600 km^2 and a watershed of ca. 164,000 km^2 including 150 major rivers and streams and is the home to over 17 million inhabitants (Figure 2; Kemp et al. 2005, Chehata et al. 2007). With a large catchment to basin ratio, the Bay is heavily influenced by precipitation within the watershed and its impact on streamflow, terrestrial runoff, water quality and ultimately biological conditions (Dauer et al. 2000. Boesch et al. 2001). As the

watershed is in a temperate region, the levels of precipitation and subsequent streamflow rates are highly seasonal, and while they can vary greatly from year to year, they generally have the same seasonal sequence (Schubel and Pritchard 1986, Harding and Perry 1997, Pionke et al. 2000). These seasonal flow patterns and associated nutrient fluxes correspond with the successional patterns of phytoplankton composition and abundance in the Bay (Marshall and Lacouture 1986, Marshall and Alden 1997). In addition to seasonal patterns, long term variability in rainfall, snowmelt, tropical storm activity, temperature changes and global climate processes all contribute to inter-annual differences in streamflow, which lead to further abiotic and biotic effects (Hagy et al. 2005, Kemp et al. 2005, Najjar et al. 2010).

Environmental conditions and their variability influence the abundance of particular organisms, along with the diversity of organisms that are present (Chesson and Warner 1981, Barton et al. 2010). There are several examples in the ecological literature of environmental gradients corresponding to varying levels of species diversity. This includes latitude, altitude, nutrient concentrations and water availability (Huston 1994). In estuarine environments, species diversity of benthic invertebrates, fish, macroalgae, shellfish, zooplankton and phytoplankton has been shown to vary with salinity, generally resulting in lower diversity found in intermediate salinities compared to the fresher and more saline waters (Remane 1934, Whitfield 2012). While these gradients generally describe spatial diversity patterns, they may also correspond to temporal changes in environmental parameters and diversity (Menge and Sutherland 1976, Steiner et al. 2005). Changing environmental conditions have been associated with varying diversity

levels on both seasonal and long term scales (Gaedeke and Sommer 1986, Calijuri et al. 2002, Barton et al. 2010).

Chesapeake Bay is not only one of the most productive estuaries in the United States, but also one of the most studied (Boesch et al. 2001). Water quality and biotic data have been gathered through various programs robustly for at least 60 years, with historical records dating back over a century (Cooper and Brush 1993, Boesch et al. 2001). Since 1984, the interagency Chesapeake Bay Monitoring Program has overseen a network of stations within the Bay and its tributaries that are monitored for a wide suite of water quality parameters and living resources (www.chesapeakebay.net). The numerous reports that have been written on the bay phytoplankton community include multiple examinations of long-term trends ranging from time periods of 5 to more than 40 years (e.g. Marshal and Alden 1994, Marshall and Nesius 1996, Harding and Perry 1997, Marshall et al. 2009c). These findings include several indications of eutrophication that include increased phytoplankton abundance and patterns of changing phytoplankton dominance, with nutrient loading tied to both land use and streamflow within the Bay ecosystem (e.g. Marshall and Alden 1997, Hagy et al. 2004, Adolf et al. 2006, Dauer et al. 2009).

Many of the examinations of eutrophication in Chesapeake Bay, and elsewhere, have utilized pigment levels as a measure of phytoplankton abundance (e.g. Flemer 1970, Harding and Perry 1997, Roman et al. 2005, Werdell et al. 2009), with fewer examinations that emphasize effects on phytoplankton community composition and diversity (exceptions include Mallin et al. 1991, Marshall 1994, Marshall and Nesius 1996, Pinckney et al. 1998, Zimmerman and Canuel 2002, Dauer et al. 2009).

Eutrophication is often associated with a shift in algal composition to one which is dominated by taxa that are considered unfavorable for a variety of reasons (Heisler et al. 2008). In freshwater habitats, this often includes the dominance of cyanobacteria, particularly bloom and even toxin producing species (O'Neil et al. 2011). Eutrophic, more saline waters may be dominated by bloom forming dinoflagellates, including those that may also produce toxins (Anderson et al. 2008, Mulholland et al. 2009). Generally, eutrophic algal communities represent lower quality food sources for zooplankton and other grazers, resulting in cascading negative effects on higher trophic levels, that may include economically important fish and shellfish populations (Riegman 1995, Ghadouani et al. 2003, Danielsdottir et al 2007). In addition, eutrophic waters often experience hypoxic or anoxic conditions through increased algal respiration, subsequent oxygen uptake during bacterial degradation, as well as higher levels of shading which can lead to a loss of seagrass beds and the fauna associated with them (Glibert et al. 2001, Burkholder et al. 2007).

A reduction of habitat quality has not only been associated with changes in abundance and species composition, but also a loss of species diversity in both terrestrial and aquatic systems (Van Horn 1983, Dobson et al. 2006). Numerous studies have linked a reduction of diversity to decline in several ecosystem level functions, e.g. productivity, stability and invasibility (Tilman et al. 1996, Lennon et al. 2003, Ives and Carpenter 2007). These linkages are of greater importance in relation to the global decline in biodiversity observed in almost all groups of organisms examined (Butchart et al.2010). Due to their ease of dispersal and apparent ubiquitous nature, microbial organisms, including phytoplankton, have also been considered less subject to much of

the pressures associated with the loss of diversity seen in other systems (Bas Becking 1934, Briggs 1991, Fenchel et al. 1997). However, both fossil and contemporary evidence suggests that this might not be the case, and that phytoplankton diversity may indeed be susceptible to declines caused by these same pressures (Bown et al. 2004, Ptacnik et al. 2008).

The objectives of this study are to examine the seasonal and inter-annual relationships of flow entering Chesapeake Bay on multiple water quality parameters over a 25 year time period, and in turn the impact on the composition and diversity of the Bay's phytoplankton community.

Methods

Streamflow data

Estimates of annual mean streamflow entering the Chesapeake Bay were obtained from records of the United States Geological Survey (USGS), based on monthly mean values of daily stream gauge data collected since 1937 (http://md.water.usgs.gov/waterdata/chesinflow/). The values represent the sum of streamflow inputs of the three major tributaries (Susquehanna, Potomac and James rivers) which account for 92% of streamflow into the Bay (Belval and Sprague 1999). Annual estimates from 1985-2009 were grouped into one of three categories as per USGS classifications (Garner 2012). These were: 1) normal (11 yrs): representing flow rates between the 25^{th} and 75^{th} percentile; 2) above normal/high flow (6 yrs): with rates in the upper 75^{th} percentile; and 3) below normal/low flow (8 yrs): with rates in the lower 25^{th} percentile. ANOVA was used to confirm that these three groups have statistically

significantly different annual flow rates (p=<0.000). Linear regression analysis of annual values was conducted to identify long-term changes in streamflow.

Chemical and physical parameters

Monthly collections have been made in the Chesapeake Bay mainstem from a network of over 20 water quality stations including 9 stations also sampled for phytoplankton composition from 1985-2009, with the exception of station CB1.1, from which phytoplankton data was collected 1985-1995 (Fig. 2). A full suite of physical and chemical parameters were measured including nutrient concentrations and chlorophyll levels using standard methods (Mallonee and Ley 2012). This study utilized water quality data from all collections concurrent with phytoplankton composition collections at the nine stations from1985-2009 (CB1.1: 1985-2009), which included salinity, secchi depth, water temperature, dissolved oxygen (DO), total suspended solids (TSS), silica (Si), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), particulate nitrogen (PN), total nitrogen (TN), orthophosphate (PO_4F), particulate phosphorus (PP), total phosphorus (TP) and the TN:TP ratio.

Biological parameters

Phytoplankton abundance, composition and relationships were determined based on microscopic examination of Lugol's preserved monthly samples collected from 1985-2009 (Marshall and Alden 1997, Lacouture 2010). Micro- and nannoplankton species densities were grouped by phyla, with chlorophytes, cyanobacteria, cryptophytes, diatoms and dinoflagellates representing greater than 97% of total phytoplankton abundance within these Bay samples. Chlorophyll concentrations were measured using standard spectrophotometric methods (Mallonee and Ley 2012), with primary

productivity rates measured using a ^{14}C uptake technique (Marshall and Nesius 1996). Algal diversity was characterized as the number of unique phytoplankton taxa for each collection (species richness), and using the Shannon diversity index, represented as H' (Shannon and Weaver, 1949): $H' = -\sum(p_i * logp_i)$ with p_i the proportion of the total sample which is composed of species i (Huston 1994).

Statistical analysis

To focus the analyses on the temporal patterns of phytoplankton diversity and composition as well as conduct the study on the entire length of the Bay mainstem, the environmental and biological data were grouped into four salinity regions using the Venice classification system (Oertli 1964), previously identified as similar in water quality and phytoplankton composition within Chesapeake Bay (Chapter 2). The polyhaline region included stations CB7.4, CB7.3E, CB6.4 and CB6.1. The mesohaline region was represented by CB5.2, CB4.3C, and CB3.3C. The oligohaline station CB2.2 and freshwater station CB1.1 each were the sole representatives of their own group. Monthly averages of all environmental and chemical data were generated each of the four groups. To evaluate the effect of streamflow on the overall water quality multivariate analysis of variance (MANOVA) was used on the monthly averages of the 14 water quality parameters (1985-2009) separately for each region with month as a covariate to test for a difference between streamflow groups (high, normal, low). When MANOVAs were significant for a region, (Wilk's Lambda p value < 0.05), univariate analysis of variance (ANOVA) was conducted on the individual response variables. This approach to ANOVA protects against inflation of Type I errors (Schenier 1993, Rubbo and Kiesecker 2005). A post hoc Ryan-Einot-Gabriel-Welsch test was used to compare

treatments when significant differences ($p<0.05$) were detected by ANOVA. The same approach was used to investigate the differences between streamflow groups on the biological parameters: chlorophyll, phytoplankton abundance, primary productivity rate, phytoplankton species richness, Shannon diversity, and the abundance of the major taxonomic groups. The database was constructed using Microsoft Access and Excel, with all statistical calculations made using IBM SPSS Statistics 20.

Results

Flow

Of the 75 years of USGS data, the annual average flow rate entering Chesapeake Bay has ranged from 45,400-121,000 ft^3sec^{-1}, with a long term mean of 78,257 ft^3sec^{-1} (Fig. 12). There has been no significant long term increase or decrease in annual average flow rate over this time period ($p=0.183$, $R^2= 0.011$). Annual averages between 63,750 and 89,675 ft^3sec^{-1} are within the 25th and 75th percentile and were classified by the USGS as normal years. During the 25 years (1985-2009) of the current study there have been 6 above normal years, 8 below normal and 11 years falling into the normal range. This period includes years with the lowest recorded annual flow (1999 and 2002) and some of the highest flow rates on record (2003, 2004 and 1996).

Intra-annual seasonal patterns of streamflow were relatively consistent between groups (high, normal, low). Flow into the Chesapeake Bay from the Susquehanna, Potomac and James rivers peaked in March and April with combined maximum values from 55,700 to 103,000 ft^3sec^{-1} (Fig. 13). Rates declined through spring into summer with minimum flow in August and September. Annual minimum values ranged from 5,800 to 29,300 ft^3sec^{-1}. During some high flow years, there were additional periods of

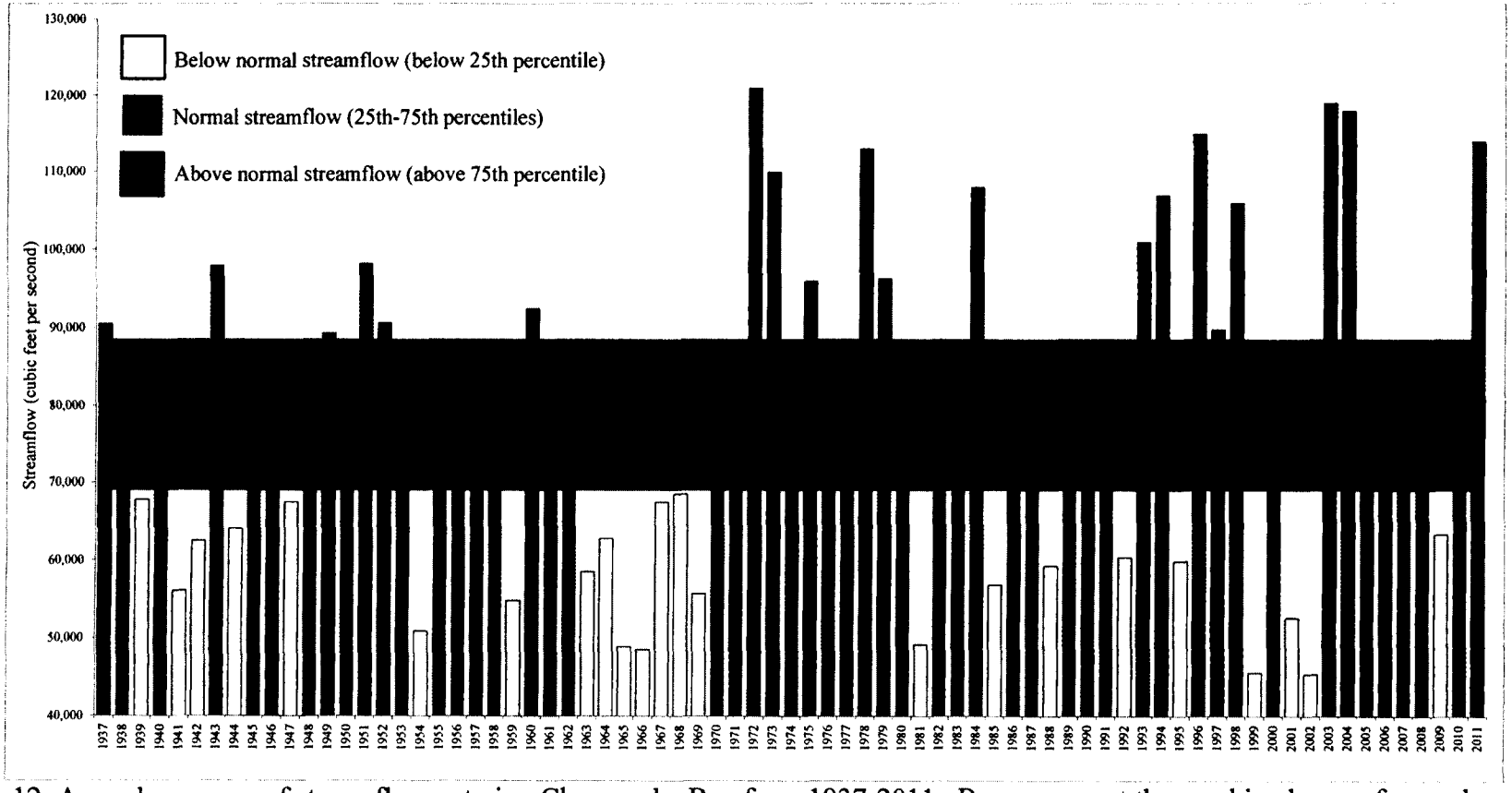

FIG. 12. Annual averages of streamflow entering Chesapeake Bay from 1937-2011. Bars represent the combined sum of annual averages of USGS flow gauge measurements from the Susquehanna, Potomac and James rivers. Years shaded in gray indicate normal years, characterized by USGS as between the 25th and 75th percentile. The current study utilizes data from 1989-2009.

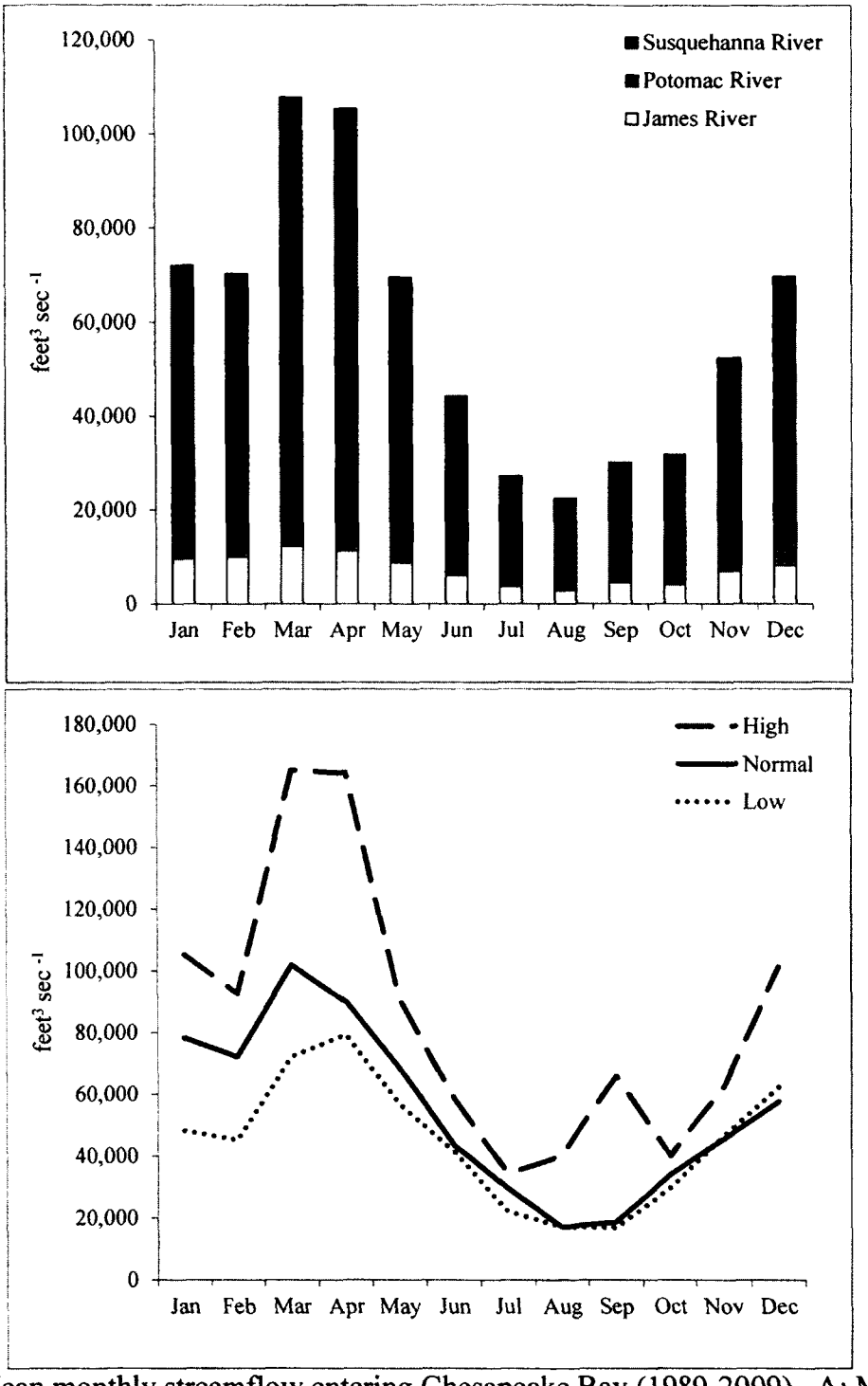

Fig. 13. Mean monthly streamflow entering Chesapeake Bay (1989-2009). A: Monthly averages of USGS flow gauge measurements from the Susquehanna, Potomac and James rivers, which together account for 92% of flow into the Bay. B: Combined average monthly flow from these rivers during periods of high, normal and low annual flow; high: annual flow in the upper 25% of long-term values, normal: 25-75%, low: lower 25%.

higher flow in September, not observed in other years (Fig. 13). Flow rates increased from October to January, with lower levels generally during February, before rising to the spring maximum. There were significant differences in flow rates throughout the year between the three flow groups ($p<0.0001$). Above normal flow years had higher levels of streamflow in the spring months and higher levels throughout the year, with summer months of below normal years having the lowest overall flow.

Water quality

There was a significant effect of annual streamflow on water quality parameters as a whole as detected by MANOVA in each of the four salinity regions (polyhaline, mesohaline, fresh $p<0.0001$, oligohaline $p= 0.003$), with subsequent ANOVA analyses identifying varying results depending on the individual parameter and region (Table 5; Figs. 14-18).

Salinity was reduced by streamflow, in the oligohaline, mesohaline and polyhaline regions with significantly lower levels in wet years than normal and dry years ($P<0.0001$). Salinity at the freshwater station remained fresh (0-0.14) in all years regardless of flow level. The salinity within the regions remained consistent to the assigned Venice classification, with the oligohaline region ranging from 1.38-3.17, the mesohaline from 10.29-13.47 and the polyhaline from 19.7 to 22.29. Seasonally, salinity was also inversely related to streamflow, with the lowest levels in April and May following the period of maximum flow (Fig. 14A). Low flow years had significantly higher salinities than wet years, particularly in summer and autumn.

Water clarity declined significantly with increased streamflow in all four regions of Chesapeake Bay (Table 4), with greater secchi depth corresponding with lower flow

TABLE 4. Water quality parameters from four salinity regions within Chesapeake Bay (1985-2009) during periods of high, normal and low annual flow; high=annual flow is in the upper 25% of longterm records, normal= 25-75%, and low= the lowest 25%. Annual averages for each parameter within each period and period shown along with results of the analysis of variance of between subject effects of streamflow treatment. Significant effects ($p<0.05$) within region in bold. Parameter abbreviations are given in the methods section.

	Polyhaline				Mesohaline			
	low	normal	high	p	low	normal	high	p
Salinity	22.29	21.55	19.70	**<0.000**	13.47	12.38	10.29	**<0.000**
Secchi (m)	2.11	1.80	1.77	**<0.000**	1.81	1.55	1.44	**<0.000**
DO (mg l^{-1})	9.2	9.3	9.6	0.285	9.2	9.0	9.4	0.598
TSS (mg l^{-1})	9.6	8.4	10.5	0.067	5.9	6.0	6.2	0.582
Temp (C)	16.2	16.0	15.4	0.858	16.6	17.2	15.8	0.703
Si (mg l^{-1})	0.19	0.26	0.28	**0.001**	0.60	0.74	0.88	**<0.000**
DIN (mg l^{-1})	0.041	0.040	0.077	**0.000**	0.246	0.249	0.393	**<0.000**
DON (mg l^{-1})	0.235	0.223	0.215	0.317	0.314	0.292	0.289	**0.002**
PN (mg l^{-1})	0.120	0.131	0.149	**0.001**	0.190	0.209	0.210	0.129
TN (mg l^{-1})	0.400	0.393	0.442	**<0.000**	0.737	0.743	0.886	**<0.000**
PO_4F (mg l^{-1})	0.0063	0.0052	0.0049	0.272	0.0052	0.0049	0.0051	0.465
PP (mg l^{-1})	0.0136	0.0133	0.0150	**0.038**	0.0166	0.0180	0.0185	**0.037**
TP (mg l^{-1})	0.0267	0.0234	0.0243	0.137	0.0304	0.0323	0.0316	0.290
TN:TP	17.11	19.16	21.03	**0.002**	28.98	26.62	31.43	0.165

TABLE 4. (continued)

	Oligohaline				Fresh			
	low	normal	high	p	low	normal	high	p
Salinity	3.17	2.56	1.38	**<0.000**	0.00	0.01	0.00	0.355
Secchi (m)	0.82	0.73	0.58	**<0.000**	0.99	0.90	0.83	**0.001**
DO (mg l^{-1})	8.6	8.7	9.3	0.244	9.6	9.6	10.3	0.347
TSS (mg l^{-1})	14.2	15.9	20.9	**0.001**	8.3	10.4	15.3	**0.022**
Temp (C)	17.1	16.7	15.5	0.621	17.2	16.1	14.6	0.425
SIF (mg l^{-1})	1.22	1.43	1.59	**0.001**	1.22	1.44	1.70	**<0.000**
DIN (mg l^{-1})	0.827	0.875	1.101	**<0.000**	1.131	1.226	1.313	**<0.000**
DON (mg l^{-1})	0.272	0.260	0.241	0.156	0.243	0.226	0.238	0.208
PN (mg l^{-1})	0.134	0.145	0.152	0.416	0.142	0.134	0.139	0.231
TN (mg l^{-1})	1.239	1.276	1.495	**<0.000**	1.511	1.589	1.683	**0.001**
PO_4F (mg l^{-1})	0.0148	0.0169	0.0164	0.325	0.0074	0.0088	0.0097	0.098
PP (mg l^{-1})	0.0259	0.0272	0.0336	**0.001**	0.0247	0.0275	0.0308	0.068
TP (mg l^{-1})	0.0484	0.0513	0.0572	**0.001**	0.0396	0.0427	0.0471	**0.029**
TN:TP	26.86	25.66	27.85	0.494	42.07	39.10	43.47	0.768

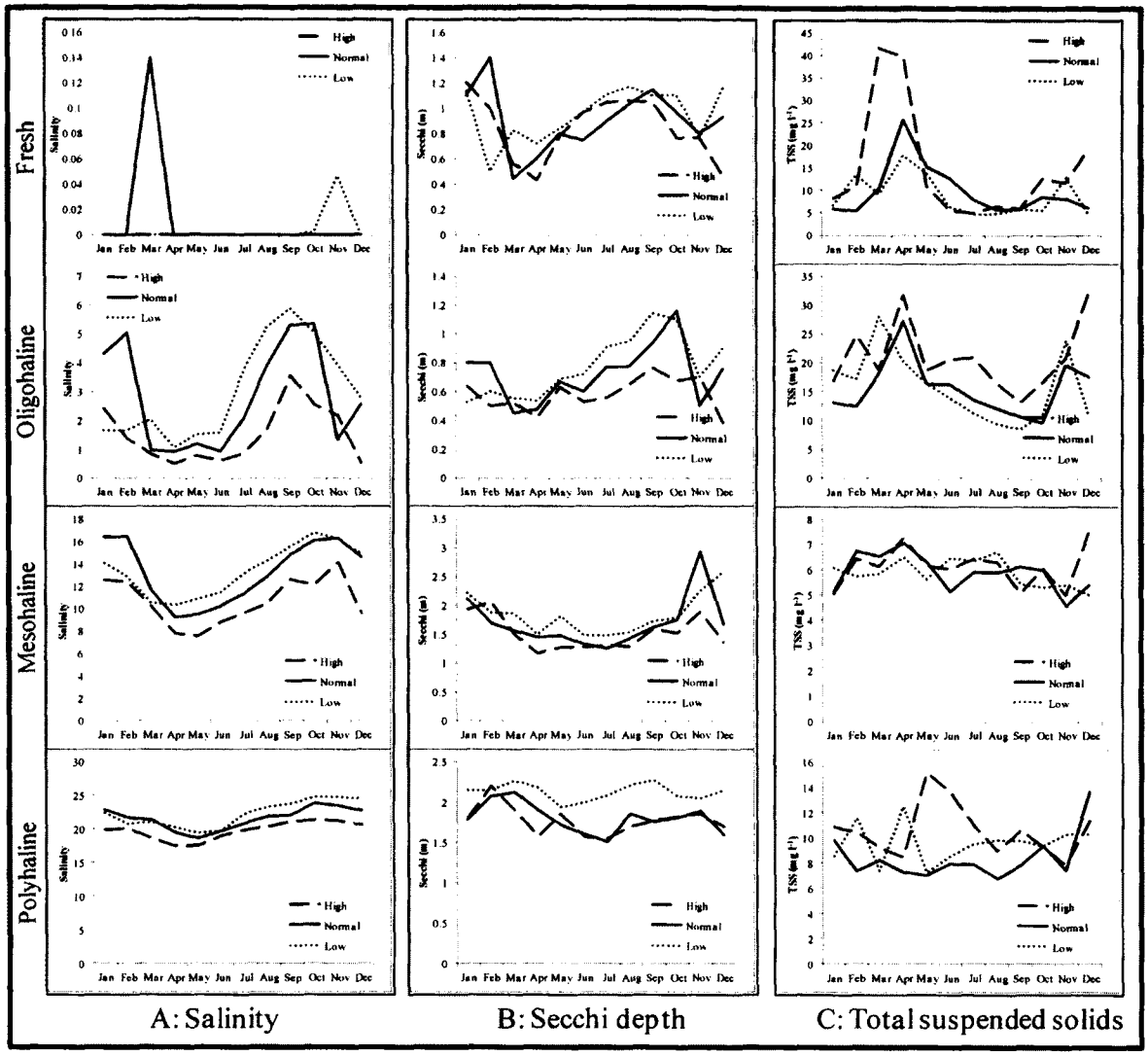

FIG. 14. Average seasonal patterns of A: salinity, B: Secchi depth, and C: Total suspended solids from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

years (Fig. 14B). Seasonally, secchi depth was greater in autumn and winter months and lowest during spring in the fresh and oligohaline regions and summer in the mesohaline and polyhaline waters. Total suspended solids were significantly greater in the fresh and oligohaline regions in years with high streamflow, with no significant difference in the meso- and polyhaline levels (Table 4). TSS was greatest in the freshwater region, particularly during March and April when streamflow was highest (Fig. 14C).

Silica concentrations were significantly increased by streamflow in all regions (Table 4). Within the polyhaline region, silica levels were lowest in spring and greatest during July with the same general pattern in the mesohaline, with reduced levels during low flow years (Fig. 15A). In the oligohaline and fresh water regions, silica levels were highest in winter, with lower concentrations in spring and summer, and higher concentrations during years of higher flow (Fig. 15A). Water temperature and dissolved oxygen both showed consistent seasonal patterns that did not differ from year to year in relation to inter-annual streamflow variations (Table 4; Fig. 15 B,C). Dissolved oxygen concentrations reflected water temperature patterns and were highest from December to February and lowest from June to September in each region (Fig. 15C).

Dissolved inorganic nitrogen concentrations were elevated with increased streamflow, with significantly higher DIN in each region during years of higher flow (Table 4). DIN was highest within the freshwater region, and declined seasonally from a maximum during winter to minimum levels in summer and autumn months (Fig. 16A). It was similar in the oligohaline, with higher concentrations during high flow years. DIN concentrations were lower in the meso- and polyhaline regions, being highest in March and April and lowest in July. Years of increased streamflow had higher DIN levels,

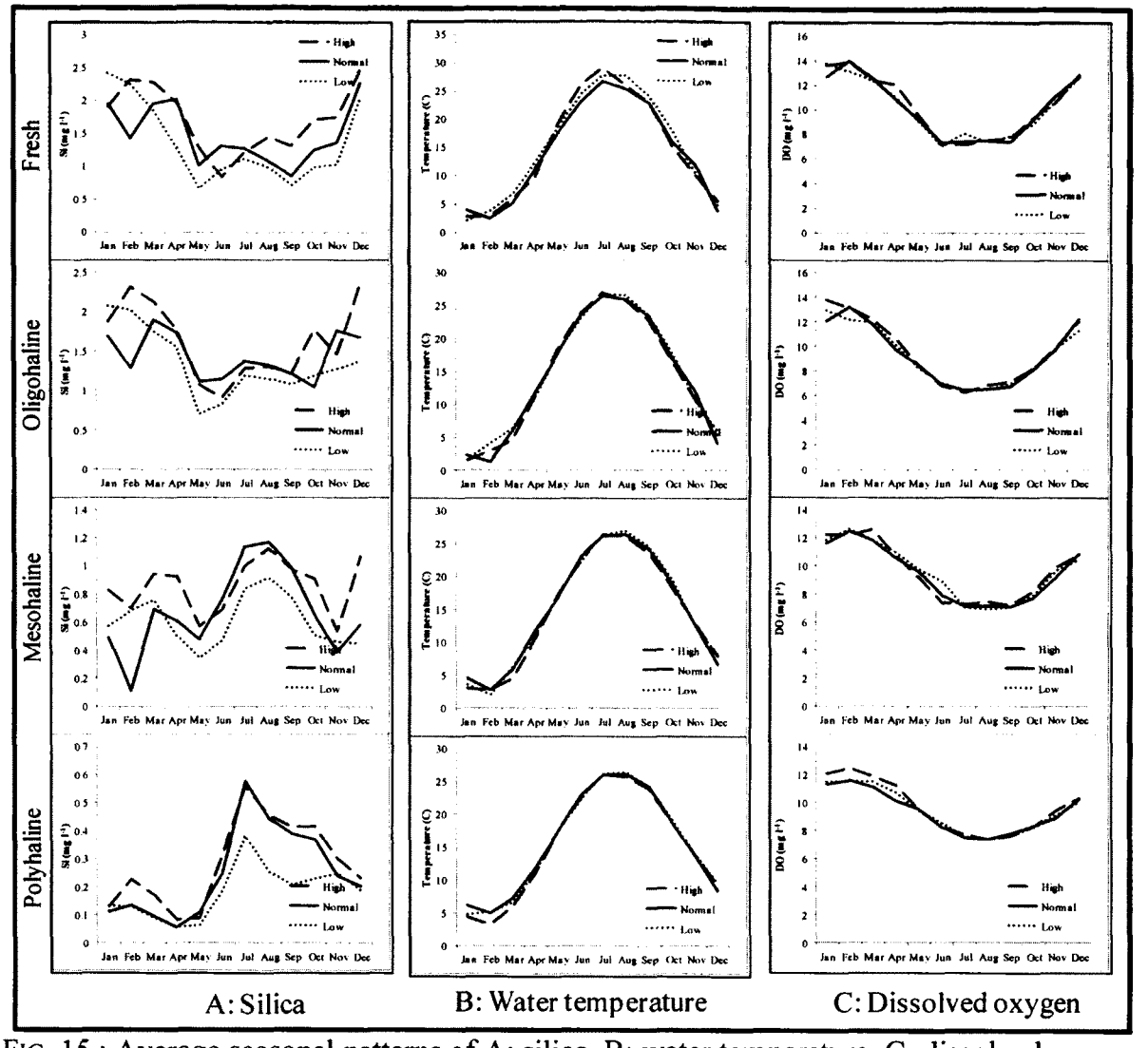

FIG. 15.: Average seasonal patterns of A: silica, B: water temperature, C: dissolved oxygen from from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

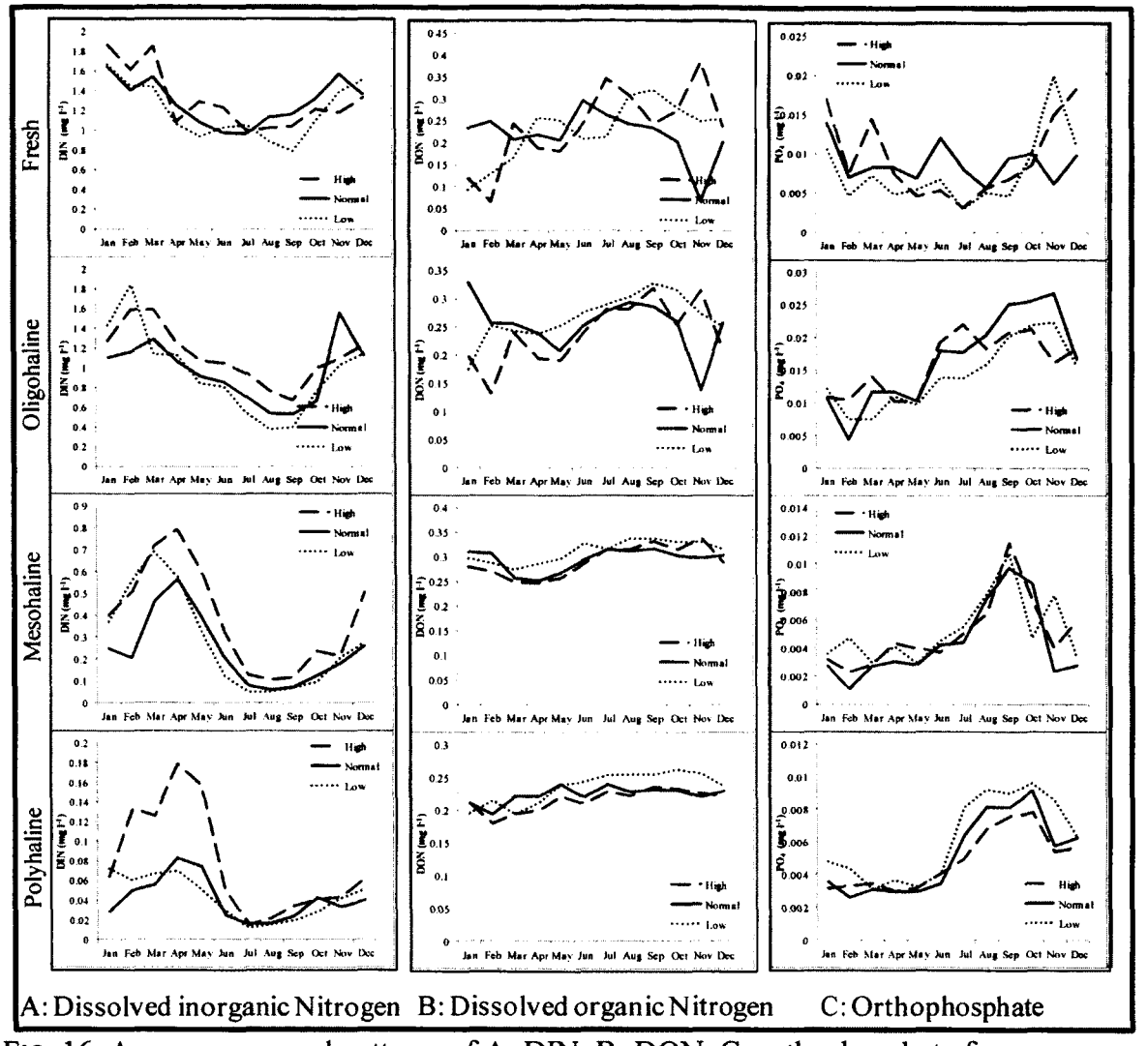

FIG. 16. Average seasonal patterns of A: DIN, B: DON, C: orthophosphate from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

particularly in winter and spring seasons (Fig. 16A). In contrast, there was no significant difference in dissolved organic nitrogen levels between streamflow groups in all but the oligohaline region (Table 4). Seasonal patterns were variable, both between regions and flow groups. In general, DON was highest in September and October, with greater concentrations during low flow years in most regions (Fig. 16B). Orthophosphate levels varied seasonally, but had lower inter-annual variability and were not significantly different between periods of different flow in any of the four regions (Table 5; Fig 16C). Within the oligo-, meso- and polyhaline sections of the Bay, PO_4 levels were lowest in winter and spring and greatest during late summer and autumn. Concentrations at the freshwater location were more variable and generally greater in winter, with lowest levels in spring and summer (Fig. 16C).

Particulate nitrogen and particulate phosphorus had similar seasonal patterns in the meso-and polyhaline regions, with highest concentrations in June and July (Fig. 17A,B). Freshwater PN levels were lowest in the winter, with greater concentrations in the other seasons, while oligohaline PN was variable throughout the year (Fig. 17A). Both fresh and oligohaline PP levels were highest in March and April, with lowest concentrations occurring during autumn (Fig. 17B). A significant difference between streamflow years in PN concentrations only occurred within the polyhaline, with highest levels during periods of high flow. Higher streamflow also was associated with greater PP, with significant differences in the oligo-, meso- and polyhaline regions (Table 4).

Total nitrogen levels were significantly increased with greater annual streamflow throughout the Bay (Table 4). Seasonally, the patterns largely reflected those of DIN, with greatest values during March and April and minimum concentrations in September

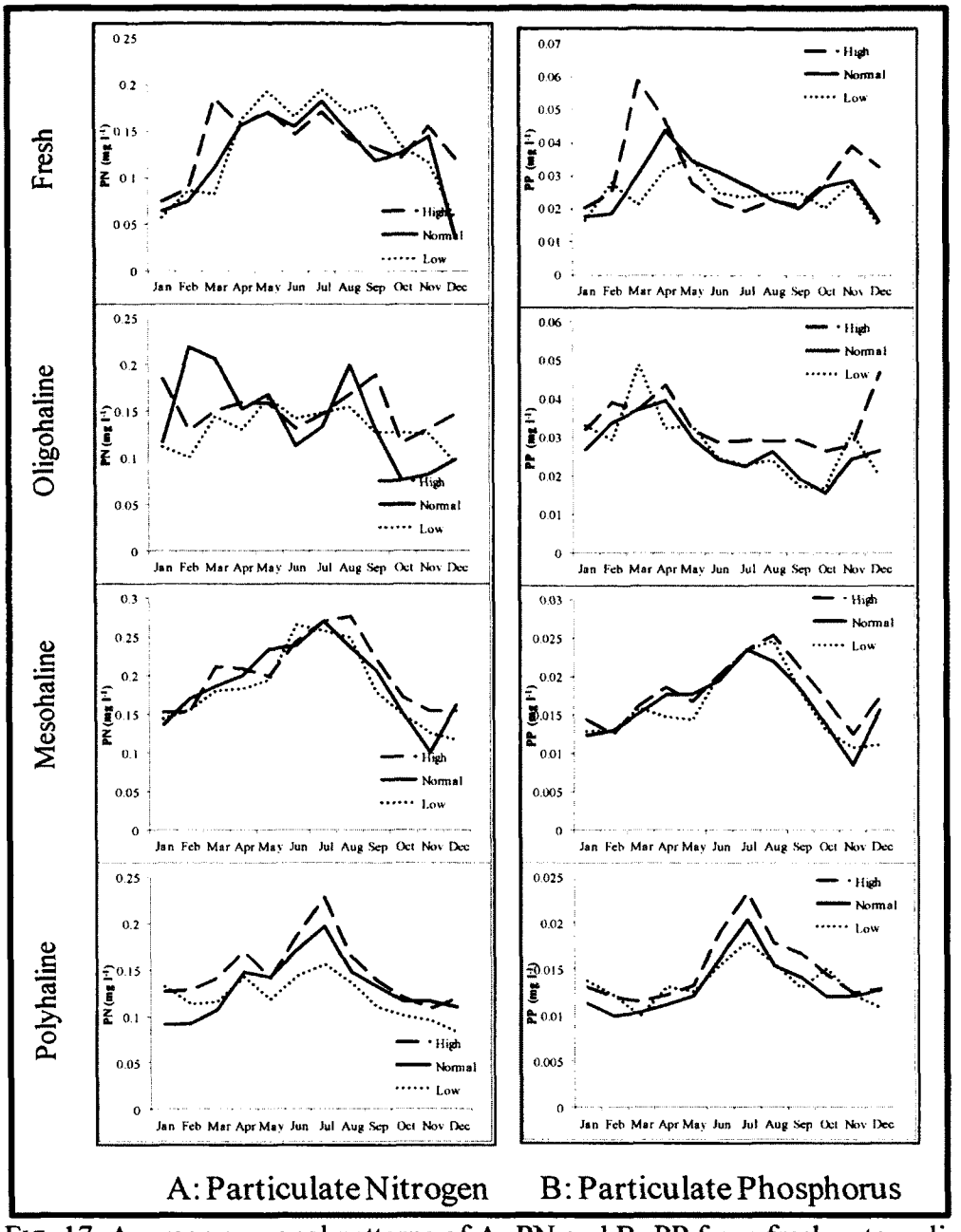

FIG. 17. Average seasonal patterns of A: PN and B: PP from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

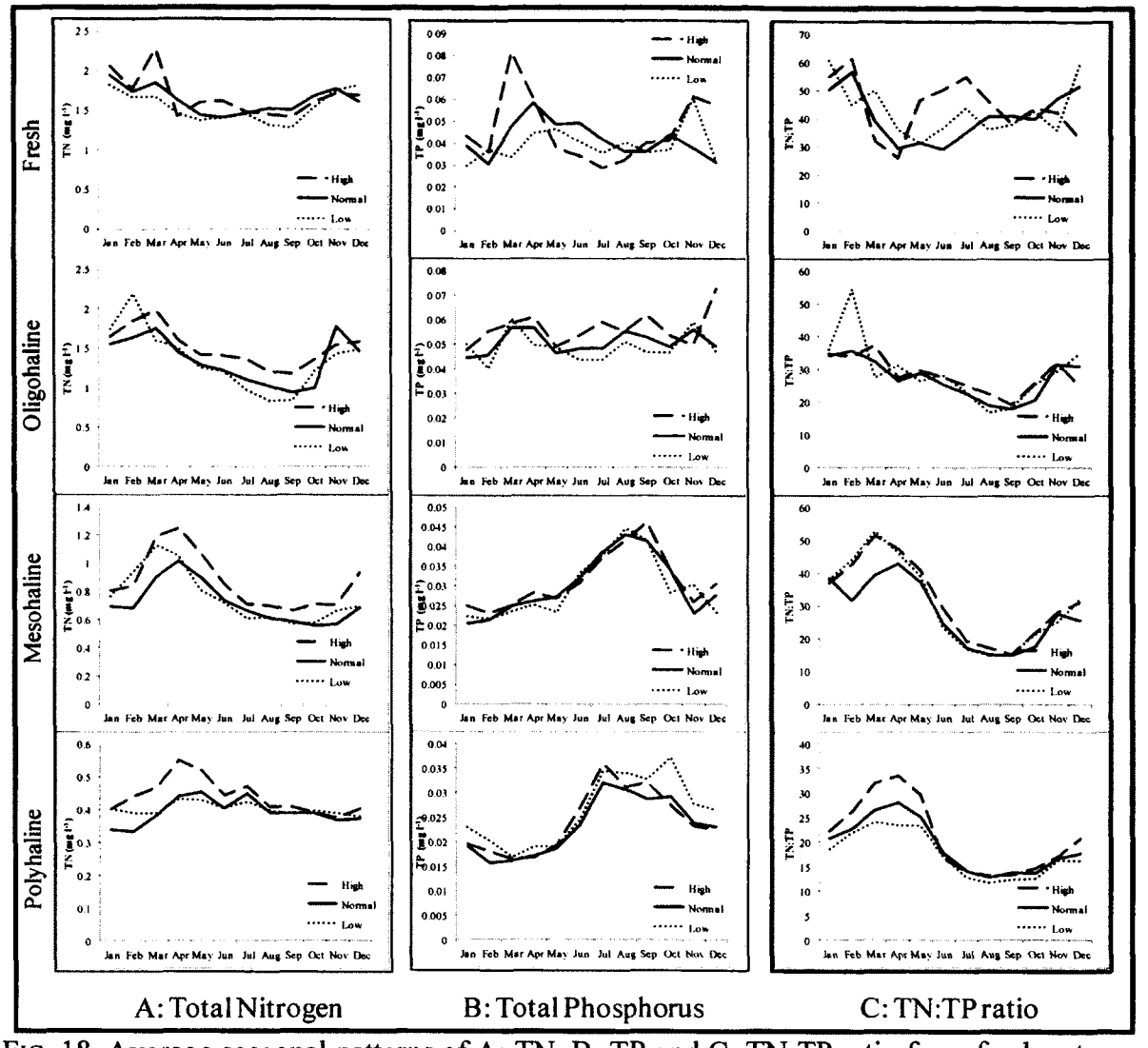

FIG. 18. Average seasonal patterns of A: TN, B: TP and C: TN:TP ratio from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

(Fig. 18A). Annual streamflow had a significant effect on total phosphorus in the fresh and oligohaline regions, with higher concentrations associated with higher flow (Table 4). TP in the meso- and polyhaline, had a consistent seasonal pattern of higher concentrations between July and September, with little interannual variation in regard to flow. The TN:TP ratio was highly variable, both seasonally and between regions ranging from an annual average of 19.1:1 in the polyhaline to 41.5:1 in the freshwater region (Fig. 18C). The meso- and polyhaline regions had clear seasonal patterns of greater TN:TP in spring, and lower ratios from July to October, with ratios less than 16 during this period in the polyhaline (Fig. 18C). Ratios were higher in the oligohaline and especially at the freshwater region, with less seasonal variation. There was a significant difference in TN:TP ratio between years of different streamflow only within the polyhaline region, with higher flow having higher ratios, particularly during spring (Table 4; Fig. 18C).

Phytoplankton abundance and productivity

There was a significant effect of annual streamflow on the biological components as a whole as detected by MANOVA in each of the four salinity regions (polyhaline and mesohaline, $p<0.0001$, oligohaline $p= 0.014$, freshwater $p=0.001$), with subsequent ANOVA analyses identifying varying differences of the individual biological metrics and regions (Table 5, Figs 19-22).

Phytoplankton abundance and productivity had a unimodal seasonal pattern in the freshwater region, with maximum chlorophyll concentrations, productivity rates, and cell abundances in summer, and minimal levels during winter (Fig. 19). This pattern was observed throughout the study, and did not vary significantly between groups of different streamflow (Table 5). Within the oligohaline region, algal productivity and abundance

TABLE 5. Biological parameters from four salinity regions within Chesapeake Bay (1985-2009) during periods of high, normal and low annual flow; high=annual flow is in the upper 25% of longterm records, normal= 25-75%, and low= the lowest 25%. Annual averages for each parameter within each period and period shown along with results of the analysis of variance of between subject effects of streamflow treatment. Significant effects ($p<0.05$) within region in bold

	Polyhaline				Mesohaline			
	low	normal	high	p	low	normal	high	p
Chlorophyll (mg l^{-1})	7.2	6.7	9.1	**0.003**	10.1	10.2	10.6	0.321
Productivity(mg C $l^{-1}h^{-1}$)	16.6	34.6	31.6	**0.001**	40.9	37.6	45.1	0.691
Species richness	39.5	37.9	35.3	**0.000**	20.0	23.0	19.2	**0.000**
Shannon index	2.8	2.8	2.7	**0.022**	2.3	2.3	2.0	**0.000**
Total abundance (cells l^{-1})	5,457,055	6,110,706	8,534,536	**0.002**	14,557,552	21,759,034	19,026,771	0.197
Diatoms (cells l^{-1})	3,535,370	3,584,779	6,088,786	**0.000**	6,063,008	6,218,357	6,322,519	0.758
Dinoflagellates (cells l^{-1})	335,678	358,512	333,602	0.449	1,180,535	1,654,379	1,549,340	0.191
Cyanobacteria (cells l^{-1})	565,173	777,564	336,117	**0.025**	5,157,081	10,762,747	8,704,394	0.481
Chlorophytes (cells l^{-1})	42,311	70,817	127,327	0.374	254,938	316,875	216,042	0.546
Cryptomonads (cells l^{-1})	910,438	1,278,311	1,570,903	**0.000**	1,656,380	2,320,775	1,861,925	**0.004**
Others (cells l^{-1})	68,086	40,724	77,801	0.398	245,609	485,902	372,551	**0.040**

	Oligohaline				Fresh			
	low	normal	high	p	low	normal	high	p
Chlorophyll (mg l^{-1})	5.3	5.4	6.1	0.881	5.4	7.3	8.1	0.057
Productivity(mg C $l^{-1}h^{-1}$)	26.5	17.1	29.3	0.174	42.1	34.8	32.5	0.284
Species richness	19.5	19.1	18.1	0.120	29.9	29.0	19.9	**0.005**
Shannon index	1.8	1.7	1.6	0.311	1.8	2.1	1.7	0.168
Total abundance (cells l^{-1})	8,463,960	7,005,489	14,032,711	0.233	25,373,487	14,983,151	17,978,219	0.628
Diatoms (cells l^{-1})	3,897,815	2,525,359	3,843,662	0.125	5,888,038	7,569,905	4,075,652	0.312
Dinoflagellates (cells l^{-1})	358,116	825,264	514,445	0.168	65,534	95,360	139,108	0.686
Cyanobacteria (cells l^{-1})	2,937,491	2,402,203	8,292,768	0.172	15,251,840	3,786,382	11,332,902	0.157
Chlorophytes (cells l^{-1})	491,062	335,089	738,310	0.208	3,145,922	2,681,566	2,033,223	0.737
Cryptomonads (cells l^{-1})	733,695	847,041	577,769	**0.012**	882,350	637,059	365,708	0.055
Others (cells l^{-1})	45,780	70,531	65,757	0.378	139,802	212,878	31,626	0.089

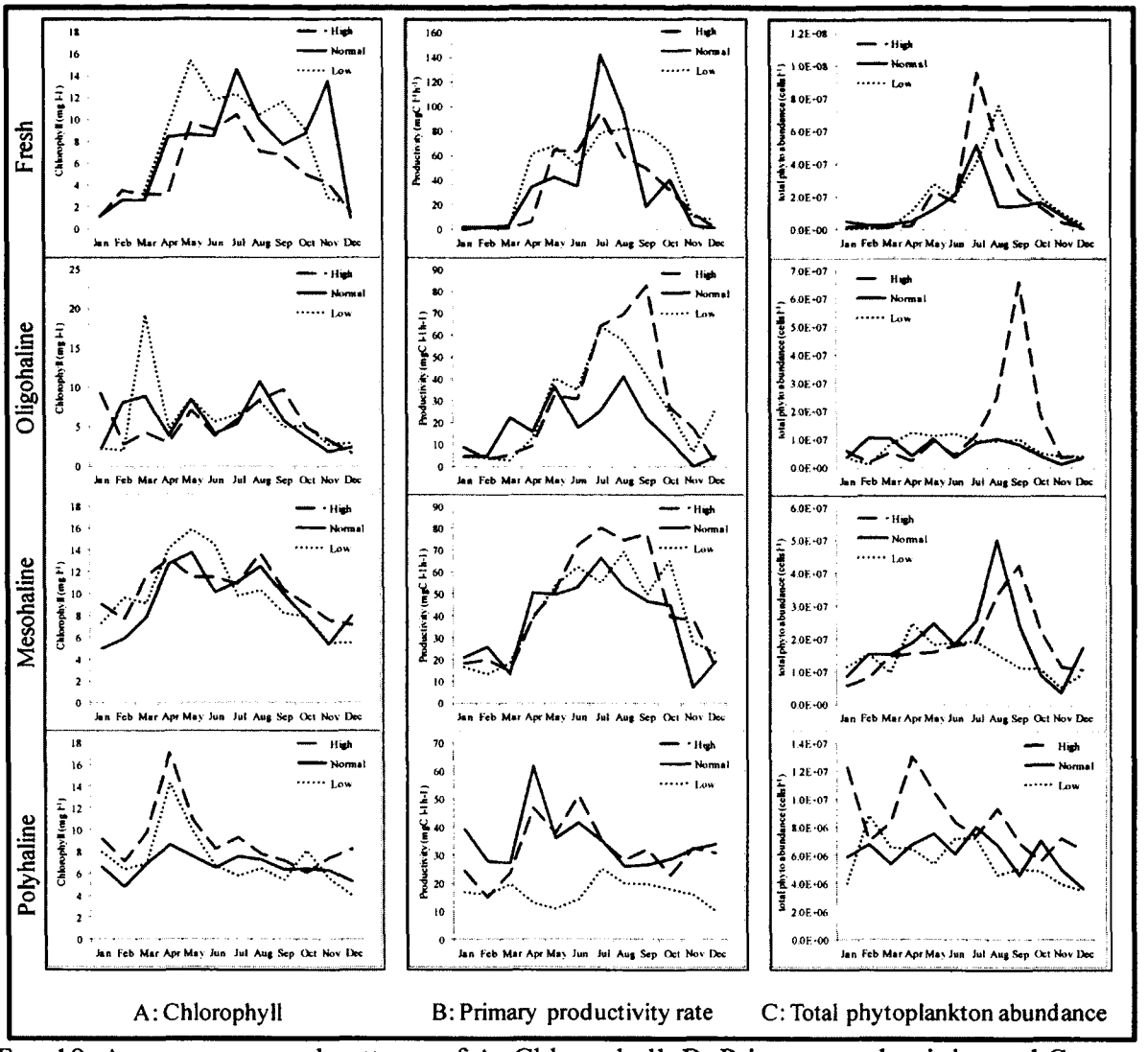

FIG. 19. Average seasonal patterns of A: Chlorophyll, B: Primary productivity and C: total phytoplankton abundance from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

were greatest in late summer, with no clear maximum period of chlorophyll development detected (Fig. 19). The mesohaline had higher chlorophyll and productivity rates during spring, summer and autumn, with lowest levels in winter. Algal abundance was greatest in late summer and autumn at this region. Within the polyhaline, there was a significant effect of streamflow on algal abundance and productivity (Table 5). Chlorophyll concentrations and cell densities were highest during periods of high streamflow (Fig. 19A,C) and productivity rates were lowest during low flow years (Fig. 19B).

Phytoplankton composition

Along with total algal abundance, densities of the major phytoplankton taxonomic groups were generally significantly different between periods of different streamflow only within the polyhaline region (Table 6). Diatom and cryptomonad densities were both significantly higher during periods of higher flow, with cyanobacteria abundance lower in high flow years in this region of the Bay (Fig. 20). Diatoms were the dominant taxonomic group throughout the season in all years of the study in each of the four regions with densities between 41-68% of the phytoplankton community (Table 2). There was not a consistent seasonal period of diatom development throughout the Bay, with maximal levels generally seen during spring and summer in freshwater and oligohaline regions, and in winter and early spring in the meso- and polyhaline Bay (Fig. 20A).

Cryptomonads represented the second most abundant phytoplankton group in Chesapeake Bay, representing 5-25% of total abundance (Table 2). Seasonally, cryptomonads displayed a broad unimodal pattern of abundance with minimal concentrations in winter and higher levels between May and October (Fig. 20B). Unlike

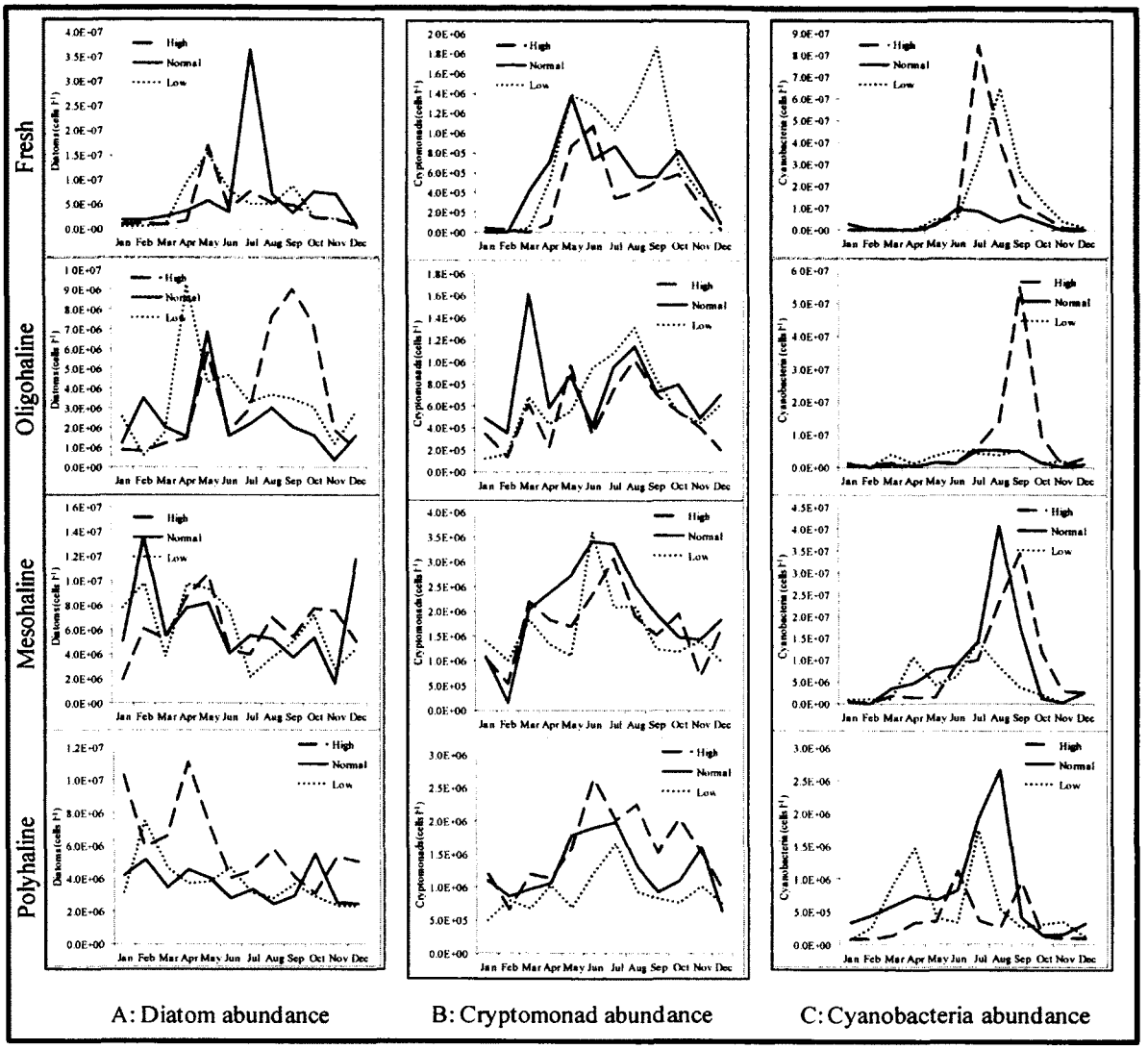

FIG. 20. Average seasonal patterns of A: Diatom, B: Cryptomonad and C: Cyanobacteria abundance from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

the other taxonomic groups, there was a significant difference in cryptomonad densities between years of different flow level in multiple regions of the Bay. Within the polyhaline and mesohaline regions, cryptomonad densities were greater during higher flow years compared to low flow years, with the reverse relationship seen in the oligohaline waters, and no significant difference observed in the freshwater region (Table 5).

Cyanobacteria concentrations were much greater in the fresh, oligo- and mesohaline regions of the Bay, where they represent an average of 27% of the phytoplankton abundance compared to 7% in the polyhaline region (Table 2). Seasonal patterns were variable between years, but densities were often highest during late summer months, and lowest in winter (Fig. 20C). Dinoflagellate abundance was also variable between regions, with the greatest concentrations in the oligo- and mesohaline regions where they accounted for an average of 10% of total algal abundance. Seasonal patterns differed between regions, with dinoflagellate abundances greatest in summer in the freshwater region, during spring in the meso- and oligohaline, and variable within the polyhaline Bay (Fig. 21A). Chlorophytes were a minor constituent (<2%) of the algal composition in all but the oligohaline and freshwater regions, where they represented between 6-16% of the total phytoplankton abundance (Table 2). In the freshwater region, where they were most prevalent, their cell densities were greatest from June to September, with minimal abundance in winter (Fig. 21B). This pattern was generally consistent between years, with no significant difference associated with flow. The remaining 1-2% of phytoplankton species, were a minor component of the algal

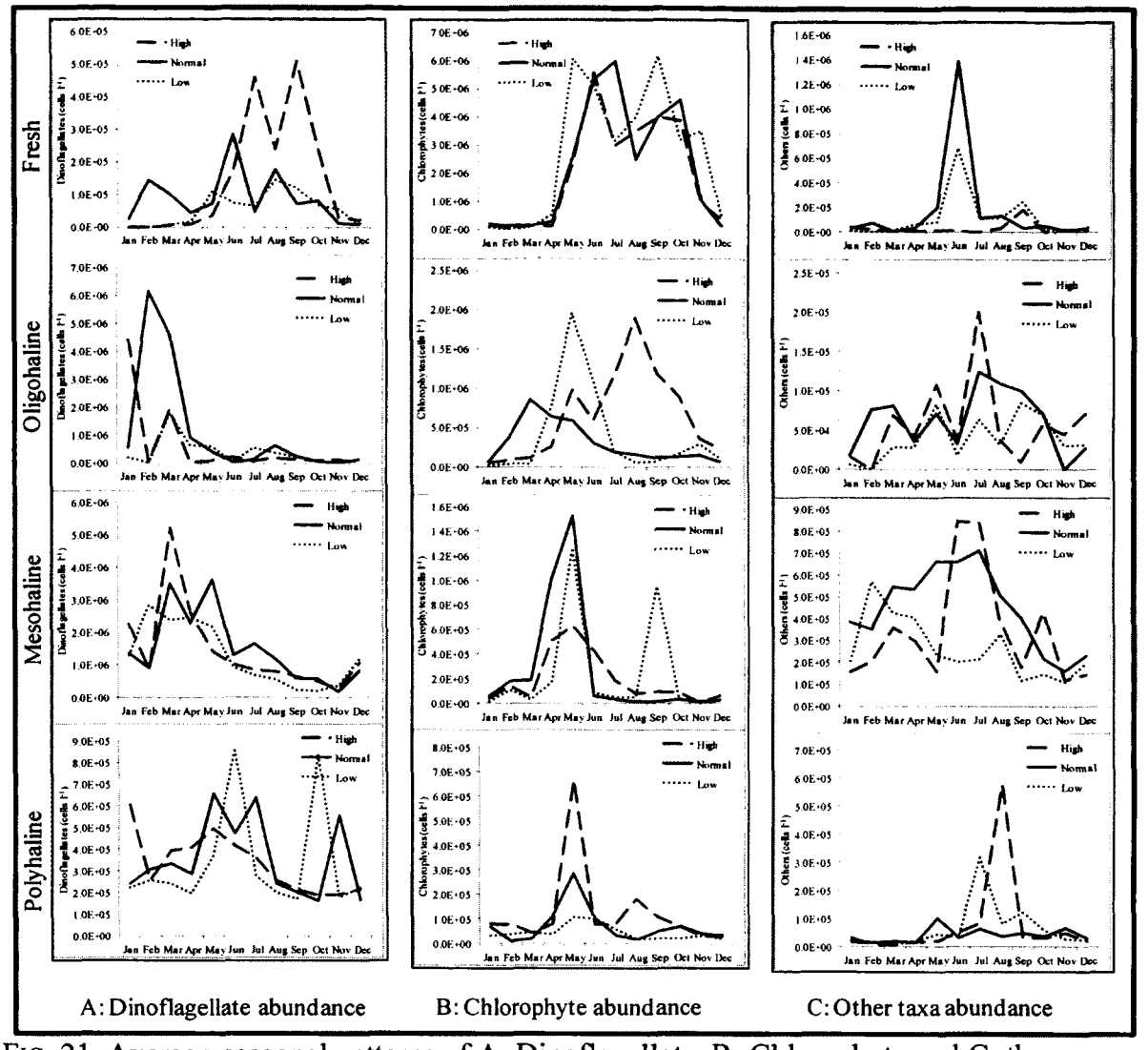

FIG. 21. Average seasonal patterns of A: Dinoflagellate, B: Chlorophyte and C: the remaining other algal taxa abundance from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

community in each of the Bay regions, and were not significantly affected by annual the streamflow rates (Fig. 21C; Table 5).

Phytoplankton diversity

Average phytoplankton species richness was reduced by high annual streamflow baywide, with significant differences in the fresh, meso- and polyhaline regions (Table 5). Seasonal patterns of richness varied between locations. Spring and summer months within the freshwater Bay had high species richness, with lower values during winter and high flow years (Fig. 22A). Richness at the oligohaline was lowest within the Bay, and remained low throughout the year, regardless of flow. The mesohaline region was more variable, with greater richness in late winter and late summer, and lower levels during spring and early summer. High flow years were associated with significantly lower richness in this region (Table 5). Species richness was greatest within the polyhaline region, with similar seasonal patterns observed in years of different flow rates (Fig. 22A). Richness was greatest in this region in winter and autumn, with minimal levels during summer, and was highest throughout the year during low flow periods, and lowest during spring and summer of high flow years (Fig. 22A). Diversity as measured with the Shannon index (H') also indicated a reduction with increased streamflow, however it was significant only within the meso- and polyhaline regions (Table 5). Seasonal patterns in H' differed between regions and from those of species richness (Fig. 22B). Within the freshwater region, H' declined between June and September, especially in high flow years. Meso- and oligohaline phytoplankton H' also declined during this same time period, a pattern not apparent, and in some cases opposite to that of species richness (Fig. 22). In the polyhaline region, H' seasonal patterns were generally consistent with those

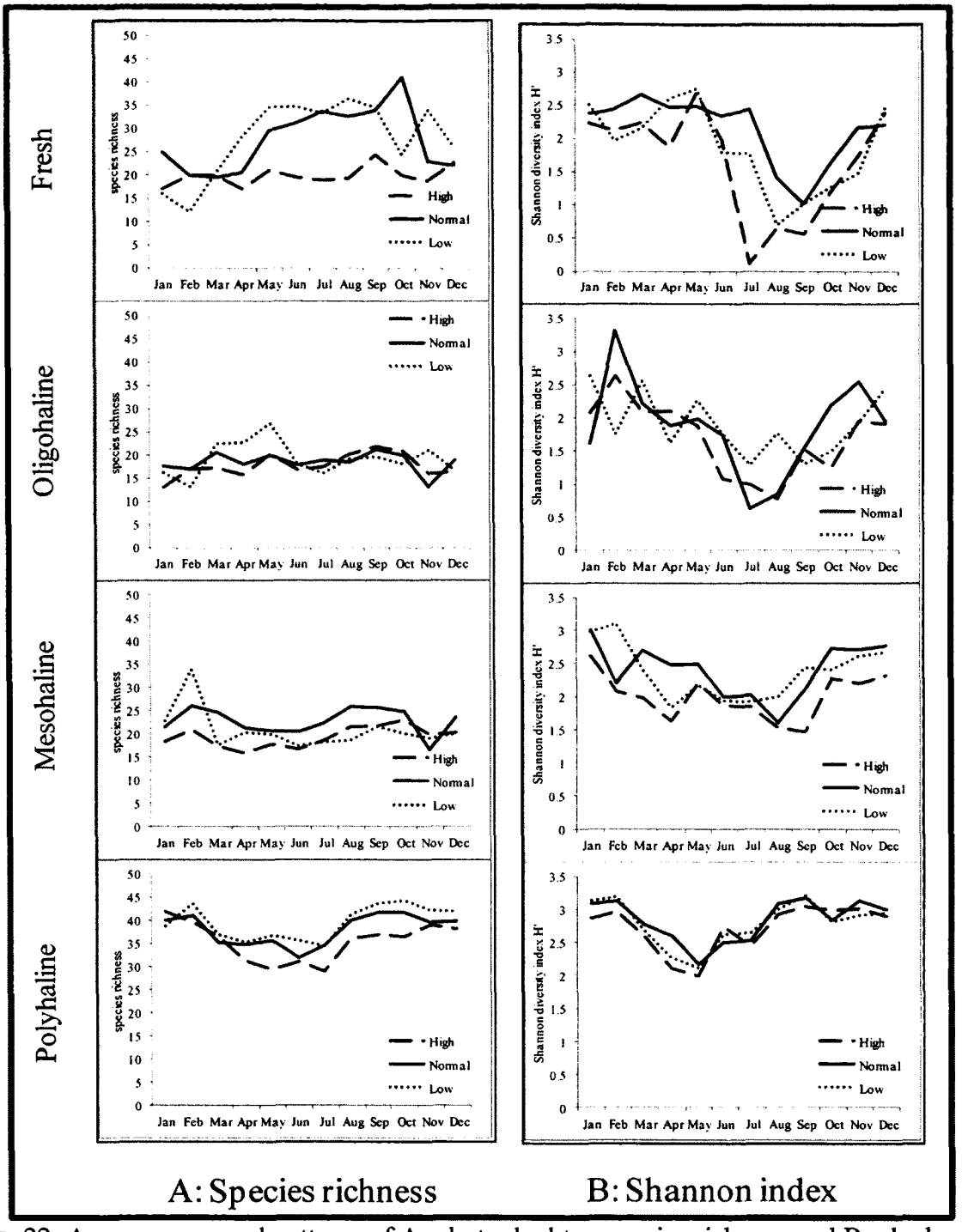

FIG. 22: Average seasonal patterns of A: phytoplankton species richness and B: algal diversity as measured using the Shannon diversity index from freshwater, oligohaline, mesohaline and polyhaline regions within Chesapeake Bay (1985-2009) during periods of high (n=6), normal (n=11), and low (n=8) annual streamflow.

of richness, both having greater values in autumn and winter, however H' was lowest during April and May while richness was lowest in June and July.

Discussion

Regional and seasonal differences

Water quality parameters and phytoplankton populations showed seasonal variability that differed greatly between salinity regions. Annual fluctuations in flow into the Bay were strongly associated with seasonal and inter-annual changes in the physical and chemical environmental conditions; however, there were considerable differences between salinity regions in the manner and extent in which they were linked. Parameters including salinity (Fig. 14A), DO (Fig. 15C), and DIN (Fig. 16A) had similar seasonal patterns Bay-wide that were consistent with seasonal streamflow fluctuations , while others such as TSS (Fig. 14C), silica (Fig. 15A), and TP (Fig. 18B) both differed between regions and in response to streamflow. These differences were greater in reference to the biological parameters. Phytoplankton abundance and productivity were seasonally most variable in the fresh and oligohaline regions, with both the lowest winter productivity and highest summer productivity observed in these sections of the Bay (Fig. 19B). In contrast, the meso- and polyhaline regions had less seasonal variability, and experienced annual maxima earlier in the year than the less saline regions. Regional different seasonal patterns in algal biomass and productivity have been previously reported in Chesapeake Bay and other estuaries (Smith and Kemp 1995, Marshall and Nesius 1996, Eyre 2000, Adolf et al. 2006). These differences are often attributed to regional differences in limiting growth factors and differences in the composition of the local dominant plankton species (Marshall and Alden 1990, Kemp et al. 2005).

Increased streamflow significantly reduced salinity both seasonally and inter-annually, however the levels at each region varied within the range associated with the Venice classification system (mesohaline remained mesohaline, polyhaline remained polyhaline, etc.). The phytoplankton taxa present within these regions are likely to have salinity tolerances that exceed the range of change experienced at each location during the course of the study (Brand 1984). While salinity appears to play a significant role in explaining the spatial patterns of phytoplankton composition and diversity within an estuary (Chapter 2, Muylaert et al. 2009), it is unlikely that the variation in salinity experienced within a region is responsible for temporal seasonal or inter-annual changes to the algal community. Instead, it appears that changes in other parameters including nutrient concentrations and turbidity play a larger role in influencing temporal changes.

Within the polyhaline lower Bay, increasing streamflow entering Chesapeake Bay was associated with more eutrophic abiotic and biotic characteristics as identified by multivariate analyses. In particular, significantly higher DIN, TN, PP concentrations as well as a higher TN:TP ratio and reduced salinity and water clarity, along with a more abundant phytoplankton community were associated with higher flow (Tables 4, 5). These linkages were not as apparent elsewhere in the Bay. Despite significantly higher DIN, TN and silica levels and reduced secchi depths in all regions of the Bay during years of higher flow, there was no significant effect of streamflow on chlorophyll or productivity in any of the three less saline regions. These results are consistent with other analyses of Chesapeake Bay showing distinct regional differences in the response of the phytoplankton community to changes in environmental variables (Williams et al. 2010, Dauer et al. 2012). While there was not a significant increase in average annual flow

over the course of the study, increased flow into the Bay has been associated with increased turbidity and phytoplankton growth (Williams et al. 2010). The results presented here, along with the analyses of Williams et al. (2009) indicated flow induced increases in nutrient concentrations are drivers of higher algal abundance, particularly in the polyhaline Bay. However, using flow adjusted analyses, there appears to be a decoupling between nutrients and the phytoplankton response, with decreasing nitrogen and phosphorus levels not being associated with any significant trend in algal abundance (Dauer et al. 2009, Dauer et al. 2012). This has been suggested as being related to nutrient conditions being higher than a saturation threshold of potentially limiting levels, above which a lack of response is not observed (Dauer et al. 2012). This hypothesis may explain why the upper Bay regions, which had much higher nutrient concentrations, did not show significant differences in chlorophyll or productivity between years of varying streamflow, with even low flow years had saturating nutrient conditions in all but the lower Bay. Decoupling between seasonal nutrient levels and phytoplankton growth has been observed in other estuaries with elevated, non-limiting nitrogen and phosphorus concentrations (Rahimibashar et al. 2009).

Phytoplankton diversity and seasonal succession

While abundance and productivity metrics differed between the Bay regions in response to streamflow, there was a more consistent effect on phytoplankton diversity. Species richness specifically was lower during years of high streamflow within each of the Bay regions (Table 6). Declines in species richness have been associated with degraded habitat quality in general and eutrophic conditions in aquatic ecosystems in particular (Wang et al. 1997, Riis and Sand-Jensen 2001). Likewise, changes in

phytoplankton evenness, reflected in diversity metrics such as the Shannon index, are often more responsive than changes in richness to nutrient enrichment, as they generally illustrate the relative dominance of a few species (Hillebrand and Sommer 2000). These changes are often associated with the characteristics of different phytoplankton groups and their affinity to specific environmental conditions.

Amongst the phytoplankton, diatoms have high growth rates and nitrogen uptake rates plus the ability to utilize a variety of nitrogen sources (Tang 1995, Lomas and Glibert 2001). This can result in a competitive advantage against other algal species that are nitrogen limited, particularly when DIN concentrations are high (Falkowski et al. 1985, Tang 1995, Del Amo et al. 1997). When nitrogen (and silicate) levels become elevated, as they do each winter/spring, especially during high flow years, this competitive ability increases, which along with rapid growth rates and a wide tolerance to temperatures (Suzuki and Takahashi 1995) produces the annual spring diatom bloom (Marshall and Lacouture 1986, Malone et al. 1996). Within Chesapeake Bay, this event is accompanied by a seasonal decrease in richness within the meso- and polyhaline regions. In addition to the data in this study, high N:P ratios (e.g. 20-50:1) have often been associated with a diatom and chlorophyte dominated phytoplankton community, while lower ratios (e.g. 5-10:1) generally have higher cyanobactiera concentrations (Bulgakov and Levich 1999, Wetzel 2001, Lagus et al 2004).

When available nitrogen levels become more limited in summer months, diatoms and other phytoplankton groups must compete with each other for a smaller pool of resources. Due in part to the ability of some taxa to fix atmospheric nitrogen, cyanobacteria can flourish in these conditions, and for a period of time may out-compete other algal groups,

with maximum abundances observed in all regions of the Bay between July to September (Fig. 20C) when DIN was lowest and phosphate levels were greatest (Fig. 26). In freshwater habitats increased phosphorus concentrations and associated decreased N:P ratios have been associated with increased productivity and cyanobacteria blooms (Wetzel 2001, Heisler et al. 2008). Cyanobacteria blooms within Chesapeake Bay are most prevalent in tidal fresh and oligohaline waters, and include *Microcystis aeruginosa* which can produce potentially fatal hemolytic toxins (Marshall et al. 2005). Large blooms of *M. aerguinosa* and harmful concentrations of its microcystin toxin have resulted in health advisories and beach closures occurred within oligohaline Chesapeake Bay tributaries during 2003 and 2004, which were years of record high streamflow (Marshall et al. 2008, Tango and Butler 2008).

In addition to cyanobacteria, dinoflagellates also form blooms in Chesapeake Bay, with spring blooms of *Heterocapsa rotundata, H. triquetra* and *Prorocentrum minimum* common annual occurrences in the oligo- and mesohaline regions. (Tango et al. 2005, Marshall et al. 2006b, Marshall and Egerton 2009a) Dinoflagellates, particularly those that are found in autumn months often have a life history which includes a resting stage that can remain dormant for the majority of the year (Rengefors and Anderson 1998). These species also are often mixotrophic, meaning that in addition to utilizing photosynthesis and the availability of dissolved nutrients, they can also take up sources of carbon, nitrogen, and other nutrients heterotrophically (Stoecker 1999). These species often cannot compete with diatoms in terms of inorganic nutrient uptake over longer periods of time, but are able to become dominant for shorter periods before returning to a resting cyst stage (Kremp et al. 2008, Kim et al. 2009). Within Chesapeake Bay, blooms

of mixtrophic dinoflagellates are most common during the summer (Bockstahler and Coats 1993) when diatom densities are generally lower, particularly in the lower bay. Included in this group, is the harmful algal bloom forming species *Cochlodinium polykrikoides* which produces dense seasonal blooms in the polyhaline Bay and its tributaries (Marshall and Egerton 2009b). Dense blooms of *C. polykrikoides* have been observed following intense storm activity and high streamflow that were preceded by extended drought periods (Mulholland et al. 2009). These rather large seasonal changes in localized streamflow and related water quality parameters can exist even during years of non-exceptional streamflow. Larger than normal blooms of *C. polykrikoides* were observed in lower Chesapeake Bay during 2007, which had annual streamflow levels within the normal range of annual streamflow (Mulholland et al. 2009).

While increased streamflow and nutrient enrichment have been associated with some dinoflagellate blooms, periods of low precipitation and reduced streamflow have also led to the proliferation of other dinoflagellate taxa. *Dinophysis acuminata*, a potentially harmful species capable of producing oxadaic acid toxin formed an unprecedented bloom within a Chesapeake Bay tributary during 2002, which had the lowest flow on record (Marshall et al. 2003b , Tango et al. 2004). The transport of this bloom was associated with increased saltwater intrusion due to the extremely low flow experienced that year and the transport of this species into northern regions of the Bay (Marshall et al. 2003b , Tango et al. 2004). Blooms of this species have not been observed within Chesapeake Bay in subsequent years.

Conclusions

Seasonal streamflow affects phytoplankton communities in a multitude of ways, with increased levels potentially either increasing or decreasing algal productivity through nutrient additions and sediment inputs (Marshall and Alden 1997). While the long term increasing trend of streamflow entering the Chesapeake is not significant (Williams et al. 2010), regionally the northeastern United States has been characterized as an area of increasing streamflow (Groisman et al. 2001). Much (89%) of the inter-annual variability in streamflow is due to changes in precipitation, with a relatively small amount due to changes in the level of evapotranspiration (Najjar 1999). Future predictions indicate that, in addition to greater precipitation and elevated total streamflow, higher levels of seasonality will be experienced, including more flow during winter and less in summer (Hayhoe et al. 2007, Pyke et al. 2008). In the Bay, these potential future conditions suggest increases in turbidity and algal biomass will occur along with changes in algal species composition and increased frequency and magnitude of algal blooms (Najjar et al. 2010). The results of this study suggest that phytoplankton diversity would also be negatively affected, with greater streamflow leading to lower species richness in Chesapeake Bay, particularly in the polyhaline region. As with other ecosystems, declines in species diversity are likely to be associated with changes in ecosystem functions and have significant impacts on higher trophic levels as well.

PHYTOPLANKTON DIVERSITY AND ECOSYSTEM FUNCTIONS IN A EUTROPHIC ESTUARY; PRODUCTIVITY, STABILITY, AND TROPHIC INTERACTIONS.

Introduction

Along with understanding the roles of environmental factors on diversity, another central concept in ecology is describing the relationships between diversity and ecosystem functions. Spurred on by the global rise in the species loss, there has been considerable research and debate examining the interaction between species diversity and broad ecosystem functions including productivity, stability and the impact on other trophic levels.

Regarding the diversity-productivity relationship, several decades of studies have produced evidence of multiple potential patterns (e.g. Huston 1979, Tilman 1982, Leibold 1999, Fukami and Morin 2003, Irigoien et al. 2004, Witman et al. 2008). Waide et al. (1999) conducted a meta-analysis of ca. 200 diversity-productivity relationships from multiple ecosystems and reported 26% were positive linear, 12% negative linear, 30% were unimodal, and 32% had no significant relationship. Similar results were noted by Grace (1999) and Mittelbach et al. (2001), with the highest number of the studies examined having a unimodal relationship between diversity and productivity, and positive linear being the second most frequent relationship observed. Certain studies have argued that the true relationship between the two parameters is unimodal, with maximum diversity observed at intermediate productivities, and that observed linear patterns are largely due to reduced sample size (e.g. Huston 1994, Rosenweig 1995, Irigoien et al. 2004). However, other data suggests that the relationships between

diversity and productivity are variable and context specific, without a single unifying pattern (e.g. Mittelbach 2001, Pärtel et al. 2007).

There has been a similar effort investigating the relationship between diversity and ecosystem stability (e.g. Walker 1989, Tilman et al. 1998, McCann 2000, Ives and Carpenter 2007). Stability of an ecosystem can be defined and measured in multiple ways, however it generally refers to the ability of a system to either remain in, or return to a static state, or equilibrium (Ives and Carpenter 2007). This includes both resistance and resilience of a system to disturbance, invasion, and other outside forces (Lawton and Brown 1994, Loreau et al. 2002). While there is some debate, there also has been a growing consensus that at the community and ecosystem level, diversity increases stability (McCann 2000, Ptacnik et al. 2008, Cleland 2012).

Within an ecosystem, the abundance and composition of one trophic level can directly lead to changes in other trophic levels (e.g. predator-prey relationships Orth et al. 1984, Egerton and Marshall 2006). Likewise, changes in species diversity present within a particular trophic level can affect other trophic levels as well (Finke and Denno 2004, Hillebrand and Cardinale 2004, Schmitz 2007, Viketoft et al. 2009). The resource competition theory indicates that varied heterogenous resources should support a higher diversity of organisms (Hutchinson 1961, Tilman 1982, Gamfeldt and Hillebrand 2011). Extending this concept to trophic interactions, a diverse primary trophic level represents a more varied set of resources available for higher trophic levels. Observational and experimental studies have indicated that consumer diversity is enhanced by or at least correlated with increased producer diversity (Pianka 1966, Sieman et al. 1998, Jetz et al. 2009).

The majority of the relationships examined between diversity and ecosystem functions have involved terrestrial macroscopic organisms, with fewer directed to aquatic systems in general and microscopic aquatic taxa in particular. This is despite the fact that marine habitats represent the largest ecosystem on Earth and that phytoplankton account for approximately half of global primary production (Falkowski et al. 1998, Irigoien et al. 2004, Ptacnik et al. 2008). In response to this aquatic data gap, there have been a growing number of ecological studies focusing on freshwater and marine diversity. In terms of aquatic diversity and productivity, there appears to be similar disagreement as terrestrial systems, with positive, negative, unimodal and non-significant relations identified (Hall et al. 2000, Smith 2007, Witman et al. 2008). Regarding phytoplankton specifically, a meta-analysis of global marine algal communities by Irigoien et al. (2004) has indicated a hump-shaped unimodal pattern, with maximal diversity (Shannon diversity index) at intermediate algal biomass. Likewise, it has been demonstrated that phytoplankton diversity is positively related to stability in terms of resource use efficiency, and is similar to that observed in terrestrial systems (Ptacnik et al. 2008). In contrast, the relationship between diversity of different trophic levels appears to be considerably different in aquatic systems, with reduced or little effect of producer diversity on grazer diversity (Parker et al. 2001, Irigoien et al. 2004).

I investigated the relationships between diversity and ecosystem functions within natural phytoplankton communities in a large tidal estuary. In particular, these were relationships between phytoplankton diversity and 1) productivity/biomass, 2) stability, and 3) zooplankton diversity. This study utilizes over 2200 estuarine plankton samples collected from Chesapeake Bay over a 25 year period (1985-2009).

Methods

Productivity can be measured using multiple metrics that quantify biomass, or a rate of growth. Phytoplankton biomass in Chesapeake Bay was determined as cell Carbon estimates based on biovolume data from microscopic cell counts of Lugol's preserved whole water samples (Smayda 1978, Marshall and Alden 1997, Lacouture 2010). Phytoplankton biomass data was collected monthly at stations within Chesapeake Bay from 1985-2009 (n= 2229). Algal primary productivity rate was measured concurrently at these stations as the Carbon assimilation rate (mgC $m^{-3} h^{-1}$) via a radiolabeled ^{14}C method from 1989-2009 (n=1774) (Nesius et al. 2007). Zooplankton samples were examined using microscopic analyses of formalin preserved net tow collections made at the same time as the phytoplankton samples from 1985-2001 (n=1281) (Carpenter 2003, Johnson 2008).

Ecosystem stability can be defined as a measure of the variability of a system, often quantified as the variance of population densities or biomass over time using the coefficient of variation (McCann 2000). This approach was used to investigate the degree of inter-annual variability in total phytoplankton biomass and productivity for each Chesapeake Bay station, with the annual mean values calculated from monthly records (1985-2009). Using the annual averages for each station, the coefficient of variation (CV) for each station was calculated as the standard deviation between years divided by the long term station mean. As the CV measures variance around the mean, lower values indicated higher stability (Tilman et al. 1998).

Phytoplankton and zooplankton diversity was characterized as the number of unique phytoplankton taxa for each collection (species richness), and using the Shannon

diversity index, represented as *H'* (Shannon and Weaver, 1949). As salinity is a significant variable in explaining the diversity of estuarine organisms, including phytoplankton in Chesapeake Bay (Chapters 2-3), its effect was extracted from the regression analysis using a two step approach performed in a similar study by Witman et al. (2008). First, the residuals of log transformed phytoplankton, log transformed zooplankton species richness and *H'* were extracted from regressions with salinity (observed log richness/*H'* minus predicted log richness/*H'*). Second, another set of regression analyses were conducted between the residuals of the diversity metrics against the productivity parameters. This is the standard analysis to remove the effect of a covariate in regression analysis (Sokal and Rohlf 1981, Witman et al. 2008). Linear and quadratic polynomial regression models were tested for each pair of variables, with a significance threshold of α=0.05 for all tests. If both regression models were significant for a particular analysis, a partial F was used to determine if the quadratic model significantly improved the explanation of the data more than the linear model (Quinn and Keough 2002, Witman et al. 2008). IBM SPSS Statistics 20 was used for all statistical analyses.

Results

Significant linear relationships were present between phytoplankton diversity and productivity, with differences in the direction (positive/negative) and percentage of the variability explained between the specific diversity (species richness and H') and productivity (biomass and productivity rates) metrics (Table 6; Fig. 23A-H). No

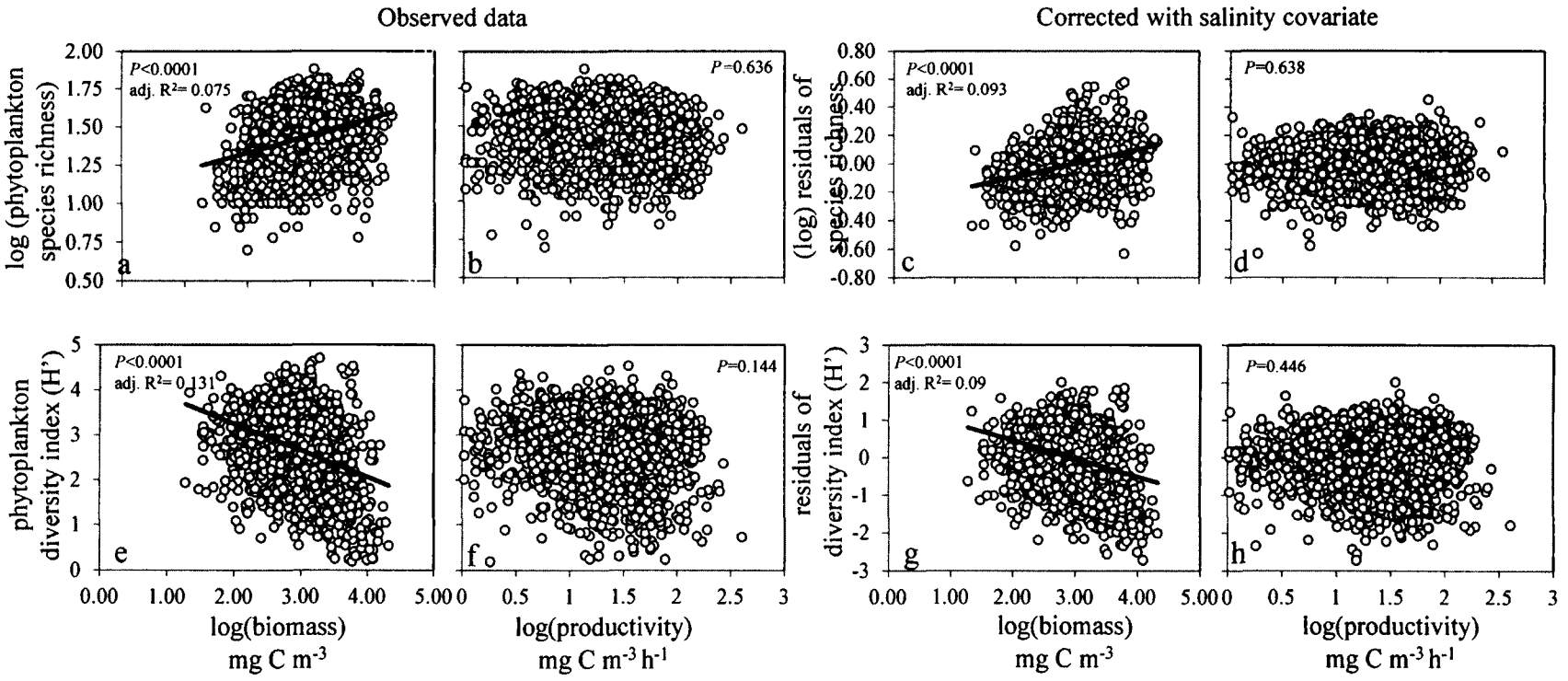

FIG. 23. Scatterplots of (log) phytoplankton species richness and Shannon diversity (*H'*) against (log) algal biomass and (log) productivity rate from Chesapeake Bay (1985-2009). Regressions in figures on the left (A, B, E, F) are based on the original observed data, while those on right (C, D, G, H) are on the residuals of the diversity values after the effect of salinity as a covariate has been extracted (see methods for details). Statistically significant relationships ($P<0.05$) shown with trendline.

TABLE 6: Results of linear regression models shown in Figs.23-25. Regressions in Fig 23 estimate phytoplankton diversity (richness and *H'*) using productivity variables (biomass and productivity rate). Regressions in Fig. 24 estimate stability (inter-annual CV of algal biomass) using phytoplankton diversity variables (richness and H'). Regressions in Fig. 25 estimate zooplankton diversity (richness and H') using phytoplankton diversity variables (richness and H').

Plot	Type	df	regression MS	residual MS	*F*	*P*
23A	Pos.	1, 2227	5.99	0.033	182.04	**<0.0001**
23B	n.s.	1,1779	0.008	0.036	0.22	0.636
23C	Pos.	1, 2227	4.44	0.019	230.09	**<0.0001**
23D	n.s.	1,1779	0.004	0.020	0.22	0.638
23E	Neg.	1,2227	165.05	0.49	337.19	**<0.0001**
23F	n.s.	1,1779	1.14	0.53	2.14	0.144
23G	Neg.	1,2227	109.70	0.49	226.41	**<0.0001**
23H	n.s	1,1779	0.295	0.507	0.582	0.446
24A	n.s.	1,7	.001	.014	0.063	0.808
24B	n.s.	1,7	0.650	0.30	2.18	0.183
24C	n.s.	1,7	0.001	0.014	0.079	0.787
24D	m.s.	1,7	0.032	0.009	3.475	0.100
25A	Pos.	1,1222	61116.25	191.37	319.36	**<0.0001**
25B	Pos.	1,1222	9439.59	90.07	104.80	**<0.0001**
25C	Pos.	1,1222	8.72	0.604	14.44	**<0.0001**
25D	n.s.	1,1222	0.53	0.53	0.99	0.32

significant hump-shaped unimodal relationships were detected. Algal biomass and productivity rates measured were variable, each ranging over three orders of magnitude (Fig. 23). Phytoplankton richness also varied greatly, and ranged from 5-76 species identified per sample collection. A positive relationship was identified between species richness and biomass, accounting for 7.5% of the variability in richness by the variability in algal biomass (Fig. 23A). When species richness was corrected with salinity as a covariate, a positive relationship was still apparent, with biomass explaining 9.3% of the variability (Fig. 23C). In contrast, there was no significant relationship between phytoplankton species richness and productivity (Carbon fixation) rate, in either the original or the salinity corrected dataset (Fig. 23 B, D). A stronger relationship was identified between algal biomass and Shannon diversity (*H'*), which measures both richness and the relative abundance of species within the community (evenness). A significant negative linear relationship between biomass and *H'* explained 13.1% of the variability in diversity by the variability in biomass (Fig. 23E). After the data was corrected with salinity as a covariate, biomass accounted for 9.2% of the variability in *H'* (Fig. 23G). In addition, no significant relationships between *H'* and productivity rate were found (Fig. 23F, H).

Temporal stability was measured as the inter-annual variability in mean algal biomass at the nine stations within Chesapeake Bay using the coefficient of variance (CV). Lower CV values indicated lower variance, and therefore higher stability. No significant relationships were identified between either species richness or *H'* with CV in the original observed dataset (Table 6; Fig. 24A, B). When the diversity values were corrected for salinity by calculating the residual values, a marginally significant

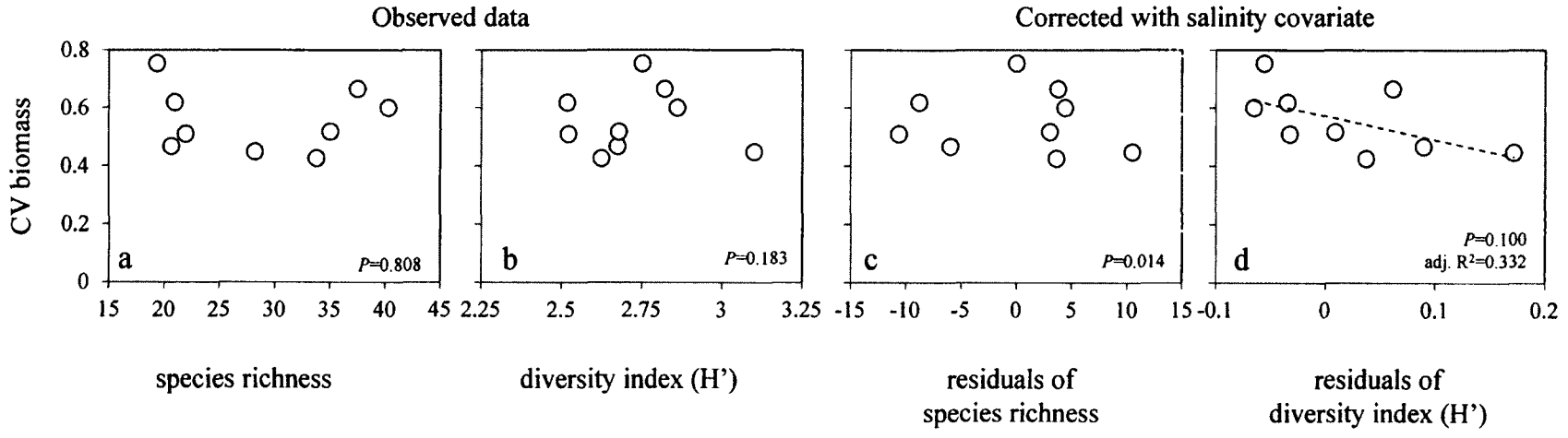

FIG. 24. Plots of temporal biomass stability as the coefficient of variance in interannual phytoplankton biomass and species richness and Shannon diversity (*H'*) at nine stations in Chesapeake Bay (1985-2009). A marginally significant (P=0.1) relationship between salinity corrected *H'* and CV biomass is shown in figure d by a dashed line indicating a positive relationship between stability and diversity.

(P=0.100) negative linear relationship between H' and CV was detected (Fig. 24C, D). In this regression, variability in phytoplankton species diversity explained 33.2% of variability in inter-annual variance of algal biomass. Stations within the Bay with higher diversity (H') were more stable, experiencing lower variability in annual mean biomass. This relationship was not indicated between stability and species richness, even after correcting for the salinity covariate (Fig. 24C).

Zooplankton diversity was generally lower than phytoplankton diversity, and equally variable, with species richness ranging from 4-91 zooplankton taxa per sample. There was a significant positive linear relation between phytoplankton and zooplankton species richness (Table 6; Fig. 25A). Twenty-one percent of the variability in zooplankton richness was explained by the variability in phytoplankton species richness. After correcting for the co-varying effect of salinity, a positive relationship remained, however the regression only explained 7.8% of the variability (Fig. 25B). When diversity was measured using H', a weak relationship between zooplankton and phytoplankton explained only 1.1% of the variability (Fig. 25C). This relationship disappeared after correcting both zooplankton and phytoplankton H' for salinity (Fig. 25D).

Discussion

Phytoplankton communities are dynamic in estuaries including Chesapeake Bay, with significant spatial and temporal variability in not only abundance and composition, but also species richness and evenness (Chapters 2,3, Marshall et al. 2005, Adolf et al. 2006). An exploratory analysis identified that algal diversity was in some cases related to multiple ecosystem functions. Correlative studies, including this study, cannot characterize the underlying causal mechanisms between variables, but are useful at

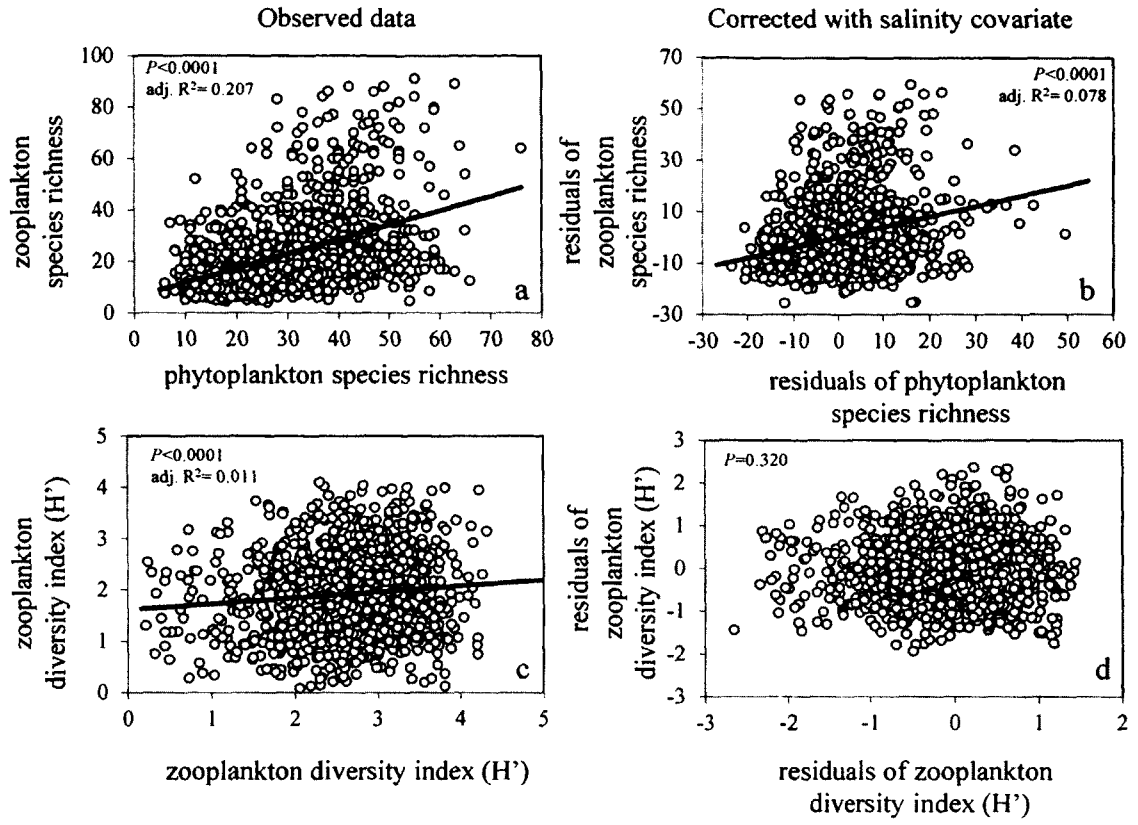

FIG. 25. Scatterplots of observed and salinity corrected phytoplankton and zooplankton species richness and *H'* from Chesapeake Bay (1985-2001). Statistically significant relationships are shown with black trendlines in A, B, C.

detecting patterns between properties in natural communities and identifying starting points for process-oriented research to begin exploring potential explanations that can be addressed in more controlled future experimental settings using hypothesis testing (Witman 2008).

Diversity/productivity relationships have been explored in numerous ecosystems for decades using a variety of measurements for both parameters (e.g. MacArthur and MacArthur 1961, Pianka 1966, Huston 1979, Tilman 1996). Although both are sometimes generalized as diversity, species richness and evenness measure very different properties of a community, and can relate to productivity in fundamentally different ways (Nijs and Roy 2000). Evenness, is an important component in describing community composition, particularly in regards to phytoplankton where densities of co-occurring species may differ by orders of magnitude (Chapter 5, Jacobsen and Simonsen 1993). A measure of evenness was examined in this study using the Shannon diversity index which incorporates evenness and richness. Likewise, examinations of the relationship with diversity have defined productivity in multiple ways including biomass and primary production rates measured using varying approaches (Waide et al. 1999, Tilman et al. 2001). By using multiple metrics, this study identified varying relationships between diversity, productivity and stability that would not have been apparent using a single set of measurements.

Both phytoplankton and zooplankton diversity are influenced by salinity (Chapter 2, Whitfield 2012). Samples analyzed in this study were collected Chesapeake Bay stations with salinities ranging from 0 to 31.9. To focus the analysis on the relationship between species richness, H', and ecosystem function, salinity was treated as a covariate

and corrected for by extracting the residuals of richness and *H'* from an initial regression against salinity (Witman 2008). If a pattern was identified in the observed data, but absent or different in the corrected dataset, it would be considered likely due to correlation with environmental conditions related to location within the estuary (i.e. salinity). While phytoplankton and zooplankton diversity may be influenced by additional, potentially confounding environmental factors, including nutrient concentrations and turbidity, these factors largely co-varied in Chesapeake Bay with salinity along the estuarine gradient (Chapter 2). Therefore, by correcting for salinity, the influence of additional covariates may also be removed, or at least reduced. In most cases, patterns identified using the original uncorrected observed data were also found using the salinity corrected data, indicating that the relationships identified were not due to salinity alone, and represented a connection between diversity and the specific ecosystem function analyzed.

Diversity-productivity relationships

Experimental manipulations and observational studies have identified positive, negative, unimodal and non-significant relationships between phytoplankton species richness and evenness and productivity rate and biomass (Mittelbach et al. 2001). Within Chesapeake Bay, a linear negative relationship was found in the current study between phytoplankton biomass and *H'* while a positive relationship existed between biomass and phytoplankton species richness (Fig. 23). Examinations of freshwater lakes have identified unimodal relationships between phytoplankton species richness and productivity of natural communities, and a negative relationship in experimentally manipulated lakes (Dodson et al. 2000). Using the Shannon diversity (*H'*) index,

Irigoein et al. (2004) described global marine phytoplankton diversity as a unimodal function of phytoplankton biomass with maximum diversity predicted at an intermediate biomass (~30 mg C m^{-3}). A similar unimodal pattern between *H'* and phytoplankton abundance was in a reservoir study within the Uruguay River basin by Chalar (2009), with maximum diversity seen at about 3000 cells ml^{-1}. No significant unimodal relationships were identified in this analysis. Previous studies have identified that the observed pattern between diversity and productivity depends on the extent of the system studied and that unimodal relationships will only be identified if there is a large enough range of productivity examined (Rosenzweig 1995, Waide et al. 1999).

Chesapeake Bay is a highly productive estuary, subject to nutrient enrichment and eutrophication (Boesch et al. 2001, Kemp et al. 2005). Algal biomass estimates based on cell biovolume in the current study ranged from 3.7 to 21,000.1 mg C m^{-3}, with a long term Bay-wide average of 1409.2 mg C m^{-3}. The unimodal relationship between plankton diversity (*H'*) and biomass described by Irigoein et al. (2004) involved a positive function below ca. 30 mg C $m^{-3}$and decreasing *H'* from approximately 30 to 1,100 mg C m^{-3}. This relationship was based on a widely distributed global dataset of 353 marine phytoplankton samples collected from the following locations: Norwegian Sea, North Atlantic Ocean, Iceland Basin, Irminger Sea, Long Island Sound, North Sea, English Channel, Benguela and Oregon upwellings, Indian Ocean, mesocosms in the Beren fjord, and five extended Atlantic Ocean meridional transects (Irigoein et al. 2004). The unimodal relationship was observed by comparing the diversity and productivity of all these habitats to each other, and was not apparent within the individual environments. When examining high productivity habitats in the analysis of Irigoein et al. (2004)

individually such as the Benguela and Oregon upwelling locations, a linear negative relationship was observed between *H'* and biomass. This is more indicative of the pattern in Chesapeake Bay, where biomass values were orders of magnitude higher than in the habitats studied by Irigoein et al. (2004) and associated with lower values of *H'* (Fig. 23).

While a unimodal relationship may exist between *H'* and biomass, the lack of sufficient low biomass samples provided little data to indicate such a pattern. Less than 3% of the sample collections had biomass values below 100 mg C m^{-3}, with less than 0.1% being below 10 mg C m^{-3}. The contrast in the pattern with *H'*, species richness, and algal biomass, indicated that decline in *H'* was due to a reduction of species evenness (Fig. 23). While it appeared that higher biomass samples contained a greater number of species, there was a greater disparity in the relative abundance of the phytoplankton taxa within the community. The proportion of rare species has been shown to increase with number of individuals within a community (Preston 1962). High biomass communities would therefore be characterized by a small number of dominant phytoplankton species along with a large number of background taxa at much lower densities. Prevalence in disproportion in the relative abundance of algal species has previously been described within Chesapeake Bay and its tributaries (Marshall and Alden 1990, Marshall and Nesius 1996, Marshall 2009). Marshall and Nesius (1996) found that less than 5% of the total phytoplankton species present in Chesapeake Bay were considered dominant (most abundant within the sample).

Although algal diversity was significantly related to biomass, no relationship was apparent regarding productivity rate. Primary productivity rates in Chesapeake Bay were

high and variable, with an average of 34 $mgCm^{-3}h^{-1}$ and ranged from 0.1 to 403.1 $mgCm^{-3}h^{-1}$. Agard et al. (1996) found marine phytoplankton species richness was positively correlated with primary productivity and plateaued at what they considered high productivity (~20 $mgCm^{-3}d^{-1}$). By comparison, daily rates calculated using an average day length of 8 hours times the hourly rate (Marshall and Nesius 1996), range from 0.8 to 3224.6 with a mean of 271.7 $mgCm^{-3}d^{-1}$. In contrast to biomass, which represents a longer standing temporal period that is more consistent with the time associated for species composition/diversity to change (ie. > than phytoplankton growth rates), productivity measurements capture the photosynthetic ability of the community for a brief moment in time (~2 hours). These measurements also do not represent the contribution of cells which are not actively undergoing photosynthesis, including species that are present but have limited productivity (ie. light limitation) and those taxa that are mixotrophic/heterotrophic. These factors would allow for variability in both richness and evenness that would not necessarily be reflected in changes in measured productivity rates, and may explain why no significant relationship between the parameters was observed.

Even though there is not a general consensus on the patterns of diversity and productivity, let alone the causal mechanism, multiple theoretical explanations of these relationships have been hypothesized (e.g. Huston 1979, Waide et al. 1999, Rajaniemi 2003). At higher diversity levels, a greater number of species should be able to utilize resources more efficiently and therefore achieve a higher overall level of productivity, assuming that different species use different resources (Huston 1994). As competition for resources increases with productivity, a relatively small number of species that are

strong competitors should survive at high productivity, a small number of species that are tolerant of resource stress at low productivity, and a larger combination of the two existing in-between where productivity and competition are at intermediate levels (Rajaniemi et al. 2003). Following this theory, in a theoretical unimodal model, phytoplankton richness at low productivity should be reduced due to nutrient limitations. At the lowest level, rock pools of rainwater have almost no primary productivity, and support very few species of any type (Dodson 1987, Waide et al. 1999).

On the other end of the spectrum are nutrient enriched eutrophic waters that are often dominated by a single algal bloom species (Jacobsen and Simonsen 1993). At high productivities, phytoplankton diversity is also thought to be limited by increased light limitation (Huisman et al. 1999). High algal biomass, such as what is present during algal blooms limits light penetration into the water column through shading and may cause a decline in phytoplankton diversity by favoring only those species that are shade tolerant (Huisman et al. 1999, Irigoien et al. 2004). Resource heterogeneity has also been identified as contributing to a potential unimodal relationship between diversity and productivity, as both very unproductive and very productive environments have low resource heterogeneity and low diversity (Tilman and Pacala 1993, Rajaniemi 2003). Both increased variance in limiting resource concentrations (temporal heterogeneity) and physical structure (spatial heterogeneity) increase phytoplankton diversity (Yamamoto and Hatta 2004, Declerck et al. 2007). Equally, nutrient enrichment reduces phytoplankton diversity by reducing heterogeneity of limiting resources at higher nutrient levels (Watson et al. 1997, Interlandi and Kilham 2001, Grover and Chrzanowski 2004).

Diversity-stability relationships

A similar degree of uncertainty and debate exists regarding the relationship between diversity and ecosystem stability, often defined, including in the current study, as the temporal variance in total community level biomass (McCann 2000). While there is debate regarding the causative mechanisms one general finding is that at higher diversity (generally species richness), there is lower temporal variability in biomass (Tilman et al. 2006, Proulx et al. 2010). Ecological theories proposed as explaining these observations include the 'insurance effect,' in which different species have different roles within a community, and that a larger number of species increases the likelihood that there is a redundancy of a particular role by multiple species (Naeem 1998, Thébault and Loreau 2005). The effect of disturbance, or a loss of individual species, is thought to be lessened in regard to the entire community when more species are present if redundancy allows for the same functional role to be carried out by a different species. High redundancy is observed in Chesapeake Bay phytoplankton within particular groups, including diatoms and dinoflagellates which are the most specious, with low representation of others (Chapter 2).

While there are a number of terrestrial studies focusing on the relationship between diversity and stability, they are less common involving aquatic habitats, particularly microbial aquatic organisms (Ptacnik et al. 2008). Examinations of phytoplankton dynamics using theoretical analyses have indicated that variable population densities caused by competition for resources by a number of different species contributes to a relatively stable level of total algal biomass (McCann et al. 1998). Steiner et al. (2005) carried out a microcosm study which included experimentally manipulated levels of freshwater algal diversity to study the effect on temporal stability.

Their findings included a negative effect of species evenness on temporal variability in community biomass, indicating a positive relationship between evenness and stability at the community level. Ptacnik et al. (2008) identified that freshwater and estuarine phytoplankton diversity was positively related to increased stability through greater resource utilization. Within Chesapeake Bay, a marginally significant ($P=0.100$, R^2 0.332) negative relationship was identified between temporal biomass variance and phytoplankton *H'* in the current study after correcting for the salinity covariate, potentially indicating greater stability at higher *H'* (Fig. 24). With no significant relationship between species richness and biomass variance identified, the association with *H'* can be attributed to variation in species evenness. While not significant at the $\alpha=0.05$ level, these results are consistent with the findings in aquatics systems of Steiner et al. (2005) and Ptacnik et al. (2008), and with ecological theory based on studies of terrestrial systems (i.e. Dodd et al. 1994, Valone and Hoffman 2003, Tilman et al. 2006). They suggest that factors that reduce phytoplankton diversity (i.e. eutrophication through increasing nutrient concentrations), may also negatively reduce the stability of aquatic primary productivity (Ptacnik et al. 2008).

Phytoplankton-zooplankton diversity

Diversity of consumers has long been considered to be related to the diversity of producers (Murdoch et al. 1972). Exanimations of producer and consumer diversity have identified a positive correlation between the two (Siemann et al. 1998; Haddad et al. 2009), although the results are not universal, with no significant relationship in several cases (Winner 1972, Boone and Krohn 2000, Hawkins and Porter 2003). In terms of aquatic habitats, Margalef (1968) states that "if the diversity of phytoplankton is high the

diversity of zooplankton and even of pelagic fishes is high also." Positive correlations between phytoplankton and zooplankton diversity have been identified, and are considered related to increased heterogeneity of resources (Lasserre 1994, Dolan et al. 2002). However, other studies have noted that in aquatic systems consumer characteristics including diversity are influenced by factors other than producer diversity (Richerson et al. 1970, Parker et al. 2001). An analysis of marine zooplankton and phytoplankton indicated little relationship (R^2=0.01) between the diversity (H') of the two groups (Irigoein et al. 2004).

In this analysis there was a positive relationship between zooplankton diversity and phytoplankton diversity in Chesapeake Bay (Fig. 25). When comparing the species richness of the two groups in the original data set, the variation in phytoplankton richness explained 20.7% of the variation in zooplankton richness. However it appeared that the majority of this relationship is due to an effect of conditions within the estuarine gradient, as the explanatory power of the regression drops to 7.8% after correcting for the salinity covariate. When relating the diversity of the groups using the diversity index H', a similar lack of relationship between the two was found (R^2=0.01) as in the study of global marine taxa (Irigoein et al. 2004). This relationship disappeared below a significant level after accounting for the salinity covariate. It has been suggested that a positive relationship observed in natural systems between certain consumer and producer diversities are not due to the diversity specifically, but the two groups responding to similar environmental factors (Hawkins and Porter 2003). Estuarine zooplankton diversity has similar trends to that described in phytoplankton, with similar associations with salinity and seasonal patterns (Whitfield et al. 2012). In Chesapeake Bay, it appears

that while most of the relationship between the two groups may be associated with a shared response to environmental conditions, a positive trend remains that suggests phytoplankton species richness may be an important component in the richness of zooplankton.

Conclusions

Multiple significant relationships were identified between phytoplankton species richness and evenness (H'), and ecosystem functions within Chesapeake Bay. Increased algal biomass was associated with higher richness and lower evenness, while no relationship was apparent regarding varying productivity rates. In contrast to current ecological theory, a unimodal relationship between phytoplankton productivity and diversity was not observed. This is explained in part by the prevalence of both very high algal biomass and productivity rates compared to studies of less productive systems.

Cultural eutrophication through increased nutrient loading has contributed to increasing trends in algal biomass in Chesapeake Bay (Harding and Perry 1997, Marshall et al. 2003a, Kemp et al. 2005, Williams et al. 2010). Although efforts have been made to reduce nutrient inputs into the Bay, little positive response has been observed in living resources including the phytoplankton community (Boesch et al. 2001, Dauer et al. 2012). The results presented here indicate that increased phytoplankton biomass is associated with changes in phytoplankton diversity, specifically a decrease in species evenness and an increase in species richness. Under these conditions, a greater proportion of the phytoplankton community would be dominated by a small number of species, with an increased number of less abundant background species.

There is also evidence that reduced levels of phytoplankton evenness may be associated with lower predictability and greater variance in annual phytoplankton biomass. A decline in diversity and stability of the primary producers of the habitat could be expected to have significant effects on the ecosystem as a whole. While species evenness of Chesapeake Bay phytoplankton does not appear to be significantly related to zooplankton evenness, there was a positive relationship regarding species richness. As decreased resource heterogeneity at the phytoplankton level, in terms of species richness appears to have a negative effect on zooplankton richness, a decline in zooplankton richness may also be expected to impact the diversity of upper trophic levels including ecologically and economically important pelagic fish communities (Eadie and Keast 1984, Jung and Houde 2003).

Predictions of the response to future changing climatic conditions within Chesapeake Bay include a continued increase in overall algal biomass, as well as an increase in harmful algal blooms (Najjar et al. 2010). In addition to the negative properties associated with harmful algal blooms (i.e. hypoxia, toxicity), they also represent very low species evenness. This reduction of diversity would contribute to future impacts on ecosystem function including lower ecosystem stability and possible negative effects on higher trophic levels as well. The results presented here and the recent findings of Chalar (2009), reinforce phytoplankton diversity as a useful metric to be used as a component, but not the only measure, in evaluating the overall condition of aquatic ecosystems.

ALGAL BLOOMS: CASE STUDIES IN PHYTOPLANKTON DIVERSITY DRIVERS AT SMALLER SPATIAL AND TEMPORAL SCALES

Preface

In the previous chapters I have addressed the large scale spatial and temporal patterns of phytoplankton diversity in Chesapeake Bay in addition to some of the impacts on associated ecosystem functions. The roles environmental factors have on influencing the composition, abundance and diversity of the algal community, particularly the importance of key variables (e.g. salinity and limiting nutrient concentrations) have also been described. Fluctuations in these environmental factors have been linked with significant changes in diversity at individual stations and Baywide at seasonal and interannual time scales. Both within a year and between years, changes in the average number of species (alpha diversity) and species turnover (beta diversity) have been associated with the fluctuations associated with streamflow (eg. DIN, secchi, salinity). The general trend is that increased streamflow, both seasonally and long-term bring increased nutrient levels, decreased water clarity, and decreased salinity. These conditions were accompanied by increased phytoplankton abundance and generally decreased algal diversity.

The Chesapeake Bay Monitoring Program contains an extensive 27 year database from a complex spatial and temporal environment. This resource has allowed for the examination of long-term trends and the assessment of biological responses to changing environmental conditions over this time period (e.g Marshall et al. 2009, Williams et al. 2010). However, as with any large scale monitoring program, it is limited in its ability to detect changes at spatial and temporal scales by the distribution and frequency structure

employed in the data collection. Given finite resources, a compromise is necessary to include a large enough spatial area as the entire Chesapeake Bay, the temporal aspects associated with seasonal conditions, plus the need to maintain the monitoring for an extended time period (decadal) to detect any long-term changes. In terms of the Chesapeake Bay Monitoring Program, this means seasonal variability is represented by monthly collections. Changes in phytoplankton composition and diversity and environmental fluctuations within shorter time periods (<30 days) may go unnoticed. Additional studies employing a higher frequency sampling period have shown that these changes can be significant (Mitchell-Innes and Walker 1991, Litaker et al. 1993).

The tradeoff between a high frequency low spatial coverage examination and a study that covers a larger area, but does so less frequently is one of data relevance. The investigator must decide if the data gained from higher sampling frequency provide sufficient additional information, particularly if it necessitates studying a smaller area. This would be more beneficial for example if there are highly dynamic conditions observed in a generally homogenous spatial environment. Similarly, in a spatially diverse habitat with lower temporal changes, resources would be better utilized in describing a larger area at a lower frequency.

To further examine the relationships between environmental variables, phytoplankton diversity and ecosystem functions over a much higher frequency time period, I have included the following month long study on a daily basis within the Lafayette River, Norfolk, Virginia. To accommodate the high sampling frequency, it was necessary to limit the study to a single station. Additionally, it was necessary to examine a location accessible on a daily basis, thus the samples were collected from shore at a site located

nearby Old Dominion University, namely the Department of Ocean, Earth and Atmospheric Sciences Center for Coastal and Physical Oceanography dock.

The study provided observations of on-going high frequency changes in algal populations and several environmental variables, and serves as a case study of a eutrophic urban estuary. The large scale patterns observed in Chesapeake Bay documented in previous chapters indicate that eutrophic conditions, particularly elevated nitrogen and increased algal productivity as a whole can be associated with lower levels of phytoplankton diversity. By studying the linkages between environmental conditions and algal diversity in a relatively degraded body of water such as the Lafayette River, it allows for the exploration of how similar conditions might relate to Chesapeake Bay as a whole.

Abstract

Algal blooms are dynamic phenomena, often attributed to multiple environmental parameters that cause responses by numerous phytoplankton taxa. To evaluate the relationships between water quality variables and algal populations, daily samples were collected over a 34 day period in the Lafayette River, a tidal tributary within Chesapeake Bay's estuarine complex, during Spring 2006. During this period two distinct algal blooms occurred; the first was a cryptomonad bloom that was followed by a bloom of the mixotrophic dinoflagellate *Gymnodinium instriatum*. Chlorophyll *a*, nutrient concentrations, and physical and chemical parameters were measured daily in addition to phytoplankton abundance and community composition. Sixty-five phytoplankton species from 8 major taxonomic groups were identified and total micro- and nano- phytoplankton cell densities ranged from 5.8×10^6 to 7.8×10^7 cells l^{-1}, while picoplankton densities

ranged from $3.7x10^6$ to $1.3x10^9$ cells l^{-1} over the same time period. During their respective blooms, cryptomonads and *G. instriatum* reached 91.6% and 99.0%, respectively, of the total phytoplankton biomass respectively. No significant changes in phytoplankton species richness were observed during the study, although there was a significant decline in the Shannon diversity index accompanying the bloom development indicating a reduction of species evenness. The cryptomonad bloom developed following a period of rainfall and concomitant increases in inorganic nitrogen concentrations. While, nitrate, nitrite and ammonium were positively lag-correlated with crytomonad abundance between 0 and 5 days prior, the *G. insriatum* bloom developed during periods of low nitrogen concentrations with abundances negatively correlated with inorganic nitrogen concentrations.

Introduction

In estuarine systems, phytoplankton communities are highly variable, and are affected by numerous environmental and ecological factors including water temperature, salinity, light intensity, nutrient availability, inter- and intra-specific competition among the algae, and predation (Hutchinson 1961, Grover and Chrzanowski 2004, Cloern and Dufford 2005, Spatharis et al. 2007). Many environmental variables vary on short time scales in estuaries, including tidal and diel fluctuations in physical/chemical parameters as well as the periodic nutrient inputs from precipitation events (Hubertz and Cahoon 1999, Morse 2011). Because of their short generation times, phytoplankton populations can respond to environmental and ecological forcing rapidly (McCormick and Cairns 1994, Buchanan et al. 2005, Paerl et al. 2007). Consequently, in estuaries, substantial changes in algal community composition can occur over relatively short time periods in

response to environmental variability (Litaker et al. 1993, Malone et al. 1996, Paerl et al. 2010). Environmental variability and species interactions also impact the biodiversity of phytoplankton communities and this can relate to changes in productivity and ecological function in estuarine systems (Duarte et al. 2006, Jouenne et al. 2007).

An example of rapid change of phytoplankton composition is an algal bloom, in which community changes can occur on the order of days resulting in near monospecific assemblages (Harris and Trimbee 1986, Glibert et al. 2001). Algal blooms appear to be increasing and nutrient over-enrichment has been implicated (Anderson et al. 2002, Heisler et al. 2008). Bloom events are often sampled opportunistically after they have been observed, and prior conditions may be unknown. Due to the speed which environmental parameters and phytoplankton communities can change, less frequent monitoring collections (i.e. monthly) may not document bloom events, and are not sufficient to record conditions prior, during and following bloom development. Daily sampling studies are more rare, but have been useful in documenting the relationship between short term variability in water quality parameters and algal composition (Mitchell-Innes and Walker 1991, Litaker et al. 1993)

The objectives of this study were to identify short-term changes in phytoplankton species composition and diversity associated with variability in water quality parameters and biological interactions that promote the development of mono-specific blooms in this tidal estuarine system. This study also investigates the relationship between algal diversity and productivity at a fine resolution scale during a period of highly variable populations.

Study site

The Lafayette River, located in Norfolk, Virginia is a tributary of the Elizabeth River that flows into the lower James River before entering the Chesapeake Bay. It is a tidal river, approximately 8km in length, with a mean depth of 1.3m, and a maximum channel depth of 7.6m (Blair et al. 1976). The river is surrounded by residential and commercial development, within an urban watershed of 43.28 km^2, and a shoreline that includes bulkheaded regions, marinas, private docks and wetland marsh of *Spartina alterniflora* (White 1972, Blair et al. 1976, Owen et al. 1976, Berman et al.2002). Freshwater input is by precipitation and shoreline drainage including from 13 storm sewers and overflow drains (White 1972, Purcell 1973). Seasonal dinoflagellate blooms common in this river include *Prorocentrum minimum* development in early spring with more recent summer and autumn blooms dominated by *Akashiwo sanguinea* and *Cochlodinium polykrikoides* (Marshall 1968, Kalenak 1982, Mulholland et al. 2009, Egerton et al. 2012). The river has been identified as a potential initiation point for large autumn regional dinoflagellate blooms dominated by *C. polykrikoides.* (Morse et al. 2011).

Methods

Surface water samples were collected once a day during the incoming tide from a stationary floating dock on the Lafayette River between April 20, 2006 and May 25, 2006. The mean water depth was 0.9m. Water temperature, salinity and dissolved oxygen were measured on station with a Hydrolab DataSonde 4a water quality multiprobe (Hach Company, Loveland, CO). Rainfall and air temperature were recorded at Norfolk International Airport, <10 km from the Lafayette River station. Chlorophyll *a* was measured fluorometrically (Welschmeyer 1994) and dissolved nitrate, nitrite, and

phosphate analyses were conducted colorimetrically with an Astoria Pacific nutrient autoanalyzer using manufacturer specifications. Ammonium was analyzed manually using the phenolhypochlorite method (Solorzano 1969). Nano- and microphytoplankton samples (500ml) were collected at the surface (<1m), preserved with Lugol's solution (1% concentration), and examined with an inverted microscope (Nikon TS100) at 150-600x following a modified Utermöhl settling and siphoning protocol (Marshall and Alden 1990). Autotrophic picoplankton samples, collected at the same time and depth were preserved with gluteraldehyde (2%) and counted using epifluorescence microscopy (Nikon E600) at 1000x (Affronti and Marshall 1994). Phytoplankton biomass was determined using volume calculations based on cell dimensions and converted to pg C using the equations of Eppley et al. (Smayda 1978). Samples examined by scanning electron microscopy were fixed with gluteraldehyde and osmium tetroxide, dehydrated through an ethanol series, dried using a critical point drier, sputter coated with gold-paladium, and analyzed using a LEO 435VP (LEO Electron Microscopy Ltd., Thornwood, NY) (Tang et al. 2008). Phytoplankton diversity was calculated daily using both species richness (number of species per sample) and the Shannon index (H') which incorporates the relative abundance of each species and therefore is commonly used as a measure of species evenness (Shannon and Weaver 1949): $H' = -\sum(p_i \log p_i)$ where p_i is the proportion of the total algal biomass of species *i.* Higher values of H' indicate a greater species diversity, and generally indicate a greater level of species evenness, with a more widely distributed range of biomass attributed to a larger number of species.

The daily abundances of phytoplankton species data and corresponding environmental variables were examined using Pearson correlation analysis. As algal

growth rates are on the order of days, a lag response of phytoplankton abundance to nutrient concentrations was expected. The daily sampling scheme allowed for algal abundances to be compared to nutrient concentrations present prior to and following potential bloom development. The lag correlation analyses conducted here compared nutrient concentrations at one day intervals over a 11 day window, from days prior to five days forward to phytoplankton abundance. Correlation analysis was conducted for the dinoflagellates and cryptomoands abundances only, as they were the most dominant phytoplankton taxa present during the sampling period, with low representation of other taxonomic groups. In addition to environmental conditions, biological interactions including competition and predation are known to influence phytoplankton composition. Therefore a lag correlation analysis of species richness, *H'*, and the abundance of other dominant phytoplankton groups was also conducted on dinoflagellate and cryptomonad abundance.

Regression analysis was used to examine the relationship between daily species diversity (both richness and H') and total algal biomass as a measure of productivity. To compare the Lafayette study to other nearby habitats, diversity and biomass measurements from Virginia Chesapeake Bay monitoring program collections (n=26) during the same time period were also included in the regression analysis. As previous studies have identified linear and non-linear (unimodal) relationships between the variables (e. g. Waide et al. 1999), analysis of variance was conducted to test for significant linear and quadratic regression models using SPSS 20 (IBM). If both regression models were significant for a particular analysis, a partial F was used to

determine if the quadratic model significantly improved the explanation of the data than the linear model (Quinn and Keough 2002, Witman et al. 2008).

Results

Meteorological and physical parameters

Over the 34-day sampling period, daytime air temperatures ranged from 11.7 to 21.7 °C, and water temperatures ranged from 15.1- 24.0 °C (Fig. 26A). Average daily wind speeds were variable and ranged from 5 to 20 mph and gusts exceeded 30 mph on 9 days with a maximum of 43mph on May 1 (Fig. 26B). During the sampling period there were 8 rain events of 0.5 cm of precipitation or more (Fig. 26C). Salinity at the sampling site decreased over the sampling period, with a maximum of 20.2 and a minimum of 17.5 ppt, salinity decreased following periods of rainfall (Fig. 26D). The water was alkaline during the study with an average pH of 8.31, and a range of 7.98 to 8.79 (Fig. 26E). Dissolved oxygen levels varied between 5.0 and 7.8 mg l^{-1} and saturation ranged from 61.6% and 98.1% (Fig. 26F)

Phytoplankton abundance, composition and diversity

Chlorophyll *a* (Chl *a*) concentrations ranged from 5.54 to 97.6 μg l^{-1} but were below 20 μg l^{-1} for 26 of the 34 days (Fig. 26G). There were high Chl *a* concentrations, 30.7 μg l^{-1}, on April 27, with the highest Chl *a* concentrations observed during the period between May 16- 25 (74- 97.6 μg l^{-1}). Total nano and microphytoplankton cell densities were high and ranged from $5.8x10^6$ to $7.8x10^7$ cells l^{-1} (Fig. 27A). Picoplankton abundances ranged from $3.7x10^6$ to $1.3x10^9$ cells l^{-1}. There was a large cryptomonad

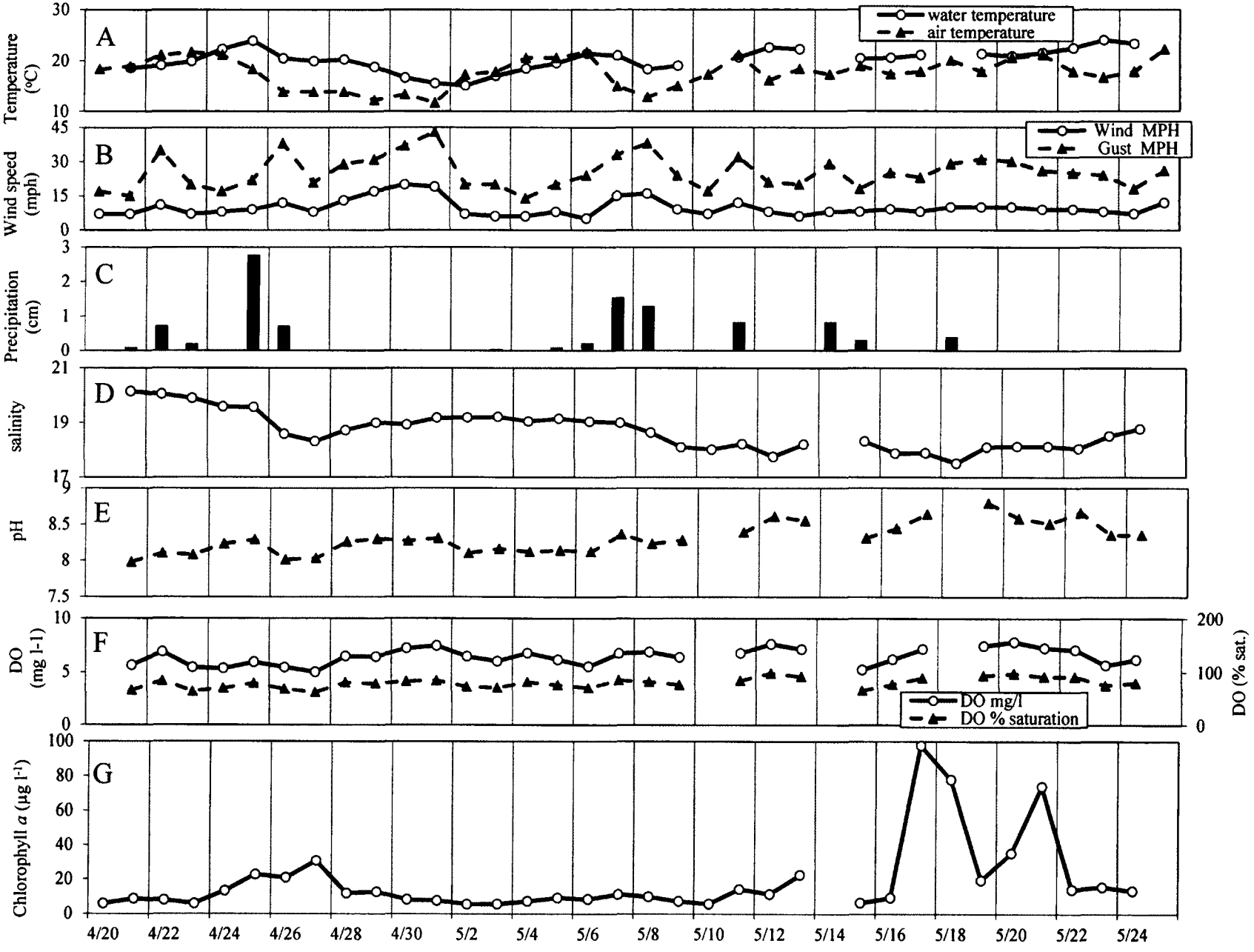
A
Temperature (°C)
30
20
10
water temperature
air temperature
B
Wind speed (mph)
45
30
15
0
Wind MPH
Gust MPH
C
Precipitation (cm)
3
2
1
0
D
salinity
21
19
17
E
pH
9
8.5
8
7.5
F
DO (mg l-1)
10
5
0
200
100
0
DO (% sat.)
DO mg/l
DO % saturation
G
Chlorophyll a (µg l-1)
100
80
60
40
20
0
4/20
4/22
4/24
4/26
4/28
4/30
5/2
5/4
5/6
5/8
5/10
5/12
5/14
5/16
5/18
5/20
5/22
5/24

FIG. 26. Daily measurements of physical and chemical parameters in the Lafayette River from April 20 to May 25, 2006. A: water temperature (^{o}C) measured on station and mean daily air temperatures measured at Norfolk International Airport (ORF). B: mean daily wind speed and maximum daily speed of wind gusts measured at ORF(miles h^{-1}). C: Daily cumulative precipitation measured at ORF (cm). D: salinity. E: pH. F: Dissolved oxygen (mg l^{-1}), and percent saturation. G: Daily chlorophyll *a* measurements (µg l^{-}).

bloom from April 24-May 1, and a second bloom dominated by the dinoflagellate *Gyrodinium instriatum* from May 16-May 24 (Fig. 27A). The morphology and size of the cryptomonads appeared consistent throughout the course of the study. The cells were comma-shaped, with a round anterior and a reflex curved pointed antapex with an average length of 18.3 μm and an average maximum width of 8.3 μm. Cryptomonad taxonomic identification is notoriously problematic due to the cells' sensitivity to chemical fixatives and small number of morphological features (Klaveness 1988, Menezes and Novarino 2003). For the purposes of this paper, even though consistent morphological features were observed during the sampling period, the cryptomonads are hereby referred conservatively as *Cryptomonas* spp., indicating the possible presence of multiple species. *Gymnodinium instriatum* was identified by its morphological features including the displacement of the cingulum and the shape of the apical groove (Fig. 28) according to Steidinger and Tangen (1996) following the most recent nomenclature of Coats and Park (2002).

Estimates of phytoplankton biomass were made using cell abundance and biovolume and were highly correlated with chlorophyll *a* concentrations ($r=.95$, $p=.000$). Nano-and microphytoplankton biomass ranged from 609 to 65,819 μg C l^{-1}, with the highest biomass measured during the *Gymnodinium* bloom from May 16 to 23 (Fig. 29A). Picoplankton biomass varied from 0.5 μg C l^{-1} at the start of the study to 181 μg C l^{-1} on May 25, but remained a minor component compared to the biomass of the nano/micro plankton size classes, contributing an average of less than 1% of total phytoplankton biomass (data not shown).

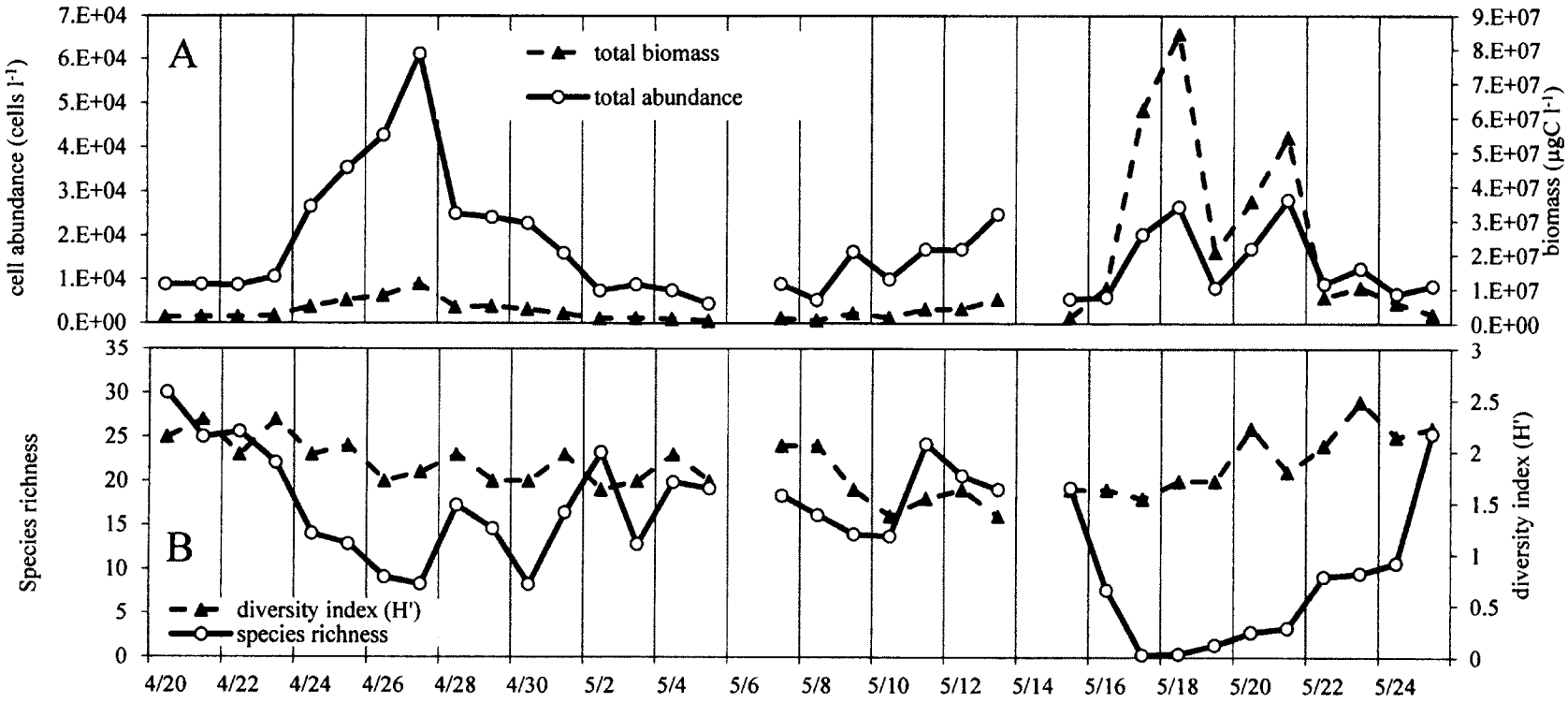

FIG. 27. Timeseries of Lafyayette River data from April 20 to May 25, 2006 showing changes in A: phytoplankton abundance and biomass, and B: varying phytoplankton diversity as measured by species richness and the Shannon diversity index *H'*.

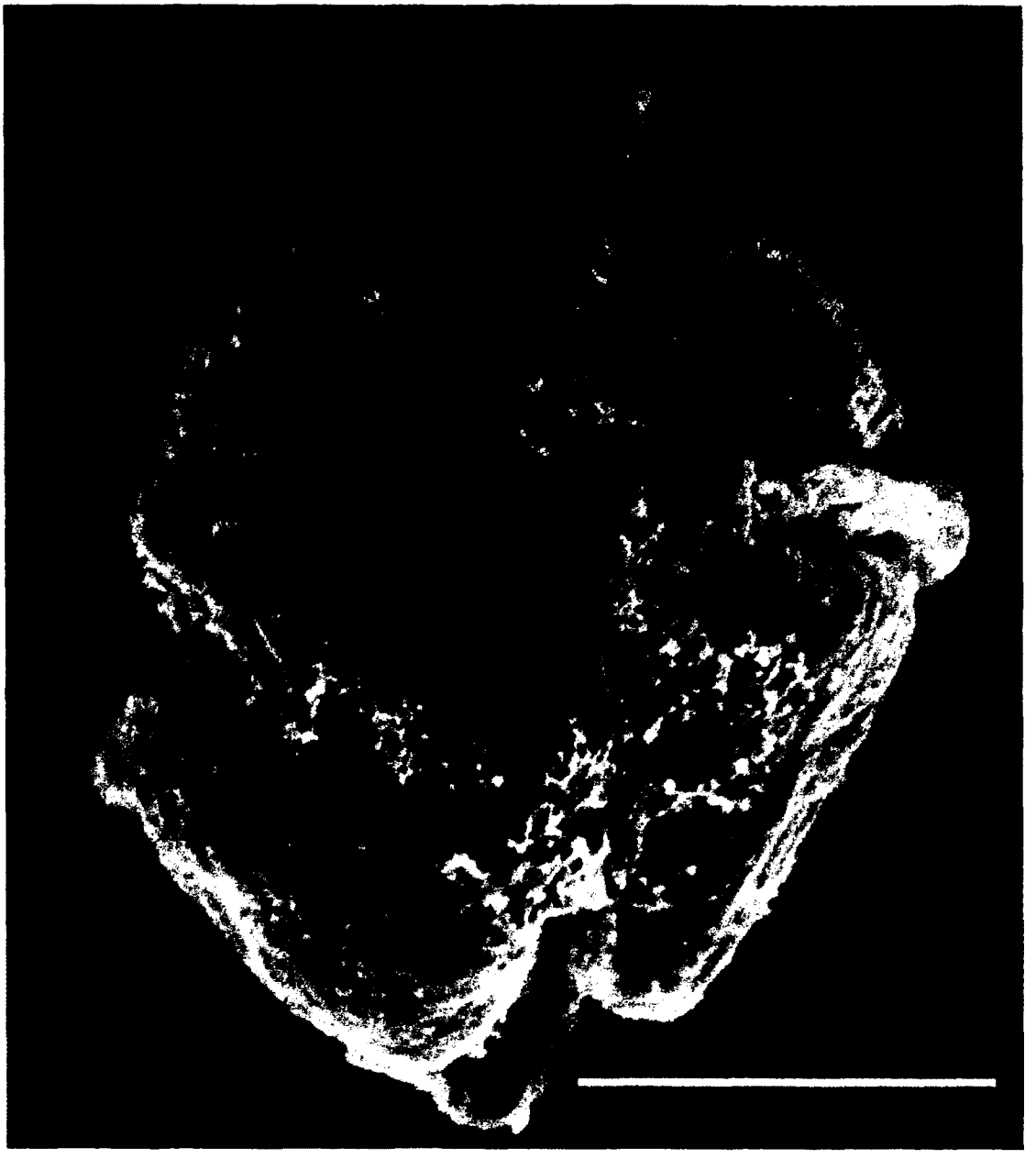

FIG. 28.Scanning electron micrograph of *Gymnodinium instriatum* vegetative cell, collected at the study site during the dinoflagellate bloom (on May 18, 2006. Scale bar = 10μm

While dominated by a single species during blooms, the phytoplankton community consisted of 65 taxa from 8 major taxonomic groups, with 41 taxa present on 5 or more days (Table 10). There were 37 species of diatoms, 17 dinoflagellates, 3 cyanobacteria, 2 silicaflagellates, 2 chlorophytes, with cryptomonads, euglenophytes and prasinophytes each represented by one taxon. While diatoms were the most diverse group, consisting of mainly centric species (eg. *Skeletonema costatum* and *Chaetoceros* spp.), they never represented more than 49% of the cells present, and were generally much less abundant than the phytoflagellates (Fig. 29B)

Phytoflagellates, specifically cryptomonads and dinoflagellates, were the dominant algae throughout the study. The most abundant taxon was *Cryptomonas* spp., reaching a maximum density of 7.7 $x10^7$ cells l^{-1} by April 27. At its peak, this group represented 96.1% of the total phytoplankton cell abundance and 91.6% of the phytoplankton biomass (Fig 29B). *Cryptomonas* spp. concentrations decreased to 4.0 $x10^6$ cells l^{-1} by May 5 before a second smaller peak of 2.6 $x10^7$ cells l^{-1} occurred May 13. As the *Cryptomonas* spp. abundance declined, the densities of *Gymnodinium instriatum* rose dramatically beginning May 15 and reached a maximum density of $3.0x10^7$ cells l^{-1} on May 18 (Fig. 29A). These concentrations represented 89.8% of the phytoplankton abundance and 99.0% of the total phytoplankton biomass (Fig 29B). *G. instriatum* densities and chlorophyll *a* concentrations decreased May 19 following a rainfall event and then increased again to $1.9x10^7$ cells l^{-1} on May 21. The high total phytoplankton densities in the Lafayette River ($5.7 x10^6 – 7.8x10^7$ cells l^{-1}) were much higher than those recorded at Virginia Chesapeake Bay Monitoring Program (CBMP) stations during the

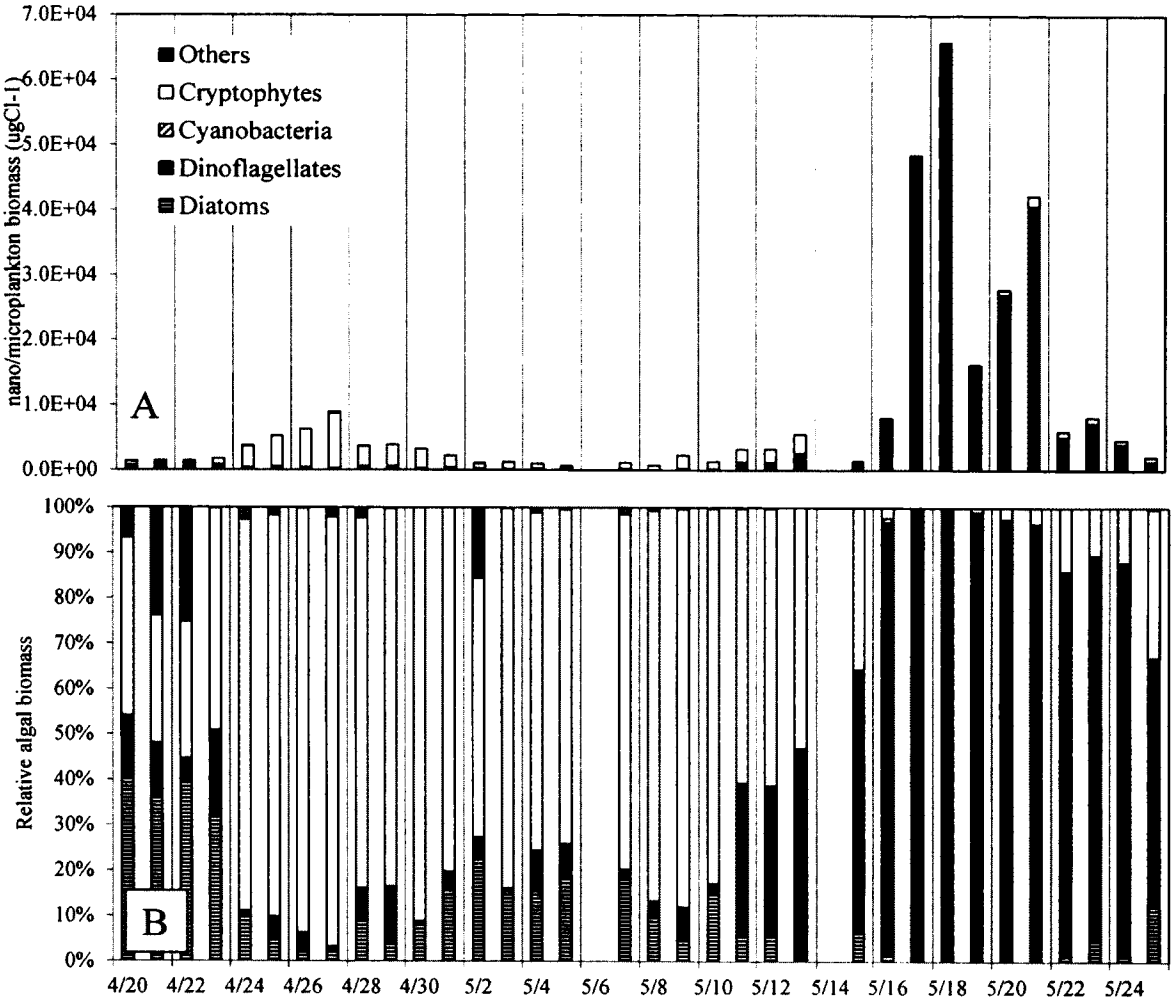

FIG. 29. Daily algal biomass (μg C l^{-1}) of the major taxonomic groups within the Lafayette River from April 20 to May 25 presented as: A stacked columns showing total daily biomass, and B: the percentage of total algal biomass accounted for by each taxonomic group.

same time period, where densities of 1.8 $x10^6$ – 1.3 $x10^7$ cells l^{-1} were reported (www.chesapeakebay.net).

Species richness was low during this Lafayette River study, ranging from 16-32 with a mean of 21 taxa identified per sample compared to an average of 32 taxa identified in samples collected from the nearby CBMP station located in the Elizabeth River (SBE5) during the same time period (www.chesapeakebay.net). The Shannon diversity index (*H'*), which includes a measure of species evenness, ranged between 0.03 and 2.57 (Fig. 27B), and was lowest during the *Cryptomonas* spp. and *G. instriatum* blooms when these species dominated the phytoplankton populations. However, even when *Cryptomonas* spp. and *G. instriatum* were at their maximum abundance and represented 96.1% and 99.0% of the biomass, respectively, there were still about 20 other phytoplankton species present and so high species richness was maintained. Levels of *H'* rapidly increased again after the abundance of the bloom species decreased (Fig. 27B). There was a significant negative relationship between phytoplankton biomass and species diversity (*H'*) over the 34 days (Fig. 30A) best described by the linear regression model (adj R^2=0.637, $p<0.0001$). This same negative relationship was also observed during the same time period at greater diversity and lower biomass levels amongst the other locations within the lower Chesapeake Bay. No significant relationship between species richness and biomass was identified ($p>0.05$) (Fig. 30B).

Nutrient concentrations

Dissolved inorganic nitrogen concentrations (nitrite, nitrate, and ammonium) fluctuated greatly from 0.54 to 14.7 μM, with concentrations lowest at the end of the study from May 17 onward when dinoflagellate abundances were highest (Fig. 31B).

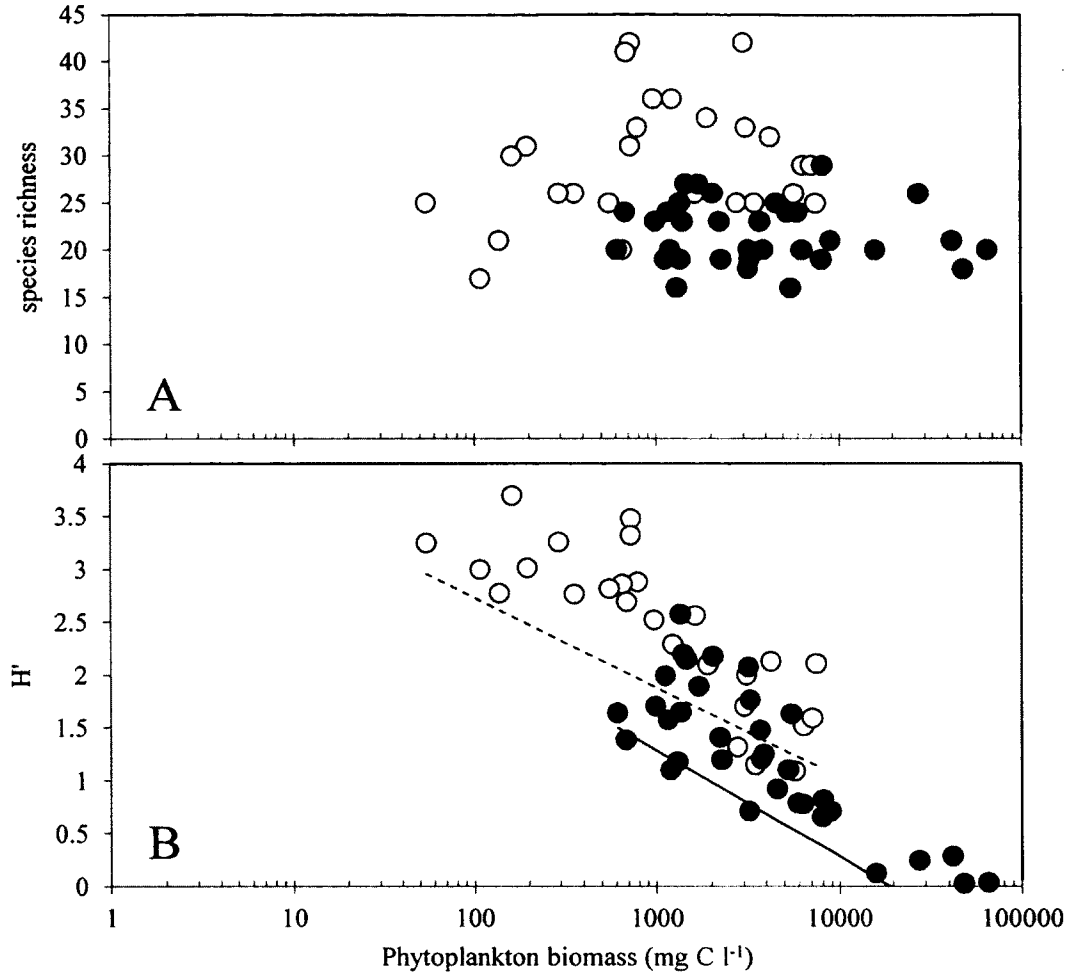

FIG. 30. Scatterplots of phytoplankton biomass and phytoplankton diversity expressed as A: species richness and B: Shannon diversity index *H'*. Black circles represent daily measurements of biomass and diversity recorded in the Lafayette River from April 20 to May 25, 2006. White circles represent algal biomass and diversity measurements recorded in 14 Chesapeake Bay Program Monitoring stations in Virginia during April and May 2006. Significant negative linear relationships exist in both datasets ($p<0.0001$), as shown by the solid trendline for the Lafayette data and the dashed trendline for the other Virginia dataset.

Dissolved organic nitrogen concentrations were relatively consistent during the study, ranging from 18.5 to 24.7 μM with the highest concentration observed on May 24 following the dinoflagellate bloom. NO_2^- concentrations accounted for less than 10% of DIN throughout the study with a maximum concentration of 0.81 μM (Fig. 31E). Concentrations of NO_2^- were highest following the *Cryptomonas* spp. bloom (April 30 to May 4), and below the detection limit (0.02 μM) during dinoflagellate bloom (May 17 to May 23). Nitrate concentrations ranged from the detection limit (0.048 μM) during the *Gymnodinium* bloom to 7.6 μM, and represented a large portion of the available DIN, with an average of 41% and a maximum of 88% of DIN during the study (Fig. 31E). NO_3^- were reduced on April 25 to the detection limit, corresponding with the highest daily precipitation during the study, and again drawn down to minimal concentrations in the days leading up to the dinoflagellate bloom.

Ammonium concentrations were highly variable over the study period ranging from 0.4 to 8.3 μM, but were never drawn down below detectable levels (<0.02 μM). NH_4^+ concentrations were highest at the beginning of the study and generally about 2-3 days following a precipitation event (ie. April 28, May 8-9). NH_4^+ measurements were low (<1 μM) in the days leading up to and during the dinoflagellate bloom (May 11 to May 23). NH_4^+ represented the dominant form of DIN throughout for the first and last third of the study, while during the period between the *Cryptomonas* spp. and *G. instriatum* blooms (May 4 to May 15) NO_3^- concentrations represented a greater percentage of DIN (52-82%) (Fig. 31E). Concentrations of urea were low throughout the study, with a mean of 0.18 μM and were at or below the detection limit (0.05 μM) for 13

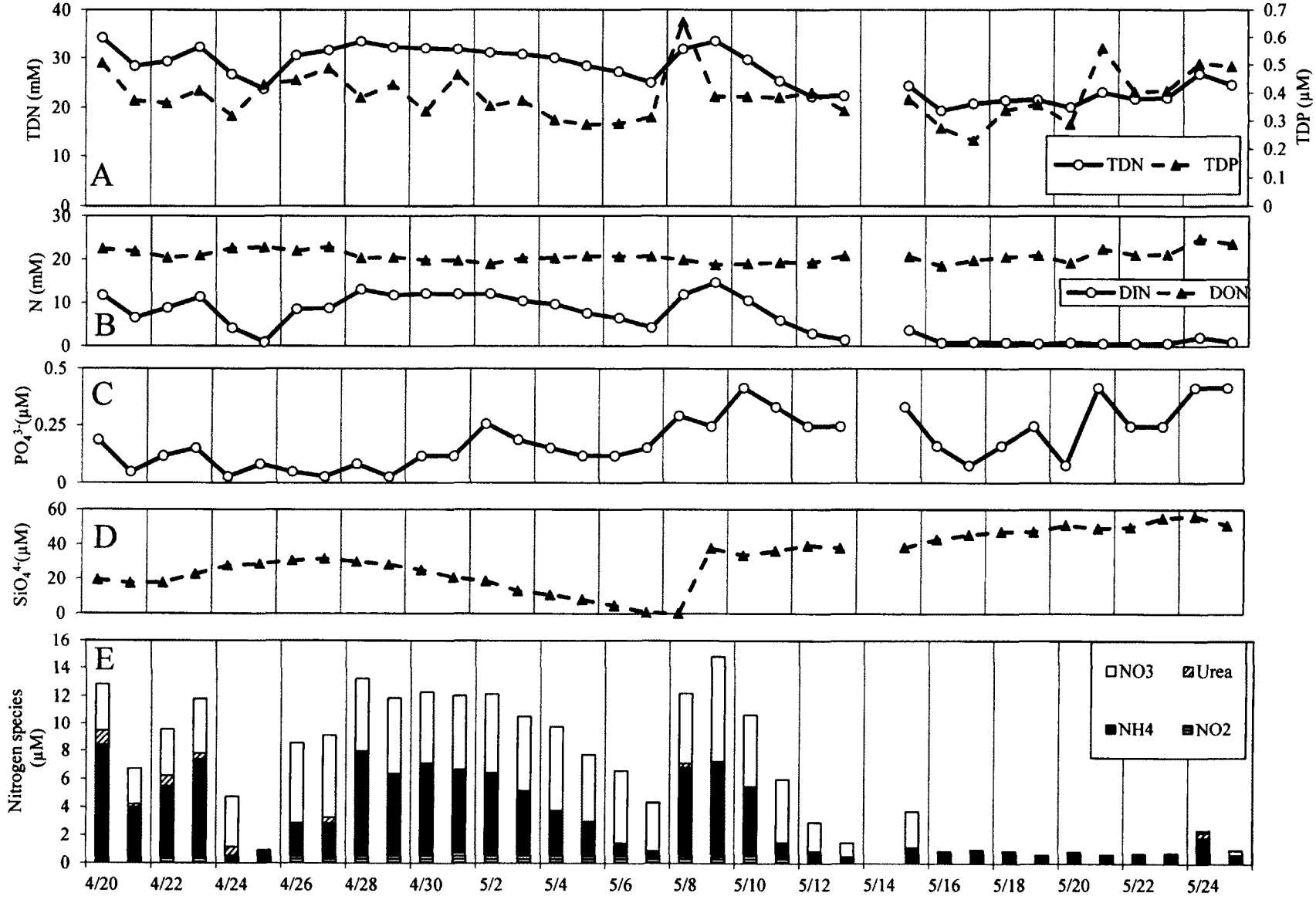
A
TDN (mM)
TDP (μM)
TDN
TDP
B
N (mM)
DIN
DON
C
PO_4^{3-}(μM)
D
SiO_4^{4-}(μM)
E
Nitrogen species (μM)
NO3
Urea
NH4
NO2
4/20
4/22
4/24
4/26
4/28
4/30
5/2
5/4
5/6
5/8
5/10
5/12
5/14
5/16
5/18
5/20
5/22
5/24

FIG. 31. Timeseries of nutrient concentrations measured in the Lafayette River from April 20 to May 25, 2006. A:Daily measurements of total dissolved nitrogen (TDN, μM N) and total dissolved phosphorus (TDP, μM P). B: Dissolved inorganic nitrogen (DIN, μM N) and dissolved organic nitrogen (DON, μM N). C: Orthophosphate (μM P). D Silicate (μM Si). E. Stacked concentrations of nitrogen species.

of the last 14 days of the sampling period (May 11 to May 25) and represented less than 1% on average of TDN (Fig. 31E).

Orthophosphate concentrations were relatively low and ranged from below the detection limit (0.027) to 0.415 μM (Fig. 31C). PO_4^+ concentrations were lowest between April 24 and 29 during the *Cryptomonas* spp. bloom, but was variable during the *Gyrdodinium* bloom with elevated concentrations on May 15 and May 21, and decreased concentrations on May 17 and May 20.

Silicate concentrations were generally high with an average of 30.6μM and a maximum concentration of 56.1 μM (Fig. 31D). However, during the period from April 27 to May 8, silicate concentrations declined from 31.7 to 0.2 μM. Following the precipitation on May 7 and May 8, silicate concentrations spiked to 37.6 μM and increased during the remainder of the study. The ratio of dissolved silicate to DIN was greater than 16 during the study with the exception of May 8, indicating that silicate concentrations were generally not considered limiting to diatom growth (Conley and Malone 1992, Morse 2011).

Time lag correlations

To understand the impact environmental and biological conditions had on the dominant phytoplankton in the study, time lagged correlations of cryptomonad and dinoflagellate abundances were analyzed. Significant positive correlations between all forms of DIN and cryptomonad abundance from 1-5 days prior were identified (Fig. 32). These results indicate that when DIN concentrations increased, cryptomonad abundances also increased between one and five days later. In contrast, significant positive correlations between cryptomonad abundance and urea and DON concentrations were

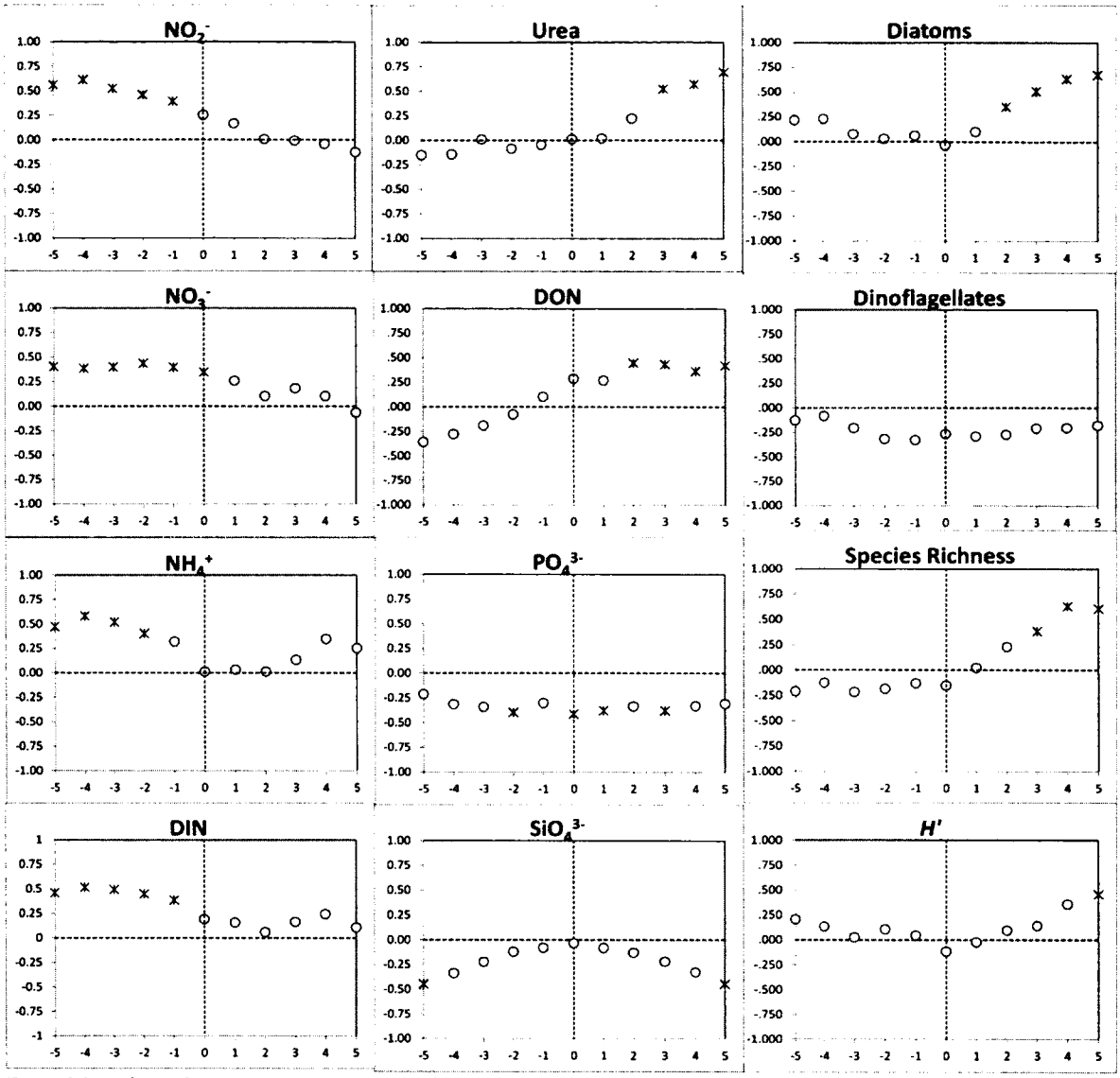

FIG. 32. Time lag Pearson correlation plots of cryptomonad abundance versus nutrient parameters, diatom abundance, cryptomonad abundance, phytoplankton species richness and diversity (Shannon index *H'*). Periods of minus five to plus five days are shown on the X-axis with 0 being present. The Pearson correlation coefficient is plotted on the Y-axis, with positive values indicating positive relationships, and negative values negative relationships. Correlations that are statistically significant at the $P<0.05$ level are indicated by asterisks.

identified between 2-5 days in forward time. Likewise, these results show that 3-5 days after abundances of cryptomonads increased, urea concentrations also increased. There was a negative correlation between PO_4^{3-} and cryptomonad abundance, with significant correlations observed between two days prior and three days forward. Silicate concentrations were generally not correlated with cryptomonad abundance, except at plus and minus five days, where negative relationships were identified. Cryptomonad abundance was positively lag correlated with diatom abundance 2-5 days forward, indicating that following periods of increased cryptomonad abundance, diatom abundances also increased. Although during the study dominance appeared to shift from cryptomonads to dinoflagellates, no significant relationship was identified between these groups. Positive relationships between cryptomonad abundance and diversity were identified, with significant correlations with species richness found 3-5 days later and *H'* after five days, indicating that diversity was greater during these periods following increased cryptomonad abundance (Fig. 32).

Dinoflagellate abundance in contrast was negatively correlated with DIN concentrations, both in reverse and forward time (Fig. 33). No significant correlations were found between urea concentrations and dinoflagellate abundance. Significant positive correlations were observed between dinoflagellate abundance and DON at minus four days, with a negative correlation at positive five days. Positive correlations between PO_4^{3-} concentration and dinoflagellate abundance were identified, again only significant on minus four and plus five days. Significant positive correlations were identified between silicate and dinoflagellate abundance, although Si is not generally considered to be limiting to phytoplankton taxa other than diatoms. Cryptomonad abundance was

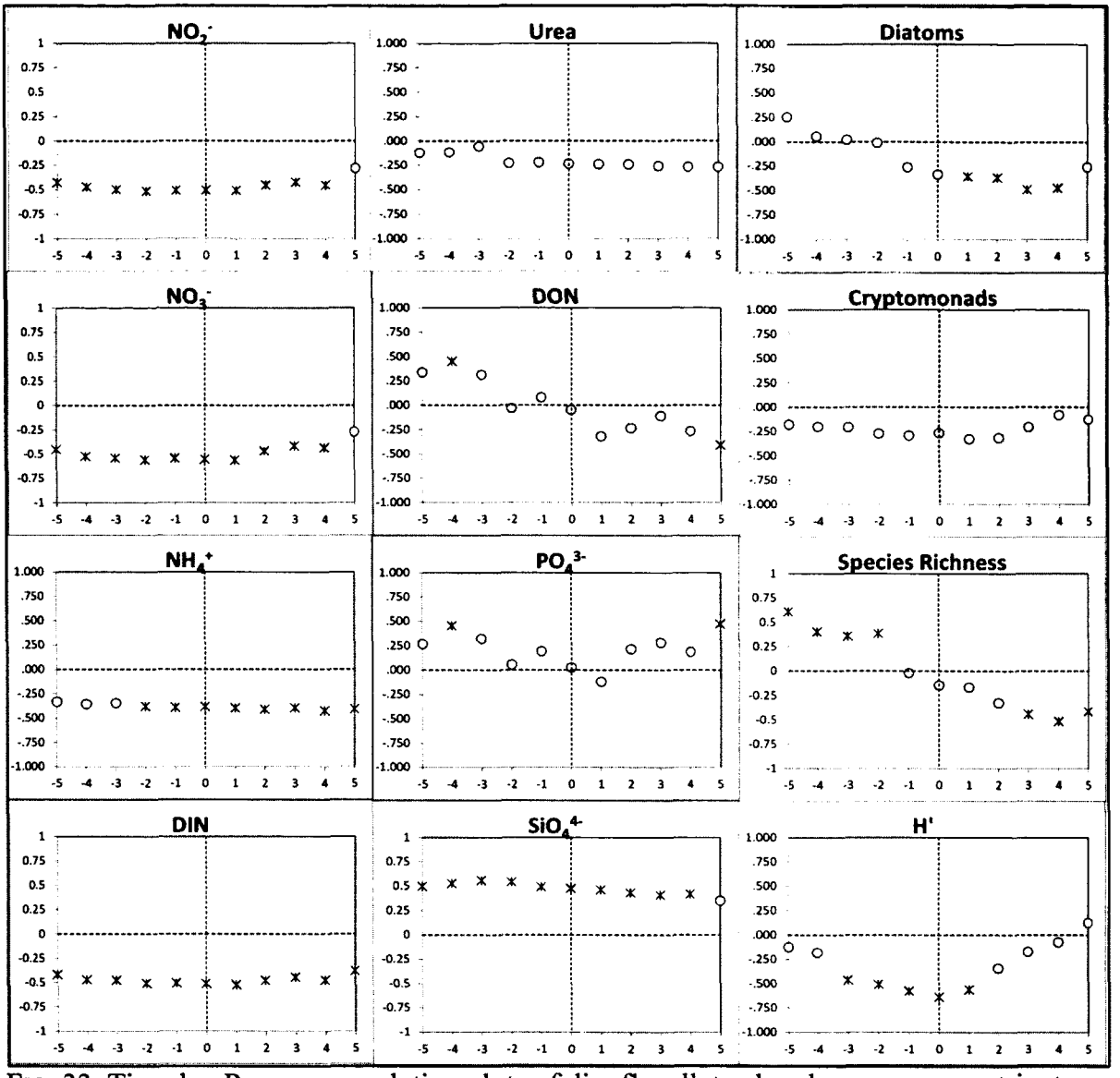

FIG. 33. Time lag Pearson correlation plots of dinoflagellate abundance versus nutrient parameters, diatom abundance, cryptomonad abundance, phytoplankton species richness and diversity (Shannon index *H'*). Periods of minus five to plus five days are shown on the X-axis with 0 being present. The Pearson correlation coefficient is plotted on the Y-axis, with positive values indicating positive relationships, and negative values negative relationships. Correlations that are statistically significant at the $P<0.05$ level are indicated by asterisks.

negatively correlated with dinoflagellate abundance, although not at a significant ($p<0.05$) level. However, diatom abundance was significantly negative correlated with dinoflagellate abundance at 1-4 days in forward time, meaning that as dinoflagellate abundances decreased, diatom abundances increased 1-4 days later. There were contrasting relationships identified between dinoflagellate abundance and diversity metrics. Significant positive correlations with species richness were identified 2-5 days prior with negative correlations 3-5 days. Negative correlations between *H'* and dinoflagellate abundance were observed from minus three days to plus one day. These results suggest that periods of higher dinoflagellate abundance generally followed periods of high richness and occurred before periods of lower richness, and that during periods of high abundance including three days prior and one day later there is lower evenness.

Discussion

Fundamental to understanding the distribution and abundance of phytoplankton groups is their relationship to environmental variables that vary over short and long timescales in estuarine environments such as the Chesapeake Bay (e.g. Marshall et al. 2009c, Williams et al. 2010). Estuaries are dynamic environments where chemical and physical parameters can vary over short time periods (e.g., tidal and sub-tidal timescales), as a result of episodic events such as storms (e.g., heavy rainfall and subsequent impacts on salinity, temperature, turbidity, and nutrient concentrations), as well as longer term climatic and anthropogenic forcing (Roberts et al. 2007, Najjar et al. 2010, Orth et al. 2010, Morse et al. 2011, Cho et al. 2012). This study was aimed at understanding how environmental and biological factors combine to favor the formation of monospecific algal blooms over a relatively short timescales during spring when rainfall and air and

water temperatures can be highly variable and result in short-term changes in salinity and nutrient concentrations in surface waters. During the course of this 34-day study, the two distinct blooms developed and dissipated, each over approximately 7-day period, and likely would not have been detected using lower frequency sampling.

Cryptomonads are a common component of estuarine phytoplankton communities throughout the year and a major source of algal biomass in Virginia estuaries (Marshall et al 2006). Their abundance has been associated with disturbances such as wind induced mixing of the water column and precipitation (Klaveness 1988, Mallin et al. 1991). Cryptomonads are also readily preyed on by grazers that include ciliates, cladocerans, copepods, and dinoflagellates (Klaveness 1988, Weise and Kirchhoff 1997, Adolf et al. 2008). *Gymnodinium instriatum* (Freudenthal et Lee) Coats is an unarmored dinoflagellate that can form dense blooms, often producing "red tides" in coastal waters throughout the world, and has been associated with shellfish mortality through oxygen depletion (Jimenéz 1993, Kim et al. 1993). *G. instriatum*, like many dinoflagellates is also capable of forming cysts when environmental conditions are undesirable (Shikata et al. 2008). While this species has a wide salinity tolerance and is considered a common member of the phytoplankton community in tropical and temperate estuaries (Nagasoe et al. 2006, Steidinger and Tangen 1996) its abundance in the Chesapeake Bay estuary is largely unknown due to its gross morphological similarity to a variety of other *Gymnodinium* and *Gyrodinium* dinoflagellates, however it has been documented within the Bay using molecular techniques (Coats and Park 2002, Malmquist 2012). *G. instriatum* is mixotrophic, and has been reported to feed on a variety of ciliates (Uchida et al. 1997). However, there are few studies which document *G. instriatum* development in

the field, and conditions associated with its growth outside of laboratory studies are rare (Nagasoe et al. 2006).

Seasonality plays a large role in the emergence of potential bloom species in the Chesapeake Bay watershed (Marshall 1980, Marshall and Lacouture 1986, Adolf et al. 2006) Seasonal changes in water temperature and water quality provide a course filter on which organisms are capable of blooming seasonally (Glibert et al. 2001, Adolf et al. 2006). When favorable environmental conditions emerge, the concentrations of particular algal species or assemblages can change rapidly, often leading to bloom conditions and reduced algal species diversity (Spatharis et al. 2007). These blooms can appear and deteriorate over short time periods or may extend for months (Mulholland et al. 2009, Morse et al. 2011).

One short-term forcing function that has been identified as impacting physical and temporal conditions in temperate estuaries is rainfall (Jordan et al. 1997, Langland et al. 2004, Najjar et al. 2010). In many estuarine environments, wetlands and aquatic shoreline vegetation work to buffer the effects of seasonal or sporadic runoff by taking up nutrients before they enter the estuary (Vought et al.1995, Laws et al.1999, Syversen and Haarstad 2005). However, urban environments such as the Lafayette River, where the shoreline is highly developed and marsh covers less than half of its shoreline, stormwater can enter the estuary directly through overland flow which is facilitated by impervious surfaces (Berman et al. 2002). Even relatively brief precipitation events can lead to large and rapid changes in water quality from storm sewer discharge and overland runoff (Nichols et al.1986, Roberts et al. 2007).

Increases in *Cryptomonas* spp. cell density in the Lafayette River were first detected 48 h after a rainfall of 0.74 cm on April 22, and cell densities reached a maximum about 48 h after a second rainfall of 2.8 cm on April 25. The rainfall resulted in a decrease in salinity and an increase in dissolved inorganic nitrogen concentrations, particularly NO_3^+ and NH_4^+. While the densities of *Cryptomonas* spp. increased rapidly, those of diatoms and other phytoplankton decreased. This was detected as reduced levels of Shannon diversity (*H'*). As there was no corresponding decline in species richness, this can be seen as reduced species evenness, as *Cryptomonas* spp. dominated the phytoplankton community, comprising 91% of the algal biomass (Fig. 27B). Based on the changes observed in daily abundances during the study, the apparent net growth rate of *Cryptomonas* sp. during this period was 0.86 divisions per day, similar to upper limits of *Cryptomonas* growth rates observed in cultures (Sciandra et al. 2000). As this estimate does not take into account potential losses due to grazing or cell advection, this rate should be considered an underestimate. Ammonium concentrations decreased steadily along with *Cryptomonas* growth, suggesting uptake by these cells. This is consistent with laboratory studies demonstrating a much higher uptake of ammonium than nitrate by *Cryptomonas* (Cloern 1977). Ammonium and nitrate levels increased following rain on May 7-8, followed by ammonium declining more rapidly than nitrate, and coinciding with renewed *Cryptomonas* growth. The positive relationship between elevated DIN concentrations prior to *Cryptomonas* growth is seen in the lag-correlation analyses at periods of 1-5 days.

Gyrodinium instriatum was at low densities (<100 cells ml^{-1}) for the first 25 days of the study. However, ca. 48hrs following the rainfall on May 14 and 15, *G. instriatum*

populations exceeded 30,000 cells ml^{-1}, having an apparent net growth rate of 3.26 divisions per day. This was over four times greater than the maximum growth rate reported for this species in laboratory cultures (Nagasoe et al.2006). A synchronous excystment of benthic dinocysts from river sediment may have contributed to these increased concentrations of *G. instriatum*. Shikata et al. (2008) have shown *G. instriatum* can excyst over a short period of time ($\leq$3days) at water temperatures of at least 20 °C, which were consistent with those present during this bloom.

Dinoflagellate cyst-beds are produced by several species, and can serve as a survival mechanism in habitats with fluctuating environmental conditions (Anderson and Wall 1978, Anderson and Rengefors 2006). Cyst formation in *G. instriatum* has been attributed to limiting N and P levels (Shikata et al.2008) and high cell densities (Uchida et al.1997). High densities of a variety of benthic dinoflagellate cysts have been identified in tributaries of the lower Chesapeake Bay, including the Elizabeth and Lafayette Rivers (Seaborn and Marshall 2008, Tang et al. 2008). The increase in blooms of the dinoflagellate *Cochlodinium polykrikoides* in the Lafayette River and elsewhere has also been attributed to local cyst-beds (Marshall et al 2008, Tomas and Smayda 2008) and as being triggered by runoff following rainfall events (Mulholland et al. 2009). Following rains of May 14 and 15, and during the subsequent *G. instriatum* bloom, increased concentrations of nitrogen were not detected in the water column, with organic and inorganic nitrogen concentrations near or below the detection limit, likely being taken up by the dinoflagellates.

While excystment and population growth of *G. instriatum* may be stimulated by increased entry of nutrients into the river, this is not strongly supported by the lag

correlation analysis. Instead, the opposite pattern was observed, with DIN concentrations negatively correlated with dinoflagellate abundance. Harmful algal blooms including dinoflagellates and other phytoplankton taxa often occur during periods of nutrient limitation, particularly low DIN (Glibert et al. 2001, Sunda et al. 2006, Mulholland et al. 2009, Morse et al. 2011). These conditions are thought to favor bloom forming dinoflagellates over other taxa such as diatoms that thrive in more nutrient replete environments (Sunda et al. 2006). Freshwater input and physical perturbations independent of nutrient additions can lead to rapid increases in dinoflagellate abundance, including through excystment (Nehring et a. 1993, Rengefors and Anderson 2002, Morse et al. 2011). This pathway is supported by the timing of the *G. instriatum* bloom after the storm. Alternative explanations include potential species interactions, such as the abundance of potential algal prey, stimulating *G. instriatum* growth. Blooms of another mixotrophic dinoflagellate, *Karlodinium veneficum* have been correlated with changes in cryptophytes abundance (Adolf et al. 2008). Increased concentrations of cryptophytes stimulated grazing and population development of *K. veneficum*, including the formation of toxic blooms (Adolf et al. 2008). While live samples were not collected, and grazing by *G. instriatum* was not observed in this study, *Cryptomonas* sp. abundances decreased as *G. instriatum* concentrations increased, and were the lowest during the dinoflagellate bloom (Fig. 29B). However, cryptomonad abundance was not significantly correlated with dinoflagellate abundance (Figs. 32, 33).

Algal diversity was greatly reduced during both blooms, particularly evenness, as illustrated by the drop in H'. This led to the significant negative regression observed between species diversity and algal biomass (Fig. 30A). Examinations of

diversity/productivity relationships in both terrestrial and aquatic systems have identified positive, negative and unimodal associations (Leibold 1999, Waide et al. 1999). Similar studies of phytoplankton communities are more limited, however it appears that at a large enough productivity gradient, the relationship appears to be unimodal, with maximum diversity at intermediate phytoplankton biomass concentrations (Irigoien et al. 2004). Within Chesapeake Bay, algal biomass is generally high, and there is a negative relationship between *H'* and biomass (Chapter 4). Due to the blooms experienced, the abundances observed in this study were as much as 10x greater than those in at other stations in the lower Chesapeake Bay at the same time period. The relationship between *H'* and biomass of the Lafayette River study follow the same pattern as those seen in the rest of the lower Chesapeake Bay estuarine system, potentially occupying the negative trailing portion of a theoretical unimodal relationship. Compared to limited resources that are generally thought to limit diversity at low productivities, species interactions, particularly competition, are a major force limiting diversity at high productivity (Guo and Berry 1998). In this case, both flagellates appear to reduce evenness through competition with other algal taxa, with the dinoflagellate also potentially limiting diversity through grazing pressure. Surprisingly, this study illustrates that even in bloom situations of high biomass and very low evenness, phytoplankton species richness is unaffected and remains relatively high.

Conclusions

Dinoflagellate blooms, including those of toxic species, appear to be increasing in magnitude and frequency in Chesapeake Bay, its tributaries, and waters where eutrophication is occurring (Glibert et al. 2007, Heisler et al. 2008, Mullholland et al.

2009, Egerton et al. 2012). The results of this study suggest that this trend will likely be associated with reduced levels of algal diversity. In addition, potentially harmful species are also being detected and in some cases becoming bloom formers at new locations in the Chesapeake Bay ecosystem (e.g. Marshall et al. 2003b, Marshall et al. 2008b, Harding et al. 2009). The distribution of cysts following blooms and their later development may contribute to this ongoing trend in a spreading geographic range. This study focused on the effects of water quality on phytoplankton species composition in an urban estuarine tributary susceptible to stormwater input and prevalent dinoflagellate blooms. The results identified subsequent changes in nutrient concentrations following rainfall, and examples of the varying responses of the phytoplankton community to these conditions. In particular, the immergence and dominance of *Cryptomonas* sp. and *G. instriatum* populations following storm events and subsequent decline in algal diversity. The rapid development and brief duration of both blooms (~5 days) emphasizes the importance of monitoring studies in detecting these events and their relationships to environmental conditions. This example demonstrates the increased complexity of explaining bloom development of mixotrophic dinoflagellates, which are influenced by water quality parameters directly as well as indirectly through potential species interactions. Further studies within this estuary focusing on the role of nutrient runoff, dinoflagellate excystment and grazing are essential to understanding not only these species, but also the influence of the habitats trophic status, the formation of algal blooms, and the effect of reduced species diversity in general.

CONCLUSIONS

Monitoring observations have revealed that phytoplankton communities are decidedly non-random with aggregate distributions that change over a broad spectrum of spatial and temporal scales. Planktonic algal species are intrinsically connected to changing environmental conditions in the aquatic environment, especially within systems as dynamic as estuaries. By examining spatial and temporal patterns of environmental parameters in relation to the species community, it is possible to build an understanding of the ecological processes that govern the abundance, composition and diversity of any group, including phytoplankton. The tidal estuarine conditions within Chesapeake Bay represent a large range of changing environmental parameters to investigate relationships with phytoplankton diversity and community characteristics.

Chesapeake Bay supports a diverse phytoplankton community comprised of multiple assemblages of algal taxa associated with spatially heterogeneous environmental conditions within the estuary. More specifically, the algal community can be characterized as one of high richness with 1480 taxa identified in these waters over two decades of monitoring (Chapter 2). An average of 35 phytoplankton taxa occurred within individual water samples, with regional species richness of between 257 and 383 taxa Baywide annually. However, the Bay should also be classified as having low species evenness, with a single species accounting for at least half of the biomass in almost one third of all samples examined. In this aspect, Chesapeake Bay contained only a relative small number of dominant taxa (less than 5%) along with a much larger number of both rare species and the more ubiquitous taxa that remain in lower concentrations. This

description is not unique to phytoplankton, as the fish community of Chesapeake Bay has also been classified as one of exceptionally low evenness (Jung and Houde 2003).

While there was considerable overlap in the distribution of certain taxa within the Bay, the dissimilarity of algal assemblages between regions suggests that the ecosystem is better described as a series of ecological boundaries, with high beta diversity occurring at these ecoclines that are related to differences in salinity. Salinity has long been recognized as a significant physical characteristic influencing the composition of phytoplankton through varied tolerances to osmotic stress between species and groups (Smayda 1958, Kirst 1990). These effects on individual taxa can also be observed in cumulative impacts on community properties including diversity (Vadrucci et al. 2008, Muylaert et al. 2009). Within Chesapeake Bay, the algal community varies considerably along the 300km estuarine gradient, with regional assemblages that differ in abundance and composition (Marshall et al. 2006b, Chapter 2). In terms of diversity, specifically species richness, the phytoplankton community of Chesapeake Bay displayed a remarkably similar pattern to the artenminimum model (Remane 1934, Remane and Schlieper 1971), having greater richness in fresh and polyhaline waters, and reduced levels in intermediate (lower mesohaline) salinities (Chapter 2). This one dimensional view of changing diversity within the estuary, while useful is misleadingly simplified however, as revealed by multivariate ordination, which illustrates the underlying complexity of multiple environmental factors that vary in the Bay along with the phytoplankton community.

In addition to phytoplankton responding to conditions changing within the spatial aspect of the estuary, there are considerable temporal changes in environmental

parameters which also elicit a response by the algal community. In Chesapeake Bay, seasonal fluctuations of precipitation and associated streamflow are coupled with changes in water quality characteristics including nutrient concentrations and turbidity which along with seasonal light and temperature flux strongly influence the phytoplankton community (Chapter 3). These same influences could vary year to year due inter-annual differences in weather patterns. The seasonal and inter-annual impact of streamflow on phytoplankton diversity varied within the estuary.

In the northernmost freshwater region, the algal community was rarely if ever nutrient limited, and therefore streamflow related changes in nutrients have little influence on abundance, composition, and diversity (Kemp et al. 2005, Chapter 3). Instead, the seasonal patterns suggest that temperature and light limitation play a larger role, with greater species richness observed during summer, and lower richness during years of high streamflow when turbidity is highest. In contrast, near the mouth of the Bay, in the polyhaline region, nutrient concentrations are lower and are often limiting to phytoplankton growth. In this region, seasonal patterns imply phytoplankton diversity is more related to seasonal and inter-annual fluctuations of streamflow linked to nutrient concentrations, particularly dissolved inorganic nitrogen and silica (Chapter 3). These findings, while novel, are to be expected, as the factors implicated in affecting phytoplankton growth and abundance within particular regions of the Bay may be predicted to also impact the diversity of the algal community. The variety of limiting factors both spatially and temporally contributes to the overall diversity of taxa within the Bay. Highest regional diversity was observed during periods of increased patchiness both in environmental conditions and phytoplankton composition, when the distinction

between salinity zones was greatest (Chapter 2, 3). Areas that contained lower levels of alpha and gamma diversity generally had higher levels of productivity and experienced higher rates of species turnover, observations which may have additional implications due to potential higher susceptibly of algal blooms.

Phytoplankton diversity, in addition to being related to a number of environmental parameters, is also related to ecosystem functions including productivity, stability and the diversity of other trophic levels. In terms of productivity, a linear relationship was observed, with increased algal biomass associated with higher richness and lower evenness, and no apparent relationship regarding algal diversity and productivity rates (Chapter 4). In contrast to current ecological theory, a unimodal relationship between phytoplankton productivity and diversity was not observed. This is explained in part by the prevalence of both very high algal biomass and productivity rates compared to studies of less productive systems. Increasing trends of algal biomass have been attributed to cultural eutrophication through increased nutrient loading in Chesapeake Bay (Harding and Perry 1997, Marshall et al. 2003a, Kemp et al. 2005, Williams et al. 2010). Although efforts have been made to reduce nutrient inputs into the Bay, little positive response has been observed in living resources including the phytoplankton community (Boesch et al. 2001, Dauer et al. 2012). The results presented here indicate that increased phytoplankton biomass was associated with changes in phytoplankton diversity, specifically a decrease in species evenness and an increase in species richness (Chapter 4).

Chapter 4 also includes evidence that reduced levels of phytoplankton evenness may be associated with lower predictability and greater variance in annual phytoplankton

biomass. A decline in diversity and stability of the primary producers in the habitat would be expected to have significant effects on the ecosystem as a whole (McCann 2000, Ives and Carpenter 2007). While species evenness of Chesapeake Bay phytoplankton does not appear to be significantly related to zooplankton evenness, there was a positive relationship regarding species richness. As decreased resource heterogeneity at the phytoplankton level, in terms of species richness appeared to have a negative effect on zooplankton richness, a decline in zooplankton richness may also be expected to impact the diversity of upper trophic levels, including the ecologically and economically important pelagic fish communities (Eadie and Keast 1984, Jung and Houde 2003).

The same negative relationship between species evenness (as illustrated by H') and algal biomass observed in the entire Chesapeake Bay dataset was observed within the Lafayette River over a 34 day study (Chapter 5). During two blooms, as much as 99% of the total algal biomass was due to the individual blooms species. Surprisingly, species richness was not significantly reduced during the blooms. The rapid development and brief duration of both blooms (~5 days) emphasizes the importance of monitoring studies in detecting these events and their relationships to environmental conditions. This study also demonstrates the increased complexity of explaining bloom development. A relatively straightforward pathway of precipitation induced nutrient loading exploited by increased abundance of a single species described the *Cryptomonas* sp. bloom. Ammonium and nitrate concentrations increased following rainfall events, with cell abundances positively lag correlated with all forms of DIN from 1-5 days prior (Chapter 5). These results are consistent with findings of an autumn study within the Lafayette

related to dinoflagellate blooms dominated by *Akashiwo sanguinea* and *Gymnodinium* sp. (Morse 2011). However, during this study conducted in spring, the dinoflagellate bloom, which followed the *Cryptomonas* sp. bloom, was associated with low nitrogen conditions. Instead, the lag correlation analysis suggested that the *G. instriatum* bloom was related to limiting DIN concentrations along with a phytoplankton community characterized by high species richness and low evenness.

Dinoflagellate blooms, including those of toxic species, appear to be increasing in magnitude and frequency in Chesapeake Bay, its tributaries, and waters where eutrophication is occurring (Glibert et al. 2007, Heisler et al. 2008, Mullholland et al. 2009). Algal blooms are thought to further increase in incidence and intensity in the Bay in response to potential changes in future climate conditions (Najjar et al. 2010). These predictions indicate that in addition to greater precipitation and elevated total streamflow, higher levels of seasonality will be experienced, including more flow during winter and less in summer (Hayhoe et al. 2007, Pyke et al. 2008). The results described in Chapter 3 suggest that phytoplankton diversity would also be negatively affected, with greater streamflow leading to lower species richness in Chesapeake Bay, particularly in the polyhaline region. In addition to the negative properties associated with harmful algal blooms (i.e. hypoxia, toxicity), they also represent very low species evenness (Chapter 5). This reduction of diversity would contribute to future impacts on ecosystem function including lower ecosystem stability and possible negative effects on higher trophic levels (Chapter 4). The analyses presented here are based on decades of monitoring results and build on previous studies which reinforce phytoplankton diversity as a useful metric to be used as a component in addition to algal abundance and composition in evaluating the

health of aquatic ecosystems such as Chesapeake Bay. Furthermore, increased high richness and greater evenness of phytoplankton communities, in part through reductions of algal blooms may be considered endpoints, or goals of restoration efforts to improve ecosystem functions of the Bay.

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APPENDIX

PHYTOPLANKTON SPECIES LIST

Phytoplankton taxa identified in Chesapeake Bay, its tidal tributaries and sub-estuaries. Frequency of taxa as such: **C:** Common: those taxa present in 10 % or more of phytoplankton samples. **I:** Intermediate: taxa present in 1-10% of samples. Entries without frequency code represent rare taxa that are present in less than 1 % of sample collections.

Taxa	Author	Frequency
Bacillariophyceae		
Centrales		
Actinocyclus normanii f. *normanii*	(Gregory) Hustedt	
Actinoptychus senarius	(Ehrenberg) Ehrenberg	
Actinoptychus splendens	(Shadbolt) Ralfs	
Actinoptychus undulatus	(J.W. Bailey) Ralfs	
Actinoptychus vulgaris	Schumann	
Asterolampra marylandica	Ehrenberg	
Asteromphalus sp.		
Asteromphalus flabellatus	(Brébisson) Greville	
Asteromphalus heptactis	(Brébisson) Ralfs	
Asteromphalus roperianus	(Greville) Ralfs	
Attheya decora	West	
Aulacodiscus sp.		
Aulacoseira sp.		
Aulacoseira distans	(Ehrenberg) Kützing	I
Aulacoseira granulata	(Ehrenberg) Ralfs	I
Aulacoseira granulata var. *angustissima*	Müller	
Aulacoseira herzogii	(Lemmermann) Simonsen	
Aulacoseira islandica	Müller	
Aulacoseira italica	(Ehrenberg) Kützing	
Aulacoseira italica var. *tenuissima*	(Grunow) Simonsen	
Auliscus sculptus	(W. Smith) Ralfs	
Azpeitia nodulifiera	(Schmidt) Fryxell & Sims	
Bacteriastrum sp.		
Bacteriastrum comosum	Pavillard	
Bacteriastrum delicatulum	Cleve	
Bacteriastrum elongatum	Cleve	
Bacteriastrum furcatum	Shadbolt	
Bacteriastrum hyalinum	Lauder	
Bacteriastrum hyalinum var. *princeps*	(Castracane) Ikari	
Bellerochea horologicalis	Von Stosch	
Bellerochea malleus	(Brightwell) Van Heurck	

Campylosira sp.		
Campylosira cymbelliformis	(Schmidt) Grunow	
Cerataulina pelagica	(Cleve) Hendey	C
Cerataulus radiatus	(Roper) Ross	
Chaetoceros sp.		C
Chaetoceros affinis	Lauder	I
Chaetoceros affinis var. *willei*	(Gran) Hustedt	
Chaetoceros atlanticus	Cleve	
Chaetoceros borealis	Bailey	
Chaetoceros brevis	Schutt	
Chaetoceros coarctatus	Lauder	
Chaetoceros compressus	Lauder	I
Chaetoceros concavicornis	Mangin	
Chaetoceros constrictus	Gran	I
Chaetoceros convolutus	Castracane	
Chaetoceros costatus	Pavillard	
Chaetoceros crinitus	Schutt	
Chaetoceros curvisetus	Cleve	I
Chaetoceros danicus	Cleve	
Chaetoceros debilis	Cleve	I
Chaetoceros decipiens	Cleve	C
Chaetoceros densus	Cleve	
Chaetoceros diadema	(Ehrenberg) Gran	
Chaetoceros didymus	Ehrenberg	
Chaetoceros didymus var. *protuberans*	(Lauder) Gran & Yendo	
Chaetoceros difficilis	Cleve	
Chaetoceros diversus	Cleve	
Chaetoceros fragilis	Meunier	I
Chaetoceros gracilis	Schutt	
Chaetoceros laciniosus	Schutt	
Chaetoceros lorenzianus	Grunow	
Chaetoceros messanensis	Castracane	
Chaetoceros muelleri	Lemmermann	
Chaetoceros neapolitanus	Schröder	
Chaetoceros neogracilis	Van Laningham	C
Chaetoceros pelagicus	Cleve	
Chaetoceros pendulus	Karsten	C
Chaetoceros peruvianus	Brightwell	
Chaetoceros pseudocurvisetus	Mangin	
Chaetoceros radians	Schutt	
Chaetoceros rostratus	Lauder	
Chaetoceros similis	Cleve	
Chaetoceros simplex	Ostenfeld	
Chaetoceros socialis	Lauder	I

Chaetoceros subtilis	Cleve	C
Chaetoceros tenuissimus	Meunier	
Chaetoceros teres	Cleve	
Chaetoceros tetrastichon	Cleve	
Chaetoceros tortissimus	Gran	
Chaetoceros wighamii	Brightwell.	
Climacodium sp.		
Climacodium biconcavum	Cleve	
Climacodium frauenfeldianum	Grunow.	
Corethron sp.		
Corethron criophilum	Castracane	I
Corethron hystrix	Hensen	
Corethron valdiviae	Karsten	
Coscinodiscus sp.		C
Coscinodiscus apiculiferus	Rattray	
Coscinodiscus argus	Ehrenberg	
Coscinodiscus asteromphalus	Ehrenberg	
Coscinodiscus centralis	Ehrenberg	
Coscinodiscus cinctus	Kützing	
Coscinodiscus concinnus	W. Smith	
Coscinodiscus gigas	Ehrenberg	
Coscinodiscus gigas var. *praetexta*	(Janisch) Hustedt	
Coscinodiscus granii	Gough	
Coscinodiscus granulosus	Grunow	
Coscinodiscus kuetzingii	A. Schmidt	
Coscinodiscus lacustris	Grunow	
Coscinodiscus marginatus	Ehrenberg	
Coscinodiscus nitidus	Gregory	
Coscinodiscus nobilis	Grunow	
Coscinodiscus obscurus	Schmidt	
Coscinodiscus oculus var. *iridis*	Ehrenberg	
Coscinodiscus perforatus	Ehrenberg	
Coscinodiscus radiatus	Ehrenberg	
Coscinodiscus rothii	(Ehrenberg) Grunow	
Coscinodiscus rothii var. *subsalsa*	(Juhlin-Dannfelt) Hustedt	
Coscinodiscus rotula	Grunow	
Coscinodiscus subbulliens	Jorgenson	
Coscinodiscus sublineatus	(Grunow) Rattray	
Coscinodiscus wailesii	Gran & Angst.	
Cyclostephanos sp.		
Cyclostephanos dubius	(Fricke) Round.	
Cyclotella sp.		C
Cyclotella atomus	Hustedt	
Cyclotella bodanica	Grunow	

Cyclotella caspia	Grunow	C
Cyclotella chaetoceros	Lemmermann	
Cyclotella choctawhatcheeana	Prasad	
Cyclotella commensis	Grunow	
Cyclotella comta	(Ehrenberg) Kützing	
Cyclotella cryptica	Reimann	
Cyclotella glomerata	Bachmann	
Cyclotella meneghiniana	Kützing	
Cyclotella stelligera	Cleve & Grunow	
Cyclotella striata	(Kützing) Grunow	C
Cyclotella stylorum	Brightwell.	
Dactyliosolen antarcticus	Castracane	
Dactyliosolen fragilissimus	Bergon (Hasle).	C
Detonula confervacea	(Cleve) Gran	
Detonula pumila	(Castracane) Gran.	I
Ditylum brightwellii	(West) Grunow.	C
Eucampia cornuta	(Cleve) Grunow	
Eucampia zodiacus	Ehrenberg.	C
Guinardia cylindrus	Cleve	
Guinardia delicatula	(Cleve) Hasle	C
Guinardia flaccida	(Castracane) Peragallo	C
Guinardia striata	(Stolterfoth) Hasle.	
Helicotheca tamesis	Shrubsole	
Hemiaulus sp.		
Hemiaulus hauckii	Grunow	I
Hemiaulus indicus	Karsten	
Hemiaulus membranaceus	Cleve	
Hemiaulus sinensis	Greville.	
Hemidiscus cuneiformis	Wallich	
Lauderia annulata	Gran	I
Leptocylindrus danicus	Cleve	C
Leptocylindrus mediterraneus	(Peragallo) Hasle	
Leptocylindrus minimus	Gran.	C
Lithodesmium sp.		
Lithodesmium undulatum	Ehrenberg.	I
Melosira ambigua	(Grunow) O. Müller	
Melosira arenaria	Moore	
Melosira dickiei	(Thwaites) Kützing	
Melosira dubia	Kützing	
Melosira hummii	Hustedt	
Aulacoseira islandica f. *curvata*	(Ehrenberg) Müller	
Aulacoseira islandica var. *helvetica*	Müller	
Melosira jurgensii	Agardh	
Melosira lineata	(Dillwyn) Agardh	

Melosira moniliformis	(Müller) Agardh	I
Melosira nummuloides	(Dillwyn) Agardh	C
Melosira sp.		I
Melosira varians	Agardh.	I
Odontella sp.		I
Odontella alternans	(Bailey) Van Heurck	I
Odontella aurita	(Lyngbye) Brébisson	
Odontella aurita var. *obtusa*	(Kützing) Hustedt	
Odontella granulata	Roper	
Odontella longicruris	Greville	
Odontella mobiliensis	(Bailey) Grunow	I
Odontella obtusa	Kützing	
Odontella pulchella	Gray	
Odontella regia	(Schultz) Ostenfeld	
Odontella reticulata	(Ehrenberg) Roper	
Odontella rhombus	Hydrax	I
Odontella rhombus f. *trigona*	(Cleve) Hustedt	
Odontella sinensis	Greville	I
Odontella tridens	(Ehrenberg) Ehrenberg	
Paralia sulcata	(Ehrenberg) Cleve	C
Plagiogramma sp.		
Plagiogramma interruptum	(Gregory) Ralfs	
Plagiogramma staurophorum	(Gregory) Heilberg.	
Plagiogrammopsis vanheurckii	Grunow.	
Planktoniella sol	(Wallich) Schutt.	
Podosira sp.		
Podosira stelligera	(Bailey) Mann.	
Porosira gracialis	(Gran) Jorgensen	
Proboscia alata	(Brightwell) Sundstrom	C
Proboscia alata f. *curvirostris*	Gran	
Proboscia alata f. *gracillima*	(Cleve) Grunow	I
Proboscia alata f. *indica*	(Peragallo) Gran	
Proboscia inermis	Castracane.	
Pseudosolenia calcar-avis	(Schultze) Sunderstrom	C
Rhizosolenia sp.		I
Rhizosolenia acuminata	(Peragallo) Peragallo	
Rhizosolenia bergonii	Peragallo	
Rhizosolenia castracanei	Peragallo	
Rhizosolenia eriensis	H. L. Smith	
Rhizosolenia formosa	Peragallo	
Rhizosolenia hebetata	Bailey	
Rhizosolenia hebetata f. *semispina*	(Hensen) Gran	
Rhizosolenia imbricata	Brightwell	C
Rhizosolenia rhombus	Karsten	

Rhizosolenia robusta	Norman	
Rhizosolenia setigera	Brightwell	C
Rhizosolenia styliformis	Brightwell	C
Rhizosolenia temperei	Peragallo.	
Skeletonema costatum	(Greville) Cleve	C
Skeletonema potamos	(Weber) Hasle.	C
Stellarima microtrias	(Ehrenberg) Hasle & Sims	
Stephanodiscus astraea	(Ehrenberg) Grunow	
Stephanodiscus Hantzschii	Grunow	
Stephanodiscus subsalsus	(Cleve) Hustedt.	
Stephanopyxis sp.		
Stephanopyxis nipponica	Gran & Yendo	
Stephanopyxis palmeriana	(Greville) Grunow	
Stephanopyxis turris	(Greville & Arnott) Ralfs.	
Thalassiosira sp.		C
Thalassiosira aestivalis	Gran & Angst	
Thalassiosira anguste-lineata	(Schmidt) Fryxell & Hasle	I
Thalassiosira antarctica	Comber	
Thalassiosira baltica	(Grunow) Ostenfeld	
Thalassiosira bioculata	(Grunow) Ostenfeld	
Thalassiosira decipiens	(Grunow) Jorgensen	
Thalassiosira delicatula	Ostenfeld	
Thalassiosira eccentrica	(Ehrenberg) Cleve	
Thalassiosira gravida	Cleve	
Thalassiosira guillardii	Hasle	
Thalassiosira hyalina	(Grunow) Gran	
Thalassiosira lacustris	(Grunow) Hasle & Fryxell	
Thalassiosira leptopus	(Grunow) Fryxell & Hasle	
Thalassiosira leptopus	Ehrenberg	
Thalassiosira lineata	Jousé	
Thalassiosira nordenskioeldii	Cleve	I
Thalassiosira oestrupii var. *venrickae*	Fryxel & Hasle	I
Thalassiosira proschkinae	Makarova	
Thalassiosira pseudonana	Hasle & Heimdal	
Thalassiosira rotula	Meunier	I
Thalassiosira subtilis	(Ostenfeld) Gran	
Thalassiosira tenera	Proschkina-Laurenko.	
Triceratium sp.		
Triceratium acutum	Ehrenberg	
Triceratium favus	Ehrenberg	
Triceratium formosum f. *pentagonale*	(Schmidt) Hustedt	
Triceratium reticulum	Ehrenberg.	
Trinacria regina	Heiberg	
Pennales		

Achnanthes sp.		I
Achnanthes clevei	Grunow	
Achnanthes danica	(Flögel) Grunow	
Achnanthes delicatula	(Kützing) Grunow	
Achnanthes fimbriata	(Grunow) Ross	
Achnanthes lemmermannii	Hustedt	
Achnanthes longipes	Agardh	
Achnanthes onegensis	(Wislouch & Kolbe) Van Landingham	
Achnanthes subsalsoides	Hustedt	
Achnanthes taeniata	Grunow.	
Amphiprora sp.		I
Amphiprora alata	(Ehrenberg) Kützing	
Amphiprora cholnokyi	Van Lan.	
Amphiprora conspicua	Greville	
Amphiprora costata	(W. Smith) Hustedt	
Amphiprora gigantea var. *sulcata*	(O'Meara) Cleve.	
Amphiprora ornata	J.W. Bailey	
Amphiprora paludosa	W. Smith	
Amphora sp.		I
Amphora angusta	Gregory	
Amphora arenaria	Donkin	
Amphora binodis	Gregory	
Amphora coffeaeformis	(Agardh) Kützing	
Amphora commutata	Grunow	
Amphora costata	W. Smith	
Amphora crassa	Gregory	
Amphora cuneata	Cleve	
Amphora cuta	Gregory	
Amphora egregia var. *interrupta*	Peragallo & Peragallo	
Amphora exigua	Gregory	
Amphora gigantea	Grunow	
Amphora grevilleana var. *contracta*	Cleve	
Amphora laevis	Gregory	
Amphora lineolata	Ehrenberg	
Amphora luciae	Cholnoky	
Amphora marina	(W. Smith) Van Heurck	
Amphora obtusa	Gregory	
Amphora ostrearia	Brébisson	
Amphora ovalis	Kützing	
Amphora peragalli	Cleve	
Amphora proteoides	Hustedt	
Amphora proteus	Gregory	
Amphora rhombica	Kitton	

Amphora robusta	Gregory	
Amphora sabyii	Salah	
Amphora spectabilis	Gregory	
Amphora szaboi	Pantocsek	
Amphora terroris	Ehrenberg	
Amphora turgida	Gregory	
Amphora veneta	Kützing.	
Asterionella formosa	Hassall	I
Asterionella gracillima	Hantzsch	
Asterionella notata	(Grunow) Grunow.	
Asterionellopsis glacialis	(Castracane) Round	C
Asterionellopsis kariana	(Grunow) Round.	
Auricula insecta	(Grunow) Schmidt	
Bacillaria paxillifer	(Müller) Hendey	I
Berkeleya rutilans	Grunow	
Bleakeleya notata	(Grunow) Round	
Caloneis sp.		
Caloneis fusioides	(Grunow) Heiden & Kolbe	
Caloneis lamella	Zakrzewski	
Caloneis lepidula	(Grunow) Cleve	
Caloneis silicula	(Ehrenberg) Cleve	
Caloneis staurophora	(Grunow) Cleve	
Caloneis subsalina	(Donkin) Hendey	
Caloneis trinodis	Schultze	
Caloneis wardii	Cleve	
Caloneis westii	(W. Smith) Hendey.	
Campylodiscus echeneis	Ehrenberg	
Campylodiscus limbatus	Brébisson.	
Catenula adhaerens	(Mereschkowsky) Mereschkowsky	
Cocconeis sp.		I
Cocconeis clandestina	Schmidt	
Cocconeis costata	Gregory	
Cocconeis disculus	(Schumann) Cleve	
Cocconeis distans	Gregory	
Cocconeis flumiatilis	Wallace	
Cocconeis molesta var. *crucifera*	Grunow	
Cocconeis pediculus	Ehrenberg	
Cocconeis pinnata	Gregory	
Cocconeis placentula	Ehrenberg	
Cocconeis scutellum	Ehrenberg	
Cocconeis scutellum var. *ornata*	Grunow.	
Cylindrotheca closterium	(Ehrenberg) Reimann &	C

	Lewin.	
Cymatopleura elliptica	(Brébisson) W. Smith	
Cymatopleura solea	(Brébisson) W. Smith.	
Cymatosira belgica	Grunow	
Cymatosira lorenziana	Grunow.	
Cymbella sp.		I
Cymbella affinis	Kützing	
Cymbella excisa	Kützing	
Cymbella helvetica	Kützing	
Cymbella tumida	Brébisson	
Cymbella turgidula	Grunow	
Cymbella ventricosa	Kützing.	
Delphineis surirella	(Ehrenberg) Grunow.	I
Diatoma sp.		I
Diatoma anceps	(Ehren.) Kirchner	
Diatoma elongatum	(Lyngbye) Agardh	
Diatoma hyemale	(Roth) Heiberg	
Diatoma tenue	Agardh	
Diatoma vulgare	Bory.	I
Dimerogramma sp.		
Dimerogramma minor	(Gregory) Ralfs.	
Diploneis sp.		I
Diploneis beyrichiana	(Schmidt) Amosse	
Diploneis bombus	Ehrenberg	
Diploneis constricta	(Grunow) Cleve	
Diploneis crabro	Ehrenberg	
Diploneis crabro var. *pandura*	(Brébisson) Cleve	
Diploneis elliptica	(Kützing) Cleve	
Diploneis gruendleri	(Schmidt) Cleve	
Diploneis interrupta	(Kützing) Cleve	
Diploneis litoralis	(Donkin) Cleve	
Diploneis obliqua	(Brun) Hustedt	
Diploneis ovalis	(Hilse) Cleve	
Diploneis smithii	(Brébisson) Cleve	
Diploneis subcincta	(Schmidt) Cleve	
Diploneis suborbicularis	(Gregory) Cleve	
Epithemia sp.		
Epithemia argus	(Ehrenberg) Kützing	
Epithemia sorex	Kützing	
Epithemia turgida	(Ehren.) Kützing.	
Eunotia sp.		I
Eunotia bidentula	W. Smith	
Eunotia lunaris	(Ehrenberg) Grunow	
Eunotia microcephala	Krasske	

Eunotia pectinalis	Rabenhorst	
Eunotia praerupta	Ehrenberg	
Eunotia serra var. *diadema*	(Ehrenberg) Patrick.	
Fragilaria sp.		C
Fragilaria capucina	Desmazieres	
Fragilaria construens	(Ehrenberg) Grunow	
Fragilaria crotonensis	Kitton	
Fragilaria hyalina	(Kützing) Grunow	
Fragilaria intermedia	(Grunow) Grunow	
Fragilaria leptostauron var. *martyi*	(Heribaud) Lange-Bertalot	
Fragilaria oceanica	Cleve	
Fragilaria pinnata	Ehrenberg	
Fragilaria schulzii	Brockmann	
Fragilaria striatula	Lyngbye	
Fragilaria virescens	Ralfs.	
Fragilariopsis cylindrus	(Grunow & Cleve) Hasle	
Fragilariopsis oceanica	Cleve.	
Frustulia sp.		
Frustulia rhomboides	(Ehrenberg) DeToni.	
Glyphodesmis distans	(Gregory) Grunow	
Gomphonema sp.		I
Gomphonema acuminatum	Ehrenberg	
Gomphonema augur	Ehrenberg	
Gomphonema constrictum	Ehrenberg	
Gomphonema exiguum	Kützing	
Gomphonema geminatum	(Lyngbye) Agardh	
Gomphonema olivaceum	(Lyngbye) Kützing	
Gomphonema sphaerophorum	Ehrenberg.	
Grammatophora sp.		
Grammatophora angulosa	Ehrenberg	
Grammatophora marina	(Lyngbye) Kützing	
Grammatophora serpentina	Ehrenberg.	
Gyrosigma sp.		I
Gyrosigma acuminatum	(Kützing) Rabenhorst	
Gyrosigma balticum	(Ehrenberg) Rabenhorst	
Gyrosigma balticum var. *silimis*	(Grunow) Cleve	
Gyrosigma distortum	(W. Smith) Cleve	
Gyrosigma distortum var. *parkeri*	Harrisson	
Gyrosigma fasciola	(Ehrenberg) Griffith & Henfrey	I
Gyrosigma hippocampus	(Ehrenberg) Hassall	
Gyrosigma macrum	W. Smith	
Gyrosigma scalproides	(Rabenhorst) Cleve	
Gyrosigma spenceri	(S. Smith) Griffith &	

	Henfrey	
Gyrosigma spenceri var. *nodiferum*	(Grunow) Cleve	
Gyrosigma wansbeckii	(Donkin) Cleve.	
Hantzchia sp.		
Hantzchia amphioxys	(Ehrenberg) Grunow	
Hantzchia marina	(Donkin) Grunow	
Hantzchia spectabilis	(Ehrenberg) Hustedt	
Licmophora sp.		I
Licmophora abbreviata	Agardh	
Licmophora flabellata	(Carmichael) Agardh	
Licmophora gracilis	(Ehrenberg) Grunow	
Licmophora inflata	Mereschkowsky	
Licmophora paradoxa	(Lygbye) Agardh	
Licmophora paradoxa var. *tincta*	(Agardh) Hustedt	
Licmophora tincta	Grunow.	
Lioloma delicatulum	Cupp	
Mastogloia sp.		
Mastogloia apiculata	W. Smith	
Mastogloia braunii	Grunow	
Mastogloia cocconeiformis	Grunow	
Mastogloia exigua	Lewis	
Mastogloia gibbosa	Brun	
Mastogloia pumila	(Grunow) Cleve	
Mastogloia rostrata	(Wallich) Hustedt	
Mastogloia smithii	Thwaites.	
Membraneis challengeri	Grunow	
Meridion circulare	(Greville) Agardh	I
Navicula sp.		C
Navicula abrupta	(Gregory) Donkin	
Navicula amphipleuroides	Hustedt	
Navicula annulata	Grunow	
Navicula apiculata	Brébisson	
Navicula arenaria	Donkin	
Navicula arvensis	Hustedt	
Navicula atomus	(Kützing) Grunow	
Navicula cancellata	Donkin	
Navicula caterva	Hohn & Hellerman	
Navicula cincta	(Ehrenberg) Van Heurck	
Navicula clavata	Gregory	
Navicula cruciculoides	Brockmann	
Navicula cryptocephala	Kützing	
Navicula cuspidata	Kützing	
Navicula cuspidata var. *ambigua*	(Ehrenberg) Cleve	
Navicula delawarensis	Grunow	

Navicula digitoradiata	(Gregory) Ralfs	
Navicula directa	(W. Smith) Ralfs	
Navicula distans	(W. Smith) Ralfs	
Navicula eidrigeana	Carter	
Navicula escorialis	Simonsen	
Navicula forcipata	Greville	
Navicula gastrum	(Ehrenberg) Kützing	
Navicula gracilis	Ehrenberg	
Navicula gracilis var. *neglecta*	(Thwaites) Grunow	
Navicula granulata	J.W. Bailey	
Navicula gregaria	Donkin	
Navicula halophila	(Grunow) Cleve	
Navicula hanseni	Möller	
Navicula hasta	Pantocsek	
Navicula hennedyii	W. Smith	
Navicula humerosa	Brébisson	
Navicula inserata	Hustedt	
Navicula irrorata	Greville	
Navicula laevissima	Kützing	
Navicula laevissima	Kützing	
Navicula longa	(Gregory) Ralfs	
Navicula lundstroemii	Cleve	
Navicula lyra	Ehrenberg	
Navicula maculata	(Bailey) Edwards	
Navicula maculosa	Donkin	
Navicula marina	Ralfs	
Navicula membranacea	Cleve	
Navicula northumbrica	Donkin	
Navicula opima	Grunow	
Navicula paleralis	(Brébison) W. Smith	
Navicula palpebralis	Brébisson	
Navicula peregrina	Ehrenberg	
Navicula phyllepa	Kützing	
Navicula placenta	Ehrenberg	
Navicula placentula	(Ehrenberg) Kützing	
Navicula praetexta	Ehrenberg	
Navicula producta	W. Smith	
Navicula pusilla	W. Smith	
Navicula radiosa	Kützing	
Navicula rhombica	Gregory	
Navicula rhynchocephala	Kützing	
Navicula salinarum	Grunow	
Navicula septentrionalis	(Grunow) Gran	
Navicula sovereignae	Hustedt	

Navicula spectabilis	Gregory	
Navicula transitans var. *asymmetrica*	(Cleve) Cleve	
Navicula tripunctata	(O.F. Müller) Bory	
Navicula tuscula	Ehrenberg	
Navicula viridula	(Kützing) Ehrenberg.	
Neidium affine	(Ehrenberg) Pfitzer.	
Neodelphineis pelagica	Takano	
Nitzschia sp.		I
Nitzschia acicularis	W. Smith	
Nitzschia actinastroides	(Lemmermann) Van Goor	
Nitzschia acuminata	(W. Smith) Grunow	
Nitzschia amphibia	Grunow	
Nitzschia angularis	W. Smith	
Nitzschia angularis var. *affinis*	Grunow	
Nitzschia angustata	Grunow	
Nitzschia apiculata	(Gregory) Grunow	
Nitzschia bergii	A. Cleve-Euler	
Nitzschia bilobata	W. Smith	
Nitzschia bilobata var. *minor*	Grunow	
Nitzschia calida	Grunow	
Nitzschia clausii	Hantzsch	
Nitzschia compressa	(J.W. Bailey) Boyer	
Nitzschia constricta	(Kützing) Ralfs	
Nitzschia denticula	Grunow	
Nitzschia dissipata	(Kützing) Grunow	
Nitzschia distans	Gregory	
Nitzschia fasciculata	Grunow	
Nitzschia filiformis	(W. Smith) Hustedt	
Nitzschia frustulum	(Kützing) Grunow	
Nitzschia gracilis	Hantzsch	
Nitzschia gracillima	Heiden & Kolbe	
Nitzschia granulata	Grunow	
Nitzschia holsatica	Hustedt	
Nitzschia hybrida	Grunow	
Nitzschia insignis	Gregory	
Nitzschia lanceolata	W. Smith	
Nitzschia liebethruthii	Rabenhorst	
Nitzschia linearis	(C. Agardh) W. Smith	
Nitzschia llorenziana var. *subtilis*	Grunow	
Nitzschia longissima	(Brébisson) Grunow	I
Nitzschia lorenziana	Grunow	
Nitzschia lorenziana var. *densistriata*	Grunow	
Nitzschia lorenziana var. *incerta*	Grunow	
Nitzschia microcephala	Grunow	

Nitzschia navicularis	(Brébisson) Grunow	
Nitzschia obtusa var. *scalpelliformis*	Grunow	
Nitzschia obtuse	W. Smith	
Nitzschia pacifica	Cupp	
Nitzschia palea	(Kützing) W. Smith	
Nitzschia palea	(Kützing) W. Smith	
Nitzschia paleacea	Grunow	
Nitzschia panduriformis	Gregory	
Nitzschia parvula	W. Smith	
Nitzschia pellucida	Grunow	
Nitzschia plana	W. Smith	
Nitzschia proxima	Hustedt	
Nitzschia punctata	(W.Smith) Grunow	
Nitzschia pusilla	Grunow	
Nitzschia recta	Hantzsch	
Nitzschia recta	Hantzsch	
Nitzschia sigma	(Kützing) W. Smith	
Nitzschia sigma var. *intercedens*	Grunow	
Nitzschia sigma var. *rigida*	(Kützing) Grunow	
Nitzschia sigmoidea	(Nitzsch) W. Smith	
Nitzschia sociabilis	Hustedt	
Nitzschia socialis	Gregory	
Nitzschia spathulata	Brébisson	
Nitzschia spectabilis	(Ehrenberg) Ralfs	
Nitzschia thermalis	(Ehrenberg) Auerswals	
Nitzschia trybionella	Hantzsch	
Nitzschia trybionella var. *levidensis*	(W. Smith) Grunow	
Nitzschia valida	Grunow	
Nitzschia vermicularis	(Kützing) Hantzsch N. vitrea Norman.	
Nitzschia vitrea	Norman	
Nitzschia vitrea var. *recta*	(Hantzsch) van Heurck	
Nitzschia vitrea var. salinarum	Grunow	
Opephora olsenii	Müller.	
Pinnularia sp.		I
Pinnularia gibba	(Kützing) Van Heurck	
Pinnularia lata	(Brebisson) W. Smith	
Pinnularia legumen	Ehrenberg	
Pinnularia major	(Kützing) Rabenhorst	
Pinnularia nobilis	(Ehren.) Ehrenberg	
Pinnularia notabilis	(Ehren.) Ehrenberg	
Pinnularia rectangulata	(Gregory) Rabenhorst	
Pinnularia trevelyana	(Donkin) Rabenhorst	
Pinnularia viridis	(Nitzsch) Ehrenberg.	

Pleurosigma sp.		C
Pleurosigma acutum	Norman	
Pleurosigma aestuarii	(Brébisson) W. Smith	
Pleurosigma angulatum	(Quekett) W. Smith	C
Pleurosigma angulatum var. *strigosa*	(W. Smith) Van Heurck	
Pleurosigma delicatulum	W. Smith	
Pleurosigma directum	Grunow	
Pleurosigma elongatum	W. Smith	I
Pleurosigma formosum	W. Smith	
Pleurosigma hamuliferum	Brun	
Pleurosigma naviculaceum	Brébisson	
Pleurosigma nicobaricum	(Grunow) Grunow	
Pleurosigma normanii	Ralfs	
Pleurosigma obscurum	W. Smith	
Pleurosigma rigidum	W. Smith	
Pleurosigma salinarum	Grun	
Pleurosigma strigosum	W. Smith.	
Pseudo-nitzschia cuspidata	(Hasle) Hasle	
Pseudo-nitzschia pseudodelicatissima	(Hasle) Hasle	
Pseudo-nitzschia pungens	(Grunow) Hasle	C
Pseudo-nitzschia seriata	(Cleve) Peragallo	C
Pseudo-nitzschia subpacifica	(Hasle) Hasle.	
Rhabdonema sp.		
Rhabdonema arcuatum	(Lyngbye) Kützing	
Rhabdonema minutum	Kützing.	
Rhaphoneis sp.		
Rhaphoneis amphiceros	(Ehrenberg) Ehrenberg.	I
Rhoicosphenia abbreviata	(Agardh) Lange-Bertalot	
Rhopalodia sp.		
Rhopalodia gibba	(Ehrenberg) O. Müller	
Rhopalodia gibberula	Ehrenberg	
Rhopalodia operculata	(C. Agardh) Håkansson.	
Scoliotropis latestriata	(Brébisson) Cleve.	
Stauroneis sp.		
Stauroneis amphioxys	Gregory	
Stauroneis anceps var. *hyalina*	Peragallo	
Stauroneis membranacea	(Cleve) F.W. Mills	
Stauroneis phoenicenteron	(Nitzsch) Ehrenberg	
Stauroneis salina	W. Smith.	
Stenopterobia anceps	(Lewis) Brébisson	
Striatella sp.		I
Striatella interrupta	(Ehrenberg) Heiberg	
Striatella unipunctata	(Lyngbye) Agardh.	
Surirella sp.		I

Surirella capronii	Brébisson	
Surirella cruciata	Schmidt	
Surirella elegans	Ehrenberg	
Surirella fastuosa	Ehrenberg	
Surirella fastuosa var. *recedens*	(Schmidt) Cleve	
Surirella gemma	Bailey	
Surirella ovalis	Brébisson	
Surirella ovata	Kützing	
Surirella pandura var. *contracta*	Peragallo & Peragallo	
Surirella patella	Ehrenberg	
Surirella robusta	Ehrenberg	
Surirella robusta var. *splendida*	(Ehrenberg) Van Heurck	
Surirella spiralis	Kützing	
Surirella striatula	Turpin	
Surirella tenera	Gregory.	
Synedra sp.		I
Synedra acus	Kützing	
Synedra closterioides	Grunow	
Synedra crystallina	(Agardh) Kützing	
Synedra fabulata	(Agardh) Kützing	
Synedra fulgens	(Greville) W. Smith	
Synedra gaillonii	(Bory) Ehrenberg	
Synedra provincialis	Grunow	
Synedra pulchella	(Ralfs) Kützing	
Synedra robusta	Ralfs	
Synedra superba	Kützing	
Synedra tabulata	(Agardh) Kützing	
Synedra tabulata var. *acuminata*	(Grunow) Hustedt	
Synedra toxoneides	Castracane	
Synedra ulna	(Nitzsch) Ehrenberg	
Synedra ulna var. *biceps*	(Kützing) Schönfeldt	
Synedra ulna var. *longissima*	(W. Smith) Brun	
Synedra undulata	(J.W. Bailey) W. Smith.	
Synedrosphenia gomphonema	(Janisch) Hustedt	
Tabellaria sp.		
Tabellaria fenestrata	(Lyngbye) Kützing	
Tabellaria flocculosa	(Roth) Kützing.	
Tetracyclus sp.		
Thalassionema sp.		
Thalassionema nitzschioides	(Grunow) Grunow & Hustedt.	C
Thalassiothrix sp.		
Thalassiothrix frauenfeldii	(Grunow) Grunow	
Thalassiothrix longissima	Cleve & Grunow	

Thalassiothrix mediterranea	Pavillard	I
Toxarium undulatum	Bailey.	
Tropidoneis sp.		
Tropidoneis lepidoptera	(Gregory) Cleve	
Tropidoneis seriata	Cleve.	
Chlorophyceae		
Chaetophorales		
Chaetosphaeridium globosum	(Nordstedt) Klebahn.	
Chlorococcales		
Acanthosphaera zachariasi	Lemmermann	
Actinastrum sp.		
Actinastrum hantzschii	Lagerheim	I
Actinastrum hantzschii var. *elongatum*	G.M. Smith	
Actinastrum hantzschii var. *fluviatile*	Schröder.	
Ankistrodesmus sp.		C
Ankistrodesmus braunii	(Nåegeli) Bruunthaler	
Ankistrodesmus convolutus	Chorda	
Ankistrodesmus falcatus	Beijerinck	C
Ankistrodesmus falcatus var. *acicularis*	(Braun) West	
Ankistrodesmus falcatus var. *mirabilis*	G.S.West	
Ankistrodesmus falcatus var. *tumidus*	(West & West) G.S. West	
Ankistrodesmus gracilis	(Reinsch) Korschikov	
Ankistrodesmus longissimus	(Lemmermann) Wille	
Ankistrodesmus spiralis	(Turner) Lemmermann.	
Arthrodesmus sp.		
Arthrodesmus incus var. *extensus*	Anderson	
Arthrodesmus octocornis	Ehrenberg	
Arthrodesmus sublatus	Kützing	
Arthrodesmus validus var. *incrassatus*	Scott & Gronblad.	
Botryococcus sp.		
Botryoccus braunii	Kützing	
Botryoccus protuberans	West & West	
Botryoccus sudeticus	Lemmerman.	
Chlorella sp.		C
Chlorella marina	Butcher	
Chlorella saccharophilia var. *ellipsoidea*	(Kruger) Gerneck	
Chlorella salina	Kufferath	
Chlorella vulgaris	Beijerinck.	
Choricystis sp.		
Closteriopsis sp.		
Closteriopsis acicularis	(G. Smith) Belcher& Swale	
Closteriopsis longissima	Lemmermann.	
Crucigenia sp.		I

Crucigenia apiculata	(Lemmermann) Schmidle	
Crucigenia crucifera	(Wolle) Collins	
Crucigenia fenestrata	Schmidle	
Crucigenia irregularis	Wille	
Crucigenia lauterbornii	Schmidle	
Crucigenia quadrata	Morren	
Crucigenia rectangularis	(A. Braun) Gay	
Crucigenia smithii	(Bourr. & Mangin) Komárek	
Crucigenia tetrapedia	(Kirchner) West & West	
Dictyosphaerium sp.		I
Dictyosphaerium ehrenbergianum	Nägeli	
Dictyosphaerium planctonicum	Tiffany & Ahlstrom	
Dictyosphaerium pulchellum	Wood	
Dictyosphaerium tetrachotomium	Printz.	
Elakatothrix sp.		
Elakatothrix gelatinosa	Wille	
Errerella bornhemiensis	Conrad	
Franceia sp.		
Franceia elongata	Korschikov	
Franceia ovalis	Lemmermann.	
Golenkinia radiata	Nägeli	
Kirchneriella sp.		
Kirchneriella contorta	(Schmidle) Bohlin	
Kirchneriella elongata	G.M. Smith	
Kirchneriella irregularis v. *spiralis*	(Smith) Korschikov	
Kirchneriella lunaris	(Kirchner) Moebius	
Kirchneriella obesa	(W.West) Schmidle	
Kirchneriella obesa var. *major*	(Bernard) G.M. Smith	
Kirchneriella subsolitaria	G.S. West.	
Lagerheimia sp.		
Lagerheimia ciliata	Chodat	
Lagerheimia citriformis	(Snow) G.M. Smith	
Lagerheimia longiseta	(Lemmermann) Printz.	
Micractinium sp.		
Micractinium crassisetum	Hortobagyi	
Micractinium pusillum	Fresenius	I
Micractinium pusillum var. *elegans*	G.M. Smith.	
Microspora sp.		
Microspora lauterbomii	Schmidle	
Microspora quadrata	Hazen.	
Monoraphidium arcuatum	(Korscikoviella) Hindák	
Monoraphidium contortum	(Thuret) Komárková-Legnerová	

Monoraphidium grifithi	(Berkel) Komárková-Legnerová	
Monoraphidium komarkovae	Nygaard	
Monoraphidium minutum	(Nägeli) Komárková-Legnerová	
Monoraphidium obtusum	(Korschikov) Komárková-Legnerová	
Monoraphidium pusillum	(Printz) Komárková-Legnerová	
Monoraphidium tortile	(West & West) Komárek.	
Nannochloris sp.		
Nannochloris atomus	Butcher.	
Nephrocytium agardhianum	Nägeli	
Nephrocytium limneticum	(G.M. Smith) G.M. Smith.	
Oocystis sp.		I
Oocystis Borgei	Snow	
Oocystis coronata	Lemmermann	
Oocystis elliptica	W. West	
Oocystis parva	West & West	
Oocystis solitaria	Wittrock.	
Pandorina sp.		
Pandorina morum	(Müller) Bory.	
Pediastrum sp.		
Pediastrum angulosum	(Ehrenberg) Meneghini	
Pediastrum biradiatum	Meyen	
Pediastrum boryanum	(Turpin) Meneghini	
Pediastrum boryanum var. *longicorne*	Reinsch	
Pediastrum duplex	Meyen	
Pediastrum duplex var. *gracillimum*	West & West	
Pediastrum duplex var. *inflata*	Wolosz	
Pediastrum duplex var. *reticulatum*	Lagerheim	
Pediastrum duplex var. *rotundatum*	Lucks	
Pediastrum duplex var. *subgranulatum*	Raciborski	
Pediastrum glanduliferum	Bennet	
Pediastrum muticum	Kützing	
Pediastrum obtusum	Lucks	
Pediastrum simplex	(Meyen) Lemmermann	
Pediastrum simplex var. *duodenarium*	(Bailey) Rabenhorst	
Pediastrum tetras	(Ehrenberg) Ralfs	
Pediastrum tetras var. *tetraodon*	Rabenhorst.	
Polydrieopsis spinulosa	Schmidle.	
Quadrigula sp.		
Quadrigula chodatii	G.M. Smith	
Quadrigula closterioides	Printz	

Quadrigula lacustris	(Chodat) G.M. Smith	
Quadrigula phitzeri	(Schröder) G.M. Smith.	
Scenedesmus sp.		I
Scenedesmus abundans	(Kirchner) Chodat	
Scenedesmus acuminatus	(Lagerheim) Chodat	I
Scenedesmus anomalus	(G.M. Smith) Ahlstrom & Tiffany	
Scenedesmus arcuatus	Lemmermann	
Scenedesmus arcuatus var. *platydisca*	G. M. Smith	
Scenedesmus armatus	(Chodat) G.M. Smith	
Scenedesmus bernardii	G. Smith	
Scenedesmus bicaudatus	Dedusenk	
Scenedesmus bijuga	(Turpin) Lagerheim	
Scenedesmus bijuga var. *alternans*	(Reinsch) Hansgirg	
Scenedesmus costato var. *alternans*	(Reinsch) Hansgirg	
Scenedesmus denticulatus	Lagerheim	I
Scenedesmus denticulatus var. *recurvatus*	Schumacker	
Scenedesmus dimorphus	(Turpin) Kützing	I
Scenedesmus ecornis	(Ehrenberg) Chodat	
Scenedesmus hystrix	Lagerheim	
Scenedesmus incrassatulus	Bohin	
Scenedesmus intermedius	Chodat	
Scenedesmus linearis	Komarek	
Scenedesmus magnis	Meyen	
Scenedesmus obliquus	Kützing	
Scenedesmus opoliensis	Richter	
Scenedesmus parisiensis	Chodat	
Scenedesmus perforatus	Lemmermann	
Scenedesmus quadricauda	(Turpin) Brébisson	I
Scenedesmus quadricauda var. *maximus*	West & West	
Scenedesmus smithii	Lemmermann.	
Schroederia planctonica	(Skuja) Philipose	
Schroederia setigera	(Schröder) Lemmermann.	
Selenastrum sp.		I
Selenastrum gracile	Reinsch	
Selenastrum minutum	(Nägeli) Collins	
Selenastrum westii	G.M. Smith.	
Tetradesmus sp.		
Tetradesmus smithii	Prescott	
Tetraëdron sp.		
Tetraëdron arthrodesmiforme	Wolszynska	
Tetraëdron caudatum	(Corda) Hansgirg	I
Tetraëdron cruciatum	West & West	
Tetraëdron gracile	(Reinsch) Hansgirg	

Tetraëdron hastatum	(Reinsch) Hansgrig	
Tetraëdron limneticum	Borge	
Tetraëdron lobulatum	(Nägeli) Hansgirg	
Tetraëdron minimum	(Braun) Hansgirg	
Tetraëdron muticum	(Braun) Hansgirg	
Tetraëdron pentaedricum	West & West	
Tetraëdron regulare	Kützing	
Tetraëdron regulare var. *incus*	Teiling	
Tetraëdron regulare var. *torsum*	Brunnthaler	
Tetraëdron triacanthum	Korschikov	
Tetraëdron trigonum	(Nägeli) Hansgirg	
Tetraëdron trigonum var. *gracile*	(Reinsch) DeToni.	
Tetrastrum sp.		
Tetrastrum elegans	Playfair	
Tetrastrum glabrum	(Roll) Ahlstrom & Tiffany	
Tetrastrum heteracanthum	(Nordstedt) Chodat	I
Tetrastrum staurogeniaeforme	(Schröder) Lemmermann.	I
Treubaria setigerum	(Archer) G.M. Smith	
Westella botryoides	(W.West) de Wildermann.	
Pediastrum duplex var. *clathratum*	(Braun) Lagerheim	
Quadricoccus euryhalinicus	Kuylenstierna	
Cladophorales		
Cladophora sp.		
Oedogoniales		
Oedogonium sp.		
Tetrasporales		
Dispora crucigenioides	Printz	
Gloeocystis vesiculosa	Nägeli	
Palmodictyon varium	(Nägeli) Lemmermann	
Ulotrichales		
Geminella subtilissima	(Langerheim) Printz.	
Hormidium Klebsii	G.M. Smith.	
Koliella longiseta	(Vischer) Hindák	
Radiophilum flavescens	G.S. West.	
Ulothrix sp.		I
Ulothrix subtilissima	Rabenhorst	
Ulothrix variabilis	Kützing.	
Volvocales		
Asterococcus limneticus	G.M. Smith.	
Carteria cordiformis	(Carter) Diesing	
Carteria fornicata	Nygaard.	
Chlamydomonas sp.		C
Chlamydomonas pertyi	Goroshankin.	
Eudorina sp.		

Eudorina cylindrica	Korschikov	
Eudorina elegans	Eherenberg.	
Gonium sp.		
Gonium pectorale	Mueller.	
Phacotus sp.		
Phacotus lenticularis	Ehrenberg	
Pleodorina sp.		
Volvox aureus	Ehrenberg	
Volvox tertius	Meyer.	
Zygnematales		
Closterium sp.		
Closterium aciculare	T. West	
Closterium acutum	Brébisson	
Closterium acutum	Lyngbye ex Ralfs	
Closterium archerianum	Cleve	
Closterium dianae	Ehrenberg	
Closterium limeatum	Ehrenberg	
Closterium parvulum	Någeli	
Closterium pronum	Brébisson	
Closterium setaecum	Ehrenberg.	
Coelastrum sp.		I
Coelastrum cambricum	Archer	
Coelastrum microporum	Nägeli	
Coelastrum reticulatum	(Dangeard) Senn	
Coelastrum sphaericum	Nägeli.	
Coenochloris mucosa	(Kors.) Hindák	
Cosmarium sp.		
Cosmarium alpestre	Roy	
Cosmarium contractum	Kirchner	
Cosmarium costatum	West & West	
Cosmarium cynthia	Denot	
Cosmarium ornatum	Ralfs	
Cosmarium rectangulare	Grunow	
Cosmarium subreniforme	Nordstedt	
Cosmarium tenue	Archer	
Cosmarium turpinii	Brébisson.	
Desmidium sp.		
Desmidium baileyi	(Ralfs) Nordstedt	
Desmidium grevellii	Kützing.	
Euastrum sp.		
Euastrum abruptum	West & West	
Euastrum gayanum	DeToni	
Gonatozygon brebissonii	Debary	
Hyalotheca sp.		

Hyalotheca dissiliens var. *tatrica*	Raciborski.	
Micrasterias sp.		
Micrasterias johnsonii	West & West	
Micrasterias pinnatifida	(Kützing) Ralfs	
Micrasterias radiata	Hass	
Micrasterias truncata	(Corda) Brébisson.	
Mougeotia sp.		
Penium sp.		
Pleurocapsa minor	Hansgirg.	
Pleurotaenium sp.		
Pleurotaenium nodulosum	(Brébisson) DeBary.	
Pleurotaenium subcoronulatum var. *detum*	(Turner) West & West	
Pleurotaenium trabecula	Nägeli	
Pleurotaenium tridentulum	(Wolle) West.	
Spirogyra sp.		
Spirogyra crassa	Kützing	
Spirogyra tenuissima	Kützing.	
Spondylosium planum	(Wolle) West & West	
Spondylosium pygmaeum	Rabenhorst.	
Staurastrum sp.		
Staurastrum americanum	(West & West) G.M. Smith	
Staurastrum chaetoceros	(Schröder) G.S. Smith	
Staurastrum cingulum var. *floridense*	Scott & Gronblad	
Staurastrum curvatum	W. West S. grande Bulnheim	
Staurastrum leptocladum	Nordstedt	
Staurastrum leptocladum var. *cornumtum*	Wille	
Staurastrum leptocladum var. *insigne*	West & West	
Staurastrum manfeldtii var. *flumenense*	Schumacher	
Staurastrum paradoxum	Meyen	
Staurastrum paradoxum var. *cingulum*	Kim	
Staurastrum pentacerum	G.M. Smith	
Staurastrum quadrispinatum	Turner	
Staurastrum tetracerum	Ralfs.	
Xanthidinium sp.		
Xanthidinium antilopeum	Ehrenberg ex Kützing	
Xanthidinium subhastiferum var. *towerii*	(Cushman) G.W. Smith	
Zygnema sp.		
Chrysophyceae		
Chrysophaerales		
Aureococcus anophagefferens	Hargraves & Sieburth	
Ochromonadales		
Calycomonas sp.		

Calycomonas gracilis	Lohmann	
Calycomonas wulffii	Conrad & Kufferath.	
Centritractus belanophorus	Lemmermann	
Centritractus brunneus	Fott	
Centritractus capilifer	Pascher	
Centritractus globulosus	Pascher.	
Chromulina parvula	Conrad	
Chromulina wislouchiana	Bourelly	
Chrysococcus minutus	(Fritsch) Nygaard	
Chrysococcus ornatus	Pascher	
Chrysococcus rufescens	Klebs	
Chrysococcus tesselatus	Fritsch.	
Dinobryon sp.		I
Dinobryon bavaricum	Imhof	
Dinobryon calciformis	Bachmann	
Dinobryon cylindricum	Imhof	
Dinobryon divergens	Imhof	
Dinobryon petiolatum	Willen	
Dinobryon sertularia	Ehrenberg	
Dinobryon sociale	Ehrenberg.	
Kephyrion sp.		
Kephyrion ovale	Lackey.	
Ochromonas sp.		I
Ochromonas caroliniana	Campbell	
Ochromonas minuscula	Conrad	
Ochromonas variabilis	Meyer.	
Paulinella ovalis	(Wulff) Johnson Hargrave & Sieburth.	
Pseudotetraedron neglectum	Pascher.	
Rhizochrysis limnetica	G.M. Smith.	
Stylococcales		
Lagynion cystodinii	Pascher	
Synurales		
Mallomonas sp.		I
Mallomonas caudata	Conrad	
Mallomonas producta	Iwanoff	
Mallomonas tonsurata	Teiling.	
Synura sp.		
Synura adamsii	G.M. Smith	
Synura uvella	Ehrenberg.	
Coccolithophoridaceae		
Coccosphaerales		
Acanthoica quattrospina	Lohmann	
Calciosolenia granii	Schiller C. murrayi Gran.	

Calyptrosphaera oblonga	Lohmann	
Discosphaera tubifer	(Murray & Blackman) Ostenfeld	
Michaelsarsia elegans	Gran	
Ophiaster hydroideus	(Lohmann) Lohmann	
Pontosphaera syracusana	Lohmann	
Rhabdosphaera claviger	Murray & Blackman	
Rhabdosphaera hispida	Lohmann	I
Rhabdosphaera longistylis	Schiller	
Rhabdosphaera stylifer	Lohmann.	
Scyphosphaera apsteinii	Lohmann.	
Syracosphaera histrica	Kamptner	
Syracosphaera pulchra	Lohmann.	
Isochrysidales		
Emiliania huxleyi	(Lohmann) Hay & Mohler.	
Hymenomonas carterae	(Braarud & Fagerland) Braarud.	
Cryptophyceae		
Cryptomonadales		
Chilomonas marina	(Braarud) Halldal.	
Chroomonas amphioxeia	(Conrad & Kufferath) Butcher	
Chroomonas salina	(Wislouch) Butcher	
Chroomonas vectensis	Carter.	
Cryptomonas sp.		C
Cryptomonas erosa	Ehrenberg	I
Cryptomonas erosa var. *reflexa*	Marsson	
Cryptomonas massonii	Skuja	
Cryptomonas ovata	Ehrenberg	
Cryptomonas ovata var. *curvata*	(Eherenberg) Lemmermann	
Cryptomonas phaseolus	Skuja	
Cryptomonas pseudobaltica	Butcher	
Cryptomonas reflexa	Skuja	
Cryptomonas rostrata	Troitzk	
Cryptomonas rostrella	Lucas	
Cryptomonas stigmatica	Wislouch.	
Hemiselmis sp.		
Rhodomonas minuta	Skuja	
Rhodomonas ovata	Ehrenberg.	
Cyanophyceae		
Chroococcales		
Aphanocapsa sp.		I

Aphanocapsa delicatssima	West & West	
Aphanocapsa elachista	West & West	
Aphanocapsa grevillei	Rabenhorst	
Aphanocapsa holsatica	(Lemmermann) Cronberg & Komárek	
Aphanocapsa pulchra	Rabenhorst.	
Aphanothece sp.		
Aphanothece gelatinosa	(Henn) Lemmermann	
Chroococcus sp.		I
Chroococcus dispersus	(Keissler) Lemmermann	
Chroococcus dispersus var. *minor*	G. Smith	
Chroococcus limneticus	Lemmermann	
Chroococcus limneticus var. *elegans*	G.M. Smith	
Chroococcus prescottii	Drouet & Daily	
Chroococcus turgidus	(Kützing) Nägeli.	
Coelosphaerium sp.		
Dactylococcopsis sp.		
Dactylococcopsis acicularis	Lemmermann	
Dactylococcopsis fascicularis	Lemmermann	
Dactylococcopsis raphidioides	Hansgirg	C
Dactylococcopsis raphidioides f. falciformis	Prinz.	
Democarpa swirenkoi	Schirsch	
Entophysalis deusta	(Meneghini) Drouet & Daily	
Gloeocapsa sp.		
Gloeocapsa aeruginosa	Kützing	
Gloeocapsa linearis	Nägeli.	
Gloeocapsa minima	(Keissler) Hollerbach	
Gloeothece sp.		
Gloeothece linearis f. *composita*	G. Smith.	
Gomphosphaeria sp.		
Gomphosphaeria aponina	Kützing	
Gomphosphaeria Naegeliana	(Unger) Lemmermann.	
Johannesbaptistia pellucida	(Dickie) Taylor & Drouet.	
Marssoniella elegans	Lemmermann.	
Merismopedia sp.		I
Merismopedia convoluta	Brébisson	
Merismopedia elegans	Braun	
Merismopedia elegans var. *major*	G. Smith	
Merismopedia glauca	(Ehrenberg) Nägeli	
Merismopedia marssonii	Lemmermann	
Merismopedia punctata	Meyen	
Merismopedia quadruplicata	(Meneghini) Brébisson	
Merismopedia tenuissima	Lemmermann.	I

Merismopedia thermalis	Kützing	
Microcystis sp.		C
Microcystis aeruginosa	Kützing	I
Microcystis firma	(Brébisson & Lemmermann) Schmidle	
Microcystis incerta	Lemmermann	I
Microcystis viridis	(Braun in Rabenhorst) Lemmermann.	
Rhabdoderma sp.		
Rhabdoderma lineare	Schmidle & Lauterborn	
Rhabdoderma sigmoidea f. *minor*	Moore & Carter.	
Rhabdogloea elenkinii	(Roll) Komárek & Anagnostidis	
Rhabdogloea smithii	(R. et F. Chodat) Komárek	
Snowella lacustris	(Chodat) Komárek & Hindák	
Synechococcus sp.		
Synechococcus elongates	Nägeli.	
Synechocystis sp.		
Synechocystis salina	Wislouch	
Woronichinia elorantae	Komárek	
Woronichinia fusca	(Skuja) Komárek.	
Anabaena sp.		I
Anabaena aequalis	Borge	
Anabaena affinis	Lemmerman	
Anabaena augstumalis var. *marchica*	Lemmerman	
Anabaena circinalis	Rabenhorst	
Anabaena confervoides	Reinsch	
Anabaena flos-aquae	Brébisson	
Anabaena limnetica	G.M. Smith	
Anabaena reniformis	Lemmermann	
Anabaena solitaria	Klebahn	
Anabaena spiroides	Klebahn	
Anabaena spiroides var. *crassa*	Lemmermann	
Anabaena wisconsinense	Prescott.	
Anabaenopsis raciborskii	Woloszynska.	
Aphanizomenon flos-aquae	(L.) Ralfs.	
Calothrix sp.		
Calothrix parietina	Thuret.	
Cylindrospermum doryphorum	Bruhl & Biswas	
Nodularia sp.		
Nodularia harveyana	(Thwaites) Thuret	
Nodularia spumigena f. *litorea*	(Kützing) Elenkin.	

Nostoc sp.		I
Nostoc commune	Vaucher.	
Richelia intracellularis	Schmidt	
Oscillatoriales		
Limnothrix planktonica	(Woloszynska) Meffert.	
Lyngbya sp.		
Lyngbya circumereta	G.S. West	
Lyngbya hieronymusi	Lemmermann	
Lyngbya planctonica		
Microcoleus sp.		
Microcoleus lyngbyaceus	(Kützing) Crouan.	
Oscillatoria sp.		C
Oscillatoria angustissima	West & West	
Oscillatoria erythraea	(Ehrenberg) Kützing	
Oscillatoria granulata	Gardner	
Oscillatoria irrigua	(Kützing) Gomont	
Oscillatoria lemmermannii	Wolosz	
Oscillatoria limosa	C.A. Agardh	
Oscillatoria lutea	Agardh	
Oscillatoria mirabilis	Bocher	
Oscillatoria pseudominima	Skuja	
Oscillatoria subbrevis	Schimdle	
Oscillatoria submembranacea	Ardissone & Strafforella	
Oscillatoria terebriformis	Agardh	
Phormidium sp.		I
Phormidium amphibium	(Agardh) Anagnostidis & Komárek	
Phormidium splendidum	(Greville) Anagnostidis & Komárek.	
Planktolyngbya contorta	(Lemmermann) Anagnostidis & Komárek	
Planktolyngbya litoralis	(Häyrén) Komárek & Hindák	
Planktolyngbya mucicola	(Naumann & Huber-Pestalozzi) Bourelly	
Planktolyngbya subtilis	(W. West) Anagnostidis & Komárek.	
Planktothrix limnetica	(Lemmermann) Komárek & Anagnostidis	
Planktothrix limnetica f. *acicularis*	(Nygaard) V. Poljanskij	
Pseudanabaena limnetica	(Lemmermann) Komárek	
Raphidiopsis curvata	Fritsch & Rich	
Schizothrix sp.		
Schizothrix arenaria	(Berkeley) Gomont	

Schizothrix calcicola	(Agardh) Gomont	
Schizothrix tenerrima	(Gomont) Drouet.	
Spirulina sp.		
Spirulina laxa	Smith	
Spirulina major	Kützing	
Spirulina subsalsa	Oersted.	
Trichodesmium lacustre	Klebahn	
Dictyochophyceae		
Dictyochales		
Dictyocha crux	Ehrenberg	
Dictyocha fibula	Ehrenberg	C
Distephanus speculum	(Ehrenberg) Haekel	I
Mesocena polymorpha	Lemmermann	
Pedinellales		
Apedinella radians	(Lohmann) Campbell	C
Dinophyceae		
Dinamoebales		
Pfiesteria piscicida	Steidinger & Burkholder	
Pfiesteria shumwayae	Glasgow & Burkholder.	
Dinophysiales		
Amphisolenia sp.		
Amphisolenia bidentata	Schröder	
Amphisolenia globifera	Stein.	
Ceratocorys horrida	Stein.	
Dinophysis sp.		I
Dinophysis acuminata	Claparede & Lachmann	I
Dinophysis acuta	Ehrenberg	
Dinophysis caudata	Kent	I
Dinophysis diegensis	Kofoid	
Dinophysis fortii	Pavillard	
Dinophysis lachmannii	Paulsen	
Dinophysis monacantha	Kofoid & Skogsberg	
Dinophysis norvegica	Claparede & Lachmann	
Dinophysis ovum	Schutt	
Dinophysis pulchella	(Lebour) Balech	
Dinophysis punctata	Jørgensen	C
Dinophysis rotundata	Claparede & Lachmann	
Dinophysis sacculus	Stein	
Dinophysis schroderi	Pavillard	
Dinophysis schuettii	Murray & Whitting	
Dinophysis tripos	Gourret.	
Ornithocercus sp.		
Ornithocercus magnificus	Stein.	
Phalacroma sp.		

Gymnodiniales		
Akashiwo sanguinea	(Hiraska) G. Hansen	I
Amphidinium sp.		C
Amphidinium acutissimum	Schiller	
Amphidinium acutum	Lohmann	
Amphidinium bipes	Herdman	
Amphidinium carterae	Hulburt	
Amphidinium crassum	Lohmann	I
Amphidinium extensum	Wulff	I
Amphidinium lacustre	Stein	
Amphidinium latum	Lebour	
Amphidinium longum	Lohmann	
Amphidinium operculatum	Claparede & Lachmann	
Amphidinium ovoideum	(Lemmermann) Lemmermann	
Amphidinium schroederi	Schiller	
Amphidinium sphenoides	Wulff	C
Amphidinium steinii	(Lemmermann) Kofoid & Swezy	
Amphidinium turbo	Kofoid & Swezy	
Amphidinium wislouchi	Hulburt.	
Cochlodinium brandtii	Wulff	
Cochlodinium helicoids	Lebour	
Cochlodinium polykrikoides	Margelef.	
Gymnodinium sp.		C
Gymnodinium arcticum	Wulff	
Gymnodinium boguensis	Campbell	
Gymnodinium coeruleum	Dogiel	
Gymnodinium costatum	Kofoid & Swezy	
Gymnodinium danicans	Campbell	
Gymnodinium dissimile	Kofoid & Swezy	
Gymnodinium flavum	Kofoid & Swezy	
Gymnodinium fusum	Stein	
Gymnodinium instriatum	(Freudenthal & Lee) Coats	
Gymnodinium marinum	Kent	
Gymnodinium mikimotoi	Miyake & Kominami	
Gymnodinium simplex	(Lohmann) Kofoid & Swezy	
Gymnodinium thompsonii	I. Kisselev	
Gymnodinium uberrimum	Kofoid & Swezy	
Gymnodinium verruculosum	Campbell.	
Gyrodinium sp.		C
Gyrodinium estuariale	Hulburt	

Gyrodinium fusiforme	Kofoid & Swezy	C
Gyrodinium lachryma	(Meunier) Kofoid & Swezy	
Gyrodinium spirale	(Bergh) Kofoid & Swezy	
Gyrodinium uncatenum	Hulburt	
Gyrodinium undulans	Hulburt.	
Karlodinium veneficum	(Ballantine) J. Larsen	I
Katodinium asymmetricum	(Massart) Loeblich III	
Oxyrrhis marina	Dujardin.	
Polykrikos hartmannii	Zimmermann	
Polykrikos kofoidii	Chatton.	C
Noctilucales		
Noctiluca scintillans	(Macartney) Ehrenberg.	I
Peridinales		
Alexandrium monilatum	(Howell) Balech	
Amphidoma sp.		
Ceratium sp.		I
Ceratium arietinum	Cleve	
Ceratium candelabrum	(Ehrenberg) Stein	
Ceratium carolinianum	(Bailey) Jorgensen	
Ceratium carriense	Gourret	
Ceratium contortum	(Gourret) Cleve	
Ceratium contrarium	(Gourret) Pavillard	
Ceratium declinatum	Karsten	
Ceratium extensum	(Gourret) Cleve	
Ceratium furca	(Ehrenberg) Claparede & Lachman	C
Ceratium fusus	(Ehrenberg) Dujardin	I
Ceratium hirundinella	(Müller) Dujardin	
Ceratium horridum	(Cleve) Gran	
Ceratium inflatum	(Kofoid) Jorgenson	
Ceratium kofoidii	Jorgensen	
Ceratium limulus	Gourret	
Ceratium lineatum	(Ehrenberg) Cleve	C
Ceratium longinum	Karsten	
Ceratium longipes	(Bailey) Gran	
Ceratium macroceros	(Ehrenberg) Vanhoffen	
Ceratium massiliense	(Gourret) Jorgensen	
Ceratium minutum	Jorgensen	I
Ceratium pentagonum	Gourret	
Ceratium pulchellum f. *semipulchellum*	Jorgensen	
Ceratium setaceum	Jorgensen	
Ceratium teres	Kofoid	
Ceratium trichoceros	(Ehrenberg) Kofoid	

Ceratium tripos	(Müller) Nitzsch.	I
Cladopyxis claytonii	Holmes	I
Diplopeltopsis minor	(Paulsen) Pavillard.	
Diplopsalis sp.		I
Diplopsalis lenticula	Bergh.	C
Glenodinium sp.		
Glenodinium armatum	Levander	
Glenodinium gymnodinium	Penard	
Gonyaulax sp.		I
Gonyaulax conjuncta	Wood	
Gonyaulax diacantha	(Meunier) Schiller	
Gonyaulax digitalis	(Pouchet) Kofoid	
Gonyaulax minuta	Kofoid & Michener	
Gonyaulax monilata	Howell	
Gonyaulax monocantha	Pavillard	
Gonyaulax polygramma	Stein	
Gonyaulax spinifera	(Claparede & Lachmann) Diesing	
Gonyaulax triacantha	Jorgensen	
Gonyaulax verior	Sournia.	
Heteraulacus polyedricus	(Pouchet) Drugg & Loeblich.	
Heterocapsa rotundata	(Lohmann) Hansen	C
Heterocapsa triquetra	(Ehrenberg) Stein.	C
Oblea rotunda	(Lebour) Balech.	
Oxytoxum crassum	Schiller	
Oxytoxum milneri	Murray & Whitting	I
Oxytoxum parvum	Schiller	
Oxytoxum reticulatum	(Stein) Butschli	
Oxytoxum sceptrum	(Stein) Schröder	
Oxytoxum scolopax	Stein	
Oxytoxum variabile	Schiller.	
Peridinium sp.		
Peridinium aciculiferum	Lemmermann	
Peridinium cinctum	Ehrenberg	
Peridinium inconspicuum	Lefevre	
Peridinium wisconsinense	(Eddy) Kützing.	
Protoperidinium sp.		C
Protoperidinium avellana	Meunier	
Protoperidinium bipes	(Paulsen) Balech	I
Protoperidinium breve	(Paulsen) Balech	I
Protoperidinium brevipes	(Paulsen) Balech	I
Protoperidinium brochii	(Kofoid & Swezy) Balech	
Protoperidinium cerasus	(Paulsen) Balech	

Protoperidinium cinctum	(Ehrenberg) Balech	
Protoperidinium claudicans	(Paulsen) Balech	
Protoperidinium conicoides	(Paulsen) Balech	
Protoperidinium conicum	(Gran) Balech	I
Protoperidinium decipiens	Parke & Dodge	
Protoperidinium depressum	(Bailey) Balech	I
Protoperidinium diabolum	(Cleve) Balech	
Protoperidinium divergens	(Ehrenberg) Balech	I
Protoperidinium fimbriatum	(Meunier) Balech	
Protoperidinium globulum	(Stein) Balech	
Protoperidinium granii	(Ostenfeld) Balech	I
Protoperidinium leonis	(Pavillard) Balech	
Protoperidinium minutum	(Kofoid) Loeblich III	I
Protoperidinium mite	(Pavillard) Balech	
Protoperidinium nipponicum	(Abe) Balech	
Protoperidinium oblongum	(Aurivillius) Parke & Dodge	
Protoperidinium oceanicum	(Vanhoffen) Balech	
Protoperidinium orbiculare	(Paulsen) Balech	
Protoperidinium ovatum	(Pouchet) Balech	
Protoperidinium pallidum	(Ostenfeld) Balech	
Protoperidinium pellucidum	Bergh	
Protoperidinium pendunculatum	(Schutt) Balech	
Protoperidinium pentagonum	(Gran) Balech	
Protoperidinium quarnerense	(Schröder) Balech	
Protoperidinium steinii	(Jørgensen) Balech	
Protoperidinium subcuvipes	(Lebour) Balech	
Protoperidinium subinerme	(Paulsen) Balech	
Protoperidinium thorianum	(Paulsen) Balech.	
Pyrocystis sp.		
Pyrocystis hamulus	Cleve.	
Pyrodinium bahamense	Wall & Dale.	
Pyrophacus sp.		
Pyrophacus horologium	Stein.	
Scrippsiella precaria	Montresor & Zingone	
Scrippsiella trochoidea	(Stein) Loeblich III.	C
Zygabikodinium lenticulatum	Loeblich & Loeblich.	
Prorocentrales		
Prorocentrum aporum	(Schiller) Dodge	I
Prorocentrum balticum	(Lohmann) Loeblich III	
Prorocentrum compressum	(Bailey) Abe	I
Prorocentrum dentatum	Stein	I
Prorocentrum gracile	Schutt	I
Prorocentrum lima	(Ehrenberg) Dodge	

Prorocentrum maximum	(Gourret) Schiller	
Prorocentrum micans	Ehrenberg	C
Prorocentrum minimum	(Pavillard) Schiller	C
Prorocentrum ovum	(Schiller) Dodge	
Prorocentrum rostratum	Stein	
Prorocentrum rotundatum	Schiller	
Prorocentrum scutellum	Schröder	
Prorocentrum triestinum	Schiller	I
Prorocentrum vaginulum	(Stein) Dodge.	
Pyrocystales		
Dissodium asymmetricum	(Mangin) Loeblich III.	
Euglenophyceae		
Euglenales		
Characium limneticum	Lemmerman	
Euglena sp.		C
Euglena acus	Ehrenberg	
Euglena agilis	Carter	
Euglena convoluta	Korshikov	
Euglena deses	Ehrenberg	
Euglena ehrenbergii	Klebs	
Euglena elastica	Prescott	
Euglena fusca	(Klebs) Lemmermann	
Euglena gracilis	Klebs	
Euglena mutabilis	Schmitz	
Euglena mutabilis var. *mainxi*	Pringsheim	
Euglena oblonga	Schmitz E. oxyuris Schmarda	
Euglena polymorpha	Dangeard	
Euglena proxima	Dangeard	
Euglena pumila	Campbell	
Euglena spirogyra	Ehrenberg	
Euglena tripteris	(Dujardin) Klebs	
Euglena virdis	Ehrenberg.	
Eutreptia sp.		I
Eutreptia lanowii	Steuer	C
Eutreptia marina	Cunha	
Eutreptia viridis	Perty.	I
Leptocinclis sp.		
Leptocinclis ovum var. *gracilicauda*	Deflandre	
Leptocinclis sphagnophila	Lemmermann.	
Phacus sp.		
Phacus caudatus	Hubner	
Phacus curvicauda	Swirenko	
Phacus latus	Pochmann	

Phacus lemmermanni	(Swirenko) Skvortzow	
Phacus longicauda	(Ehrenberg) Dujardin	
Phacus monilatus	Stokes	
Phacus orbicularis	Huebner	
Phacus perkinensis	Skvortz	
Phacus suecicus	Lemmermann	
Phacus triqueter	Dujardin.	
Rhabdomonas spiralis	Pringsheim	
Strombomonas affinis	(Lemmermann) Deflandre	
Strombomonas asymmetrica	(Roll) Popova	
Strombomonas australica	Deflandre.	
Strombomonas borysteniensis	(Roll) Popova	
Trachelomonas sp.		I
Trachelomonas acanthophora	Stokes	
Trachelomonas acanthostoma	(Stokes) Deflandre	
Trachelomonas armata var. *longa*	Deflandre	
Trachelomonas bulla	(Stein) Deflandre	
Trachelomonas charkowiensis	Swirenko	
Trachelomonas globularis var. *boyeri*	Conrad	
Trachelomonas hispida	(Perty) Stein	
Trachelomonas hispida var. *coronata*	Lemmermann	
Trachelomonas intermedia	Dangeard	
Trachelomonas planctonica var. *oblonga*	Drezepolski	
Trachelomonas raciborskii	Woloszynska	
Trachelomonas regulosa	Deflandre	
Trachelomonas scabra var. *longicollis*	Playfair	
Trachelomonas similis	Stokes	
Trachelomonas superba	Deflandre	
Trachelomonas superba var. *duplex*	Deflandre	
Trachelomonas varians	Deflandre	
Trachelomonas verrucosa	Stokes	
Trachelomonas volvocina	Enrenberg	
Trachelomonas volvocina var. *punctata*	Playfair.	
Prasinophyceae		
Chlorodendrales		
Heteromastix pyriformis	(Carter) Manton	
Heteromastix rotunda	(Carter) Manton.	
Pyramimonas sp.		C
Pyramimonas amylifer	Conrad	
Pyramimonas grossii	Parke	
Pyramimonas micron	Conrad & Kufferath	
Pyramimonas obovata	Carter	
Pyramimonas plurioculata	Butcher	
Pyramimonas torta	Conrad & Kufferath.	

Tetraselmis sp.		
Tetraselmis gracilis	(Kylin) Butcher	
Tetraselmis maculata	Butcher.	
Prymnesiophyceae		
Isochrysidales		
Isochrysis galbana	Parke	
Pavlovales		
Pavlova homersandii	Campbell	
Pavlova salina	(Carter) Green.	
Prymnesiales		
Chrysochromulina sp.		I
Chrysochromulina minor	Parke & Manton.	
Raphidophyceae		
Chattonellales		
Chattonella subsalsa	Giecheler	
Chattonella verruculosa	Hara & Chihara	
Heterosigma sp.		
Heterosigma akashiwo	(Hada) Hada ex. Hara & Chihara	
Olisthodiscus sp.		
Olisthodiscus luteus	Carter	
Xanthophyceae		
Chloramoebales		
Nephrochloris sp.		
Nephrochloris salina	Carter	
Mischococcales		
Botrydiopsis arhiza	Borzi	
Botrydiopsis eriensis	Snow.	
Characiopsis subulata	(A. Braun) Gorzi	
Dichotomococcus curvatus	Korschikoff	
Gleobotrys limneticus	(G.M. Smith) Pascher	
Goniochloris pulcherrima	Pascher.	
Isthmochloron lobulatum	(Nägeli) Skuja	
Monodus sp.		
Monodus guttula	Pascher.	
Ophiocytium capitatum var. *longispinum*	Lemmermann	
Ophiocytium cochlerare	A. Braun	
Pseudotetraedron neglectum	Pascher	
Tetraedriella spinigera	Skuja	
Tribonematales		
Tribonema sp.		
Tribonema aequale	Pascher	
Tribonema affine	West	
Tribonema ambiguum	Skuja	

Tribonema minus	(Wille) Hazen	
Tribonema monochloron	Pascher & Geitler	
Tribonema pyrenigerum	Pascher	
Tribonema subtilissimum	Pascher	
Tribonema viride	Pascher	
Tribonema vulgare	Pascher	

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Publications

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