ABSTRACT

Title of Document: PHYTOPLANKTON DYNAMICS AND HARMFUL ALGAL SPECIES IN THE POTOMAC RIVER ESTUARY

Meghann E. Niesen, Master of Science, 2013

Directed By: Lora A. Harris, Assistant Professor
Marine Estuarine Environmental Science

Phytoplankton populations are a primary driver of chemical and biological dynamics and are therefore important sentinel organisms for monitoring environmental perturbations. Additionally, long term ecological monitoring in the Potomac River estuary provides opportunities to examine phytoplankton dynamics. Annual blooms of the cyanoHAB *Microcystis* were observed in the 1970's and 80's, and since declined in frequency. A large *Microcystis aeruginosa* bloom occurred, summer 2011, prompting investigation of forecasting efforts for harmful algal species. Three prediction methods were investigated, with binary linear regression identified as the most appropriate forecasting tool. Coastal marine ecosystems are also at risk from climate change and phytoplankton provide a crucial monitoring tool. Extensive time series analysis revealed changes in phytoplankton phenology in response to climate indicators, mainly a shift in the timing of maximum abundance of diatoms and cryptophytes. It is likely that this change in phenology has an effect on energy transfer to higher trophic levels.

PHYTOPLANKTON DYNAMICS AND HARMFUL ALGAL SPECIES IN THE CHESAPEAKE BAY, FOCUSING ON THE POTOMAC RIVER ESTUARY

By

Meghann Elizabeth Niesen

Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Science
2013

Advisory Committee:
Assistant Professor Dr. Lora A. Harris, Chair
Professor Dr. Walter R. Boynton
Professor Dr. Allen Place

ACKNOWLEDGEMENTS

I would like to express the deepest appreciation to my committee chair Assistant Professor Lora Harris for her patience, motivation, enthusiasm, and immense knowledge. Without her guidance and persistent help this thesis project would not have been possible.

I would like to thank my committee members, Professor Walter Boynton and Professor Allen Place, whose work demonstrated to me the benefits of hard work and thought provoking science. Their encouragement and insightful comments have helped to lead me in the learning process of this masters thesis. .

I would also like to thank the District of Columbia Water and Sewer Authority for their financial support granted through their year round student research internship program. I thank my fellow labmates, students, and friends at CBL and IMET for all of the stimulating discussions and moral support. I am especially thankful to Mike O'Brien for his support from the beginning. Finally, I would like to thank my family, from whom I rely on for encouragement and strength.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Predicting *Microcystis aeruginosa* blooms in the Chesapeake Bay

INTRODUCTION

In aquatic systems, phytoplankton are frequently the main contributors to primary production. Bloom conditions characterized by high abundances, often of a single species, may have dramatic impacts on an ecosystem. A harmful algae bloom (HAB) occurs when the bloom species causes detrimental effects to the local environment or produces toxins. While HABs are a natural occurrence, there has been a global increase in their frequency, largely attributed to anthropogenic nutrient inputs (Pearl et al. 2001). CyanoHABs are blooms of photosynthetic cyanobacteria (as opposed to eukaryotic phytoplankton) and cause HABs in freshwater regions around the world. Environmental conditions known to influence cyanobacteria bloom formation are solar radiation, pH, temperature, stratification and nutrient concentrations, including the stoichiometric ratio of nitrogen and phosphorus (Sellner et al. 2003; Wicks and Thiel 1990).

Microcystis aeruginosa is one species of cyanobacteria that can cause recurrent HAB events in freshwater rivers and lakes throughout the US with characteristic extensive green slime collecting on the water surface and along banks (Lewitus et al. 2012). *M. aeruginosa* can produce the toxin microcystin under the right environmental conditions and there are documented cases of this toxin causing liver problems and lesions in aquaculture organisms, as well as harmful effects in humans and wildlife upon external contact and when ingested (Paerl et al. 2001; Gorham and Carmichael 1988).

The combined effects of unsightly surface scums and human health problems make this species of interest for environmental management and research.

The Chesapeake Bay has a history of CyanoHAB events, frequently in the tributaries and sub-tributaries where tidal freshwater ecosystems are most frequently located. The Potomac River estuary, the largest of these tributaries, has experienced frequent summer *M. aeruginosa* blooms. These blooms were especially prevalent in the 1960s and 1970s and decreased in frequency during the late 1980s (Krogmann et al. 1986) (Table 1). This decrease in HAB occurrence is mainly attributed to improvements in phosphorus removal at the major waste water treatment plant in Washington DC, Blue Plains (Thomann et al., 1985). Previous studies have shown that sediment phosphorus processes have a large impact on *M. aeruginosa* growth in the Potomac and other Chesapeake Bay tributaries (Seitzinger 1991, Gao et al 2012). Other tributaries of Chesapeake Bay also experiencing *M. aeruginosa* blooms include the Sassafras, James and Susquehanna rivers (Figure 1). In July and August of 2011 there was a substantial *M. aeruginosa* bloom in the Potomac River that extended from the Woodrow Wilson Memorial Bridge in Washington, DC to Mallows Bay, Maryland. This bloom prompted renewed interest in the factors affecting *M. aeruginosa* blooms and possible prediction methods for the Potomac River.

When forecasting HABs it is important to employ a prediction method to fit the needs of management. Within the concept of Occam's razor, ecological modelers have long recognized the need to balance complexity of formulations without over parameterization. A prediction tool for the Chesapeake Bay must consider this principle

while also insuring that any HAB prediction is efficient and easily accessible to local government agencies and policy makers. There are many forecasting methods in use to predict HABs, including those designed for *M. aeruginosa* specifically. Sullivan(1987) used hydro-meteorological data to develop an "algae encouragement index" (AEI) specific to the Potomac River for the Metropolitan Washington Council of Governments' Department of Environmental program. The AEI attempted to compute the likelihood of an algae bloom occurring in any given summer. In other ecological indices for the Chesapeake Bay, algae species are often used as indicators of water quality. Lacouture et al.(2006) created an Index of Biotic Integrity for the Chesapeake Bay and its tributaries in which the presence or absence of certain species, along with physical parameters, was indicative of water quality in a given location. There are also known seasonal successional patterns in algal functional groups for the Potomac (Marshall et al. 2005) that could facilitate an investigation into how changes in the community composition can impact *M. aeruginosa* bloom formation.

Many types of linear regression techniques have also been applied to forecasting bloom formation. Generalized linear modeling has proven successful in other phytoplankton modeling efforts in the Chesapeake Bay and globally using both general linear regression and binary logistic regression (Anderson et al. 2010; Lane et al. 2009; Kruk et al. 2010; Imai et al. 2009; Rost et al. 2011;Carvalho et al. 2011). Mechanistic models that couple hydrodynamic models with satellite remote sensing data have had success with *M. aeruginosa* blooms in the Great Lakes, USA (Wynne et al 2011; Wynne et al 2010; Stumpf et al 2012). Neural networks are the most prevalent method for prediction of *M. aeruginosa* bloom formation (Wei et al 2001, Jeong et al 2006,

Recknagel et al 1997). Here I investigate three possible forecasting methods and their applicability to predict a *M. aeruginosa* bloom for the freshwater regions of the Chesapeake Bay. Revisiting the historical prediction tools, I first evaluated the applicability of the AEI developed by Sullivan (1987). Because more recent regional efforts have revealed seasonal patterns in functional diversity, I then analyzed community composition as a predictor of bloom formation. Finally I targeted evaluating statistical models to predict bloom formation using generalized linear modeling.

MATERIAL AND METHODS

Study Site and Available Data

For this study I focused on two major tributaries of the Chesapeake Bay; the Potomac and the James Rivers (Figure 1). Each have a history of *M. aeruginosa* cyanoHAB events and are included as sampling locations in long term environmental monitoring records. Both of these systems are under U.S. Environmental Protection Agency regulation through Total Maximum Daily Loads (TMDLs) designed to reduce anthropogenic nutrient inputs and improve water quality. *M. aeruginosa* blooms are an urgent issue for improvements in water quality because of their toxicity and implications for human health.

Several sources were mined for environmental and biotic data to support the exploration of various prediction methods. The USGS National Water Information System (http://water.usgs.gov/) documents measurements and estimates of average river

discharge, as well as nutrient loading, for the Potomac River at Little Falls, MD and for the James River near Richmond VA (Figure 1). Nutrient loading from Blue Plains wastewater treatment plant in Washington DC and Richmond wastewater treatment plant are available from the Chesapeake Bay Program data hub (http://www.chesapeakebay.net/data). Average wind speeds and light data are available from Ronald Reagan Washington National airport and Richmond International airport via the NOAA national climatic data center (http://www.ncdc.noaa.gov/). Light measurements were reported as both percent sunshine, a measure of the minutes in a day where sunshine was observed, and total daily integrated photosynthetic active radiation (PAR). I supplemented these data with measurements from the National Estuarine Research Reserve System centralized data management office for the Jug Bay Wetlands Sanctuary and Taskinas Creek, as well as data from the Chesapeake Bay Program Historical Data sets (http://cdmo.baruch.sc.edu/, http://archive.chesapeakebay.net/data/historicaldb/historicalmain.htm).

Phytoplankton identifications and abundances, as well as corresponding environmental data, were downloaded from the Chesapeake Bay Program data hub for the tidal fresh portion of the Potomac River and the tidal fresh James River (Figure 1). Environmental data listed in Table 1 ranged from direct measurements such as nutrient concentrations, pH, and salinity to indirect metrics such as the difference between bottom and surface water temperatures (DeltaT). The Chesapeake Bay phytoplankton monitoring program reports phytoplankton identifications at the lowest possible taxonomic designation, commonly to the species and variation level. Each designation has a unique code and these can be analyzed as a whole or condensed into larger functional groupings

based on genus level taxonomy. Summarized methods for the monitoring program can be found in Marshall et al (2006).

Algae encouragement index

Given the long time series now available to revisit the AEI developed by Sullivan (1987), I investigated its use as a predictor index for current *M. aeruginosa* bloom dynamics in the Potomac River and James River using the updated data set. The AEI includes three factors important to the growth of *M. aeruginosa*; percent sunshine, wind speed, and river discharge. Together, Sullivan (1987) proposed a formulation to evaluate the joint occurrence of environmental conditions which he hypothesized would encourage a bloom. The AEI is calculated according to equation1 with terms defined in Table 2.

$$\text{Light term} = \frac{(S - \bar{S})}{D_S} \qquad \text{Wind term} = \frac{(\bar{W} - W)}{D_W} \qquad \text{Discharge term} = \frac{(\overline{LQ} - LQ)}{D_{LQ}} \tag{1-3}$$

$$\text{AEI} = \text{Light term} + \text{Wind term} + \text{Discharge term} \tag{4}$$

Each component of the AEI is calculated as the difference of the summer average from the long term mean, giving each variables anomaly from the long term mean. For wind speed and river discharge a value lower than the mean correlates to positive *M. aeruginosa* growth while for percent sunshine a value higher than the mean correlates to positive growth, thus the change in component calculation.

In order to evaluate the AEI as a potential prediction method, several steps were carried out to parameterize the index equation with currently available datasets. For example, percent sunshine data were not available after 1998, therefore I calculated a

modified AEI index using total daily integrated PAR data collected from 1953-1980 to determine if PAR light data would be a viable substitute for percent sunshine. Figure 2 shows a comparison of the AEI computed using the same dataset reported by Sullivan (1987) but with a modified AEI calculated using PAR data. The AEI showed little change when calculated with PAR data rather than percent sunshine, therefore I determined that PAR data could be substituted in later years when percent sunshine measurements are no longer available. Using PAR light data I extended the AEI through 2011 using 1985-2005 for the long term mean in the calculations. I then compared the calculated index with *M. aeruginosa* abundances reported from the tidal fresh Potomac River. To test its applicability for other regions in the Chesapeake Bay I also calculated the AEI for the tidal fresh James River Estuary for 1986 - 2011.

Community Composition

Regional analyses of the Chesapeake Bay long term plankton data base have revealed seasonal patterns in community composition (Marshall et al 2005), therefore I investigated the potential of developing a forecasting method using community composition as an indicator of *M. aeruginosa* bloom formation. I used a combination of non-metric multi-dimensional scaling (MDS) and redundancy analysis (RDA) to show patterns in species related to *M. aeruginosa* abundances. RDA is a form of constrained ordination that examines how much of the variation in one set of variables explains the variation in another set of variables. It is the multivariate analog of simple linear regression. A Bray-Curtis similarity matrix was constructed from species abundance data normalized with a log transformation (Primer-E) at each sampling time. An MDS graph

was then prepared by plotting the similarity matrix in space with the best 2D and 3D representations (Primer-E) to investigated similarity patterns among communities under varying conditions. This analysis was performed with environmental data collected at the same time at the community composition as well as a one-sampling-time step lag, representing environmental conditions in the previous month. I ran a RDA of phytoplankton communities using the Vegan package (2.0-7) of R version 3.0.0 (R development Core Team, 2001), which is a free software available at http://r-project.org.

Statistical modeling

I used two GLM techniques, the logistic regression and a binary response framework, to predict the likelihood of *M. aeruginosa* bloom occurrence. For the two GLM techniques, I combined the data from the Potomac and James River Estuaries to increase the sample size and bloom incidence for better predictive power. In a single river alone there are so few bloom observations, statistical modeling efforts would not be able to accurately predict future blooms. These two tributaries of the Chesapeake Bay are both tidal estuaries subject to influence by river discharge, land based nutrient inputs and have regionally similar climate. For these models I used environmental data collected from 1981-2011 (Table 2). The environmental variables included in model estimations were all chosen because they have a possible direct impact on *M. aeruginosa* growth rates or indirect impact through water condition. Some of these influential parameters include, river discharge, temperature, light levels, wind speed (DiToro 1981, Fitzpatrick et al 1988), alkalinity, pH (Seitzinger 1991, Jaworski 1990), and river nutrient conditions (Seitzinger 1991, Selner et al 1988). I also evaluated these models on a one-sampling-

time step lag to look for variables that have a longer response lag for *M. aeruginosa* growth (Table 2).

Linear model regression was performed with R version 3.0.0 (R development Core Team, 2001) using the base programming and the supplemental package, glmulti (Calcagno 2010). A log transformation was used for *M. aeruginosa* abundances to combat bias in cell count data. These linear regressions were calculated using all abundance and environmental variables, fitted to a glm function using all subsets of possible models and reported model significances according to Akaike information criterion (AIC). Binary logistic regression was also run using the base R programming and the glmulti supplemental package following the same sequence of full model fitting and all possible subset selection (Burnham & Anderson 2002) . In contrast to linear model regression which employs a continuous linear relationship between the predicted and observed variables, a binary regression predicts the probability of bloom occurrence in a bloom vs. no bloom scenario. This logistic regression was run in conjunction with linear regression to combat any errors due to possible problems with normality in the data as well as to investigate the possibility of a continuous response to environmental variables or a threshold response. This process of model fitting was repeated on a one-sampling-time step lag, which in most cases denotes a month difference.

RESULTS AND DISCUSSION

Algae encouragement index

Figure 3 shows a plot of modified AEI values using PAR data over the available dataset for the Potomac River Estuary. There is not a strong correlation in the Potomac River Estuary between calculated AEI values and *M. aeruginosa* abundances. Similarly, AEI values calculated in the James River Estuary pictured in Figure 4 do not show a strong correlation to *M. aeruginosa* abundances and even greater levels of variability are apparent. The AEI is not effective, and this is most apparent in Figures 3 and 4 where a low base line level of cell abundance can occur over a range of index values in both systems. Furthermore, there is a breakdown in the AEI for the Potomac, where anomalous high cell abundances occur at low index values (Figure 3). In order to better visualize the components of the AEI and explore whether any single variable was particularly critical to the AEI for a given year, I plotted histograms of each environmental term and the corresponding AEI values for each year Figure 5 and Figure 6. However, there is no one variable that is the major driver of index variability in either estuary.

When using a static index for tracking HAB activity it is important to remember that a system can change in a 30 year time period. When the original index was developed for the Potomac using data collected between 1960 and 1980, it was a good tool for indicating bloom likelihood. Applying that index to more recent datasets markedly decreased its applicability. This is most likely due to changes in the system and the way that light, discharge, and wind affect bloom dynamics. This is most clearly seen

in Figure 7, which displays the AEI and contributing terms for anomalous years with low index values but high *M. aeruginosa* abundances. For the years in this subset of values falling after 1990, a negative river discharge AEI term coincides with the Blue Plains wastewater treatment plant full implementation of new phosphorus removal techniques, as well as nationwide efforts to ban phosphorus from detergents. Prior to these management changes, it is likely that the early AEI included a negative relationship between high discharge and *M. aeruginosa* abundances because high flows lead to increases in flushing, which is detrimental to bloom formation. However with a change in nutrient inputs in the 1990s, the main source for phosphorus to the system is now through upstream river discharge. When terms are included in an index that relate to indirect effects, as is the case for river discharge, formulations should be revisited and revised on a regular basis.

The use of indices in ecology is prevalent and ongoing in the Chesapeake Bay (Lacouture et al. 2006; Gastrich and Wazniak 2002; Borja et al. 2008; Pinto et al. 2009; Williams et al. 2009).However, there are inherent drawbacks to using an index as a predictive tool. The AEI assumes proportional increases in growth with increases in each variable. Because the AEI is an additive index, a negative and positive value in the same year results in a net sum of zero that may obscure the signal of the other components. Fisheries scientists have previously identified these drawbacks and the associated diminished effectiveness of indices (Cone 1989).

An example of these shortcomings can be understood by considering a scenario where high light and low wind conditions are combined with high river discharge to

result in a moderate index value, even as similar AEI values could also be achieved with moderate conditions for wind, light, and discharge measurements. When looking at the index values for the Potomac in years 1996, 2001, and 2005, all have values very close to zero. However these zero index values signify very different conditions for plankton in the estuary. While an index is a very simple and easy to use method, it doesn't capture the full complexity of the Chesapeake Bay tributaries.

Community Composition

Looking in depth at the community composition associated with *M. aeruginosa* blooms, there are differences that suggest the possibility of using community characteristics in a forecasting context. The results of multi-dimensional scaling analyses pictured in Figure 8 exhibit a gradient change in phytoplankton community similarity associated with high, medium, or low abundances of *M. aeruginosa.* However, when looking at the community composition preceding high abundance blooms as pictured in Figure 9, there is no distinct community that could be used as a predictor of subsequent *M. aeruginosa* abundances. Figure 10 shows an RDA of phytoplankton species as they are correlated with increasing *M. aeruginosa* abundance. Species in the top right are mostly diatoms and are correlated with low or no *M. aeruginosa*, while those species in the bottom left constitute mostly other cyanobacteria and are associated with higher abundances. Some of those species associated with high abundances are also known nitrogen fixers. The RDA shows the community shifts seen in the MDS plots and how the species change along the gradient observed.

When looking at community composition as a prediction method for *M. aeruginosa* bloom formation the most critical drawback preventing predictive ability is sampling frequency. Routine monitoring occurs once a month with only occasional biweekly sampling. Therefore, for this analysis a one-sampling-time step lag could be either two weeks or a full month difference. For looking at phytoplankton with a high population turnover time this sampling is not frequent enough. This deficiency could be bridged through satellite pigment analysis as has been suggested and attempted in lakes (Stumph et al. 2012; Wynne et al. 2011; Lewitus et al. 2005; Wynne et al. 2010).

Statistical modeling

The GLM analyses yielded more encouraging results. The all possible subsets regression analysis not only identified the best fit model, but resulted in the finding that alkalinity, the AEI light term, DeltaT, and pH were the most influential terms for predicting *M. aeruginosa* abundance as seen in Figure 11. The general liner regression model with the best fit to the data, shown as Equation 5, included those parameters as well as two others; normalized wind speed (WI) and dissolved inorganic phosphorus (DIP).

$$\log(\text{Micro}) \sim 1.75*\text{pH} + 38.83*\text{DIP} - 1.45*\text{DeltaT} - 0.42*\text{WI} - 0.1*\text{LI} + 0.04*\text{Alkalinity} - 2.54 \quad (5)$$

I considered two models in the binary logistic regression approach, one defining a bloom as more than 15,000 cells per milliliter (BloomH) and another at a lower cutoff of more than 10,000 cells per milliliter (BloomM). From the all possible subsets analysis the most important terms for predicting *M. aeruginosa* abundances at high bloom conditions

were the AEI light term, alkalinity and dissolved inorganic nitrogen (DIN) while at medium bloom conditions total suspended solids (TSS), DeltaT, and AEI wind term were also important terms (Figure 12). The best fit model for both high and medium bloom cutoffs are shown in equations 6 and 7.

$$\text{BloomH} \sim 0.15*\text{pH} + 5.31*\text{DIP} - 0.17*\text{DIN} - 0.11*\text{DeltaT} + 0.05*\text{Alkalinity} - 0.1*\text{LI} - 1.41 \quad (6)$$

$$\text{BloomM} \sim 0.16*\text{pH} - 0.35*\text{DIN} - 0.01*\text{TSS} - 0.22*\text{DeltaT} + 0.01*\text{Alkalinity} - 0.08*\text{LI} - 0.13*\text{WI} - 1.32 \quad (7)$$

Due to the long residence time of the Potomac River Estuary I examined several environmental conditions using a time lag. This is to look for a time delay in onset of a variable and the reaction of plankton community. When examining models on a one-sampling-time step lag, only one variable stands out as most important for both linear regression and binary logistic regression and that was the AEI light term. For the general linear regression the top model also included difference in water temperature (DeltaT) and waste water treatment plant phosphorus loads (WWTPload). However, for the binary logistic models, light was the only term in both high and mid abundance level cutoff models.

$$\log(\text{Micro}) \sim 0.15*\text{Wtemp} - 0.14*\text{LI} - 0.001*\text{WWTPload} + 11.2 \quad (8)$$

$$\text{BloomH} \sim 0.08 - 0.09*\text{LI} \quad (9)$$

$$\text{BloomM} \sim 0.16 + 0.06*\text{LI} \quad (10)$$

In other studies where general linear regressions are used for HAB prediction, model validation methods further test each model output (Anderson et al 2010). Anderson et al. (2010) used part of a data set to create a best model scenario, and then validated the model with the remainder of the dataset. However, this is not possible with the current data set for the Chesapeake Bay because of limitations in the number of bloom events. Relatively fast growth rates result in high turnover of the microbial community, on the order of days to weeks. However, once a *M. aeruginosa* bloom has established it can last for weeks to months. A sampling frequency of once a month cannot capture rapid turnover and often misses the start of a bloom event, a very important part of understanding bloom dynamics.

General linear regression provides a good model tool for predicting *M. aeruginosa* abundances for the Chesapeake Bay. The two regression techniques could be used together or separately to give advanced warning for *M. aeruginosa* bloom formation. When looking at the effects of a time lag on importance to bloom formation, normalized light was clearly the best indicator for long term bloom prediction. Years with low average PAR levels are at a low risk for *M. aeruginosa* bloom formation while years of high average PAR should be considered for further analysis as to the likelihood of bloom formation. Regression models also lend themselves better to adaption for dynamic systems. As new data are collected, a model can be re-tested and evaluated to fine tune the model equation. It is also possible to efficiently reanalyze top model selections for changes in the importance of variables.

The benefit to using model regression techniques, especially those using model ranking techniques based on information theory like those presented here, is the incorporation of the principle of parsimony to capture the complexity inherent in the system without over parameterization. This model is practical, providing information to the public and policy makers as simply and efficiently as possible. Current approaches to HAB monitoring are dependent on reactive sampling methods, where information is collected and reported to environmental managers with a lag time which is dependent upon field collection, laboratory analysis, and reporting efforts. These factors lead to little preparation time when a bloom does occur for planned monitoring efforts and public notices. The models described here can give more advanced warning of bloom formation and therefore more forethought in monitoring efforts. Environmental parameters can be quickly analyzed and run through a model to look for likelihood of bloom formation.

CONCLUSION

Both the AEI and phytoplankton community composition seem to be weak predictors for *M. aeruginosa* bloom formation for data available over the past 20 years. The use of more advanced statistical methods, especially the multivariate regression models and model ranking approach presented here, gives greater explanatory power while maintaining ease of use. It is important to maintain and update these methods of prediction of bloom formation in dynamic systems that are typical of the Chesapeake Bay tributaries. However, their applicability and value may enable managers to more quickly identify and predict a HAB, warn the local community, and trigger more intensive

monitoring efforts to protect public health. Under current motoring efforts a possible bloom must be identified before action is taken. With the use of regression modeling it is possible to know the likelihood of bloom formation and take proactive steps to monitor the situation. There is still work needed to fully understand formation and maintenance of *M. aeruginosa* blooms in tidal ecosystems, especially the advancement of remote sensing techniques that have shown potential in lakes. However, the application of GLM techniques is a promising direction to take in leveraging existing monitoring infrastructure for the Chesapeake Bay.

Table 1. Reported algae blooms in the Potomac River until 1983 adapted from Krogmann et al 1986.

Year	Organism	Location	Date
1959	*M. aeruginosa*	Anacosita and Potomac River	August
1965	"algae of a poisnous variety"	Potomac River	September 28
1963	"So much algae the river turned green"	Potomac River	July 8
1963	"Fish kills… resulting from a severe algal bloom"	Potomac River	August 24
1965	"Algae that grows in thick profusion"	Potomac River	August 1
1966	"Algae"	Potomac River	August 23
1966	*M. aeruginosa*	Potomac River, Piscataway Creek	June
1968	*M. aeruginosa*	Potomac River below Chain Bridge	August 19
1970	*M. aeruginosa*	Potomac River, Tidal Basin	
1983	*M. aeruginosa*	Potomac River, Piscataway Creek	August 20
1983	*M. aeruginosa*	Potomac River	July

Table 2. Environmental parameters used in statistical modeling and their associated abbreviations. Normalized parameters are calculated based on the formulation for the AEI. Those parameters denoted with a (*) are only used in time lag model.

Environmental Parameter		**Model abbreviation**	**Units**
pH		pH	SU
Molar ratio of total nitrogen to total phosphorus		N/P	mg/L
Dissolved inorganic nitrogen		DIN	mg/L
Dissolved inorganic phosphorus		DIP	mg/L
Alkalinity		Alkalinity	mg/L
Total suspended solids		TSS	mg/L
Difference in water temperature between surface and bottom waters		DeltaT	deg C
AEI wind term		WI	m/sec
AEI river discharge term		DI	m^3/sec
AEI light term		LI	E/m^2/sec
Water temperature	*	Temp	deg C
Wastewater treatment plant nitrogen loading	*	WWTNload	kg/day
Wastewater treatment plant phosphorus loading	*	WWTPload	kg/day
Headwater nitrogen loads	*	RNload	kg/year
Headwater phosphorus loads	*	RPload	kg/year
Hydraulic fill time	*	Hydro	days

Table 3: Variable terms and abbreviations for Sullivan (1987) AEI equation

Variable	**Units**	**Definition**
Light		(S - $\bar{S}$) / D_S
S	(min/day) or (E/m2/sec)	Average summer percent sunshine or daily integrated PAR
$\bar{S}$		Long term average of percent sunshine or PAR
D_S		Standard deviation of long term average of percent sunshine or PAR
Wind		($\bar{W}$ – W) / D_W
W	(m/sec)	Average summer wind speed
$\bar{W}$		Long term average of wind speed
D_W		Standard deviation of long term average of wind speed
River Discharge		($\overline{LQ}$ – LQ) / D_{LQ}
LQ	(m^3/sec)	Common logarithm of average summer river discharge
$\overline{LQ}$		Long term average of river discharge
D_{LQ}		Standard deviation of long term average of river discharge

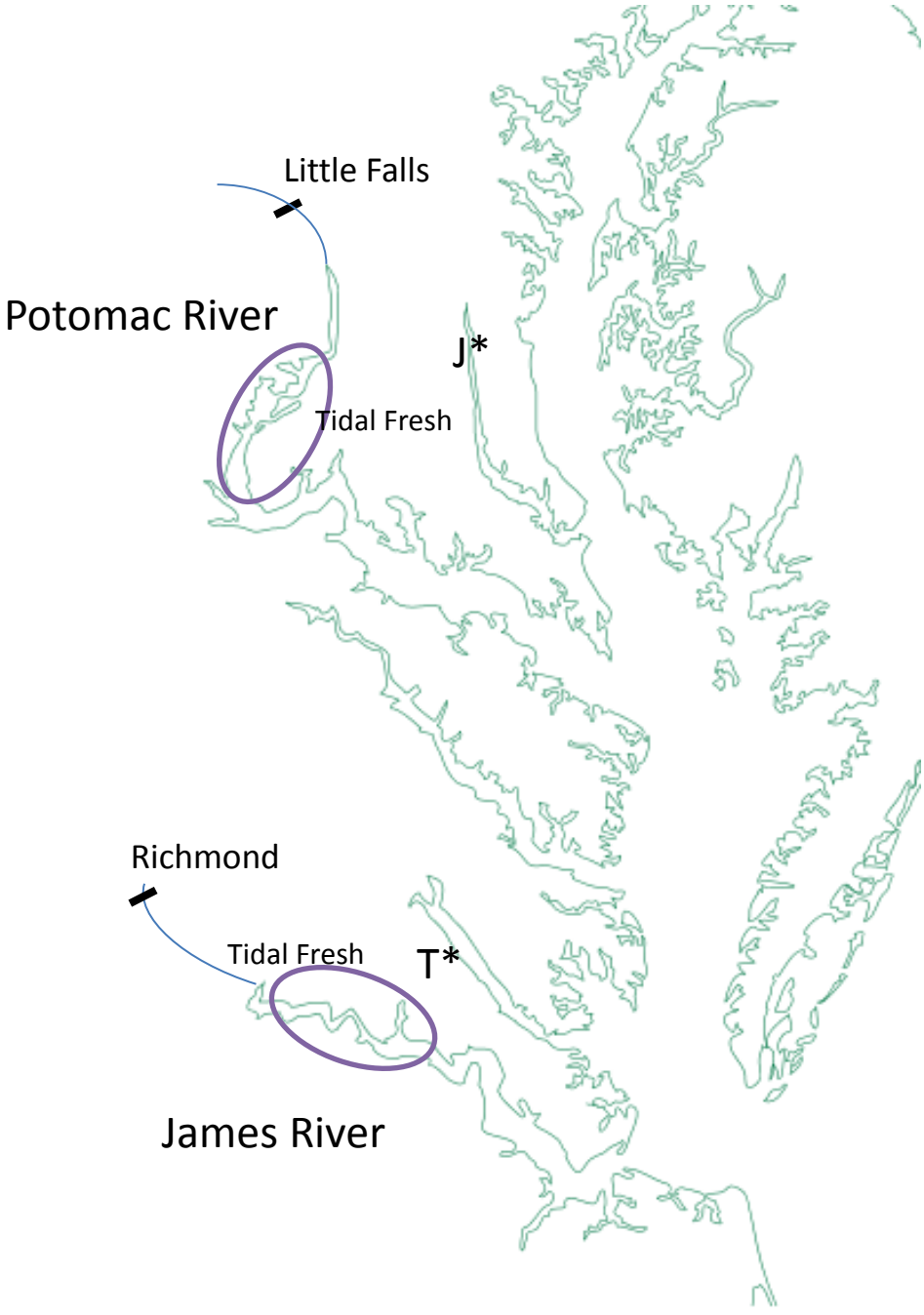


Figure 1. Map of Chesapeake Bay with study sites highlighted. Potomac and James Rivers. Tidal Fresh portion of the estuaries circled, Taskinas creek and Jug Bay marked with a T* and J* respectively, and river discharge sites marked as Little Falls and Richmond.

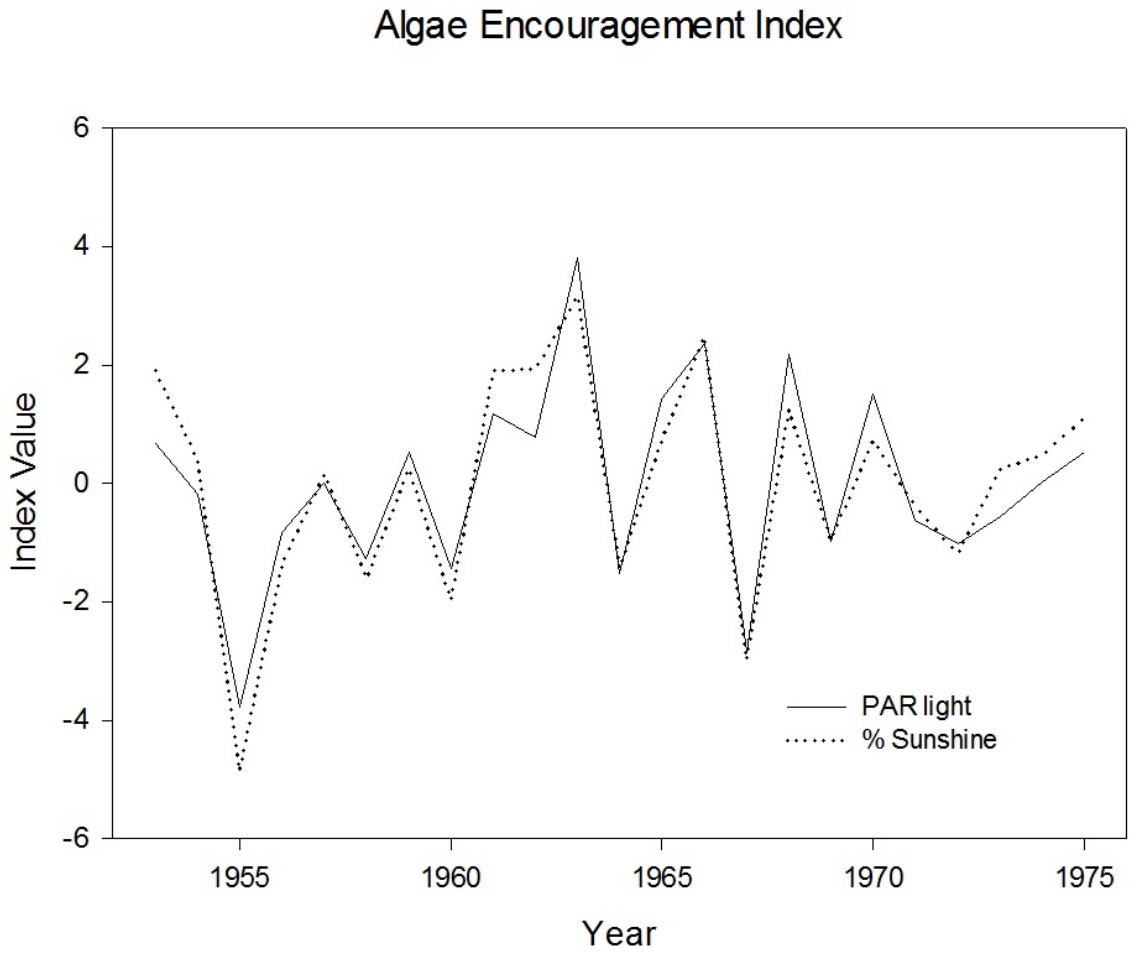


Figure 2. Graph of AEI calculated using PAR light data and percent sunshine data over the time period originally used to develop the AEI. Higher AEI values indicate years of high *M. aeruginosa* bloom favorability.

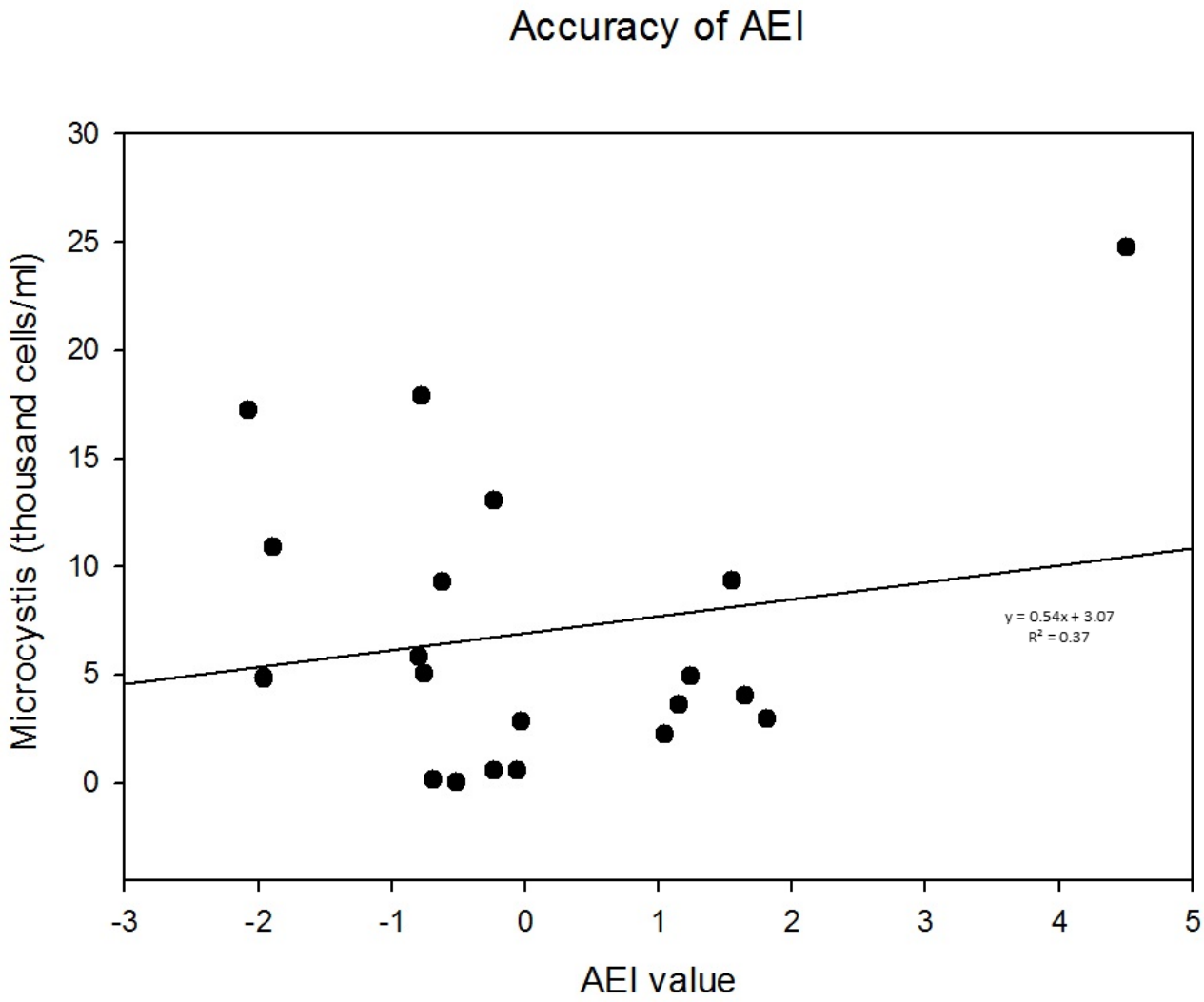


Figure 3. Plot of calculated AEI values against reported *M. aeruginosa* abundances for the tidal fresh Potomac River Estuary. With linear regression line shown, associated equation, and R^2 value.

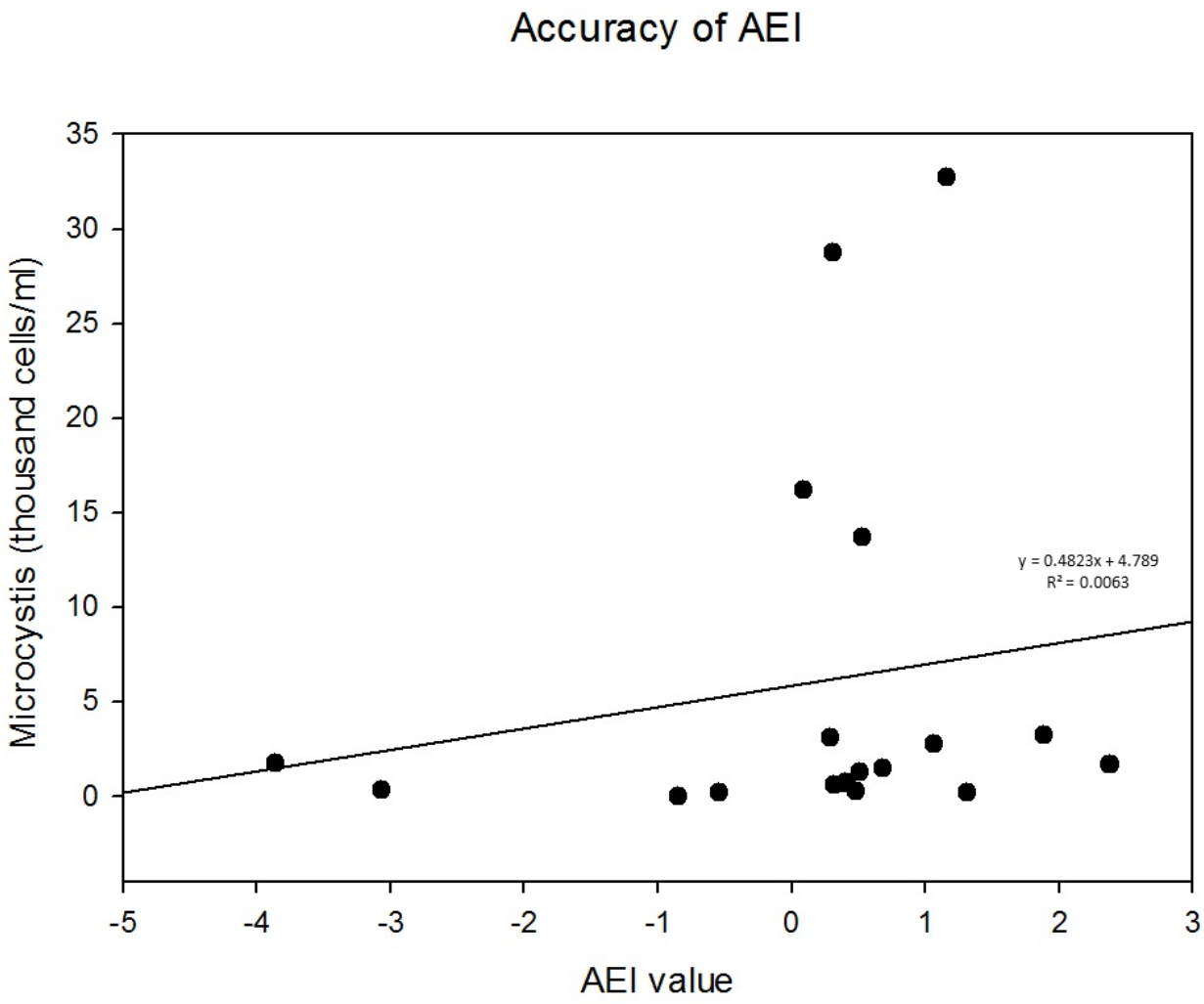


Figure 4. Plot of calculated AEI values against reported *M. aeruginosa* abundances for the tidal fresh James River Estuary. With linear regression line, associated equation, and R^2 value.

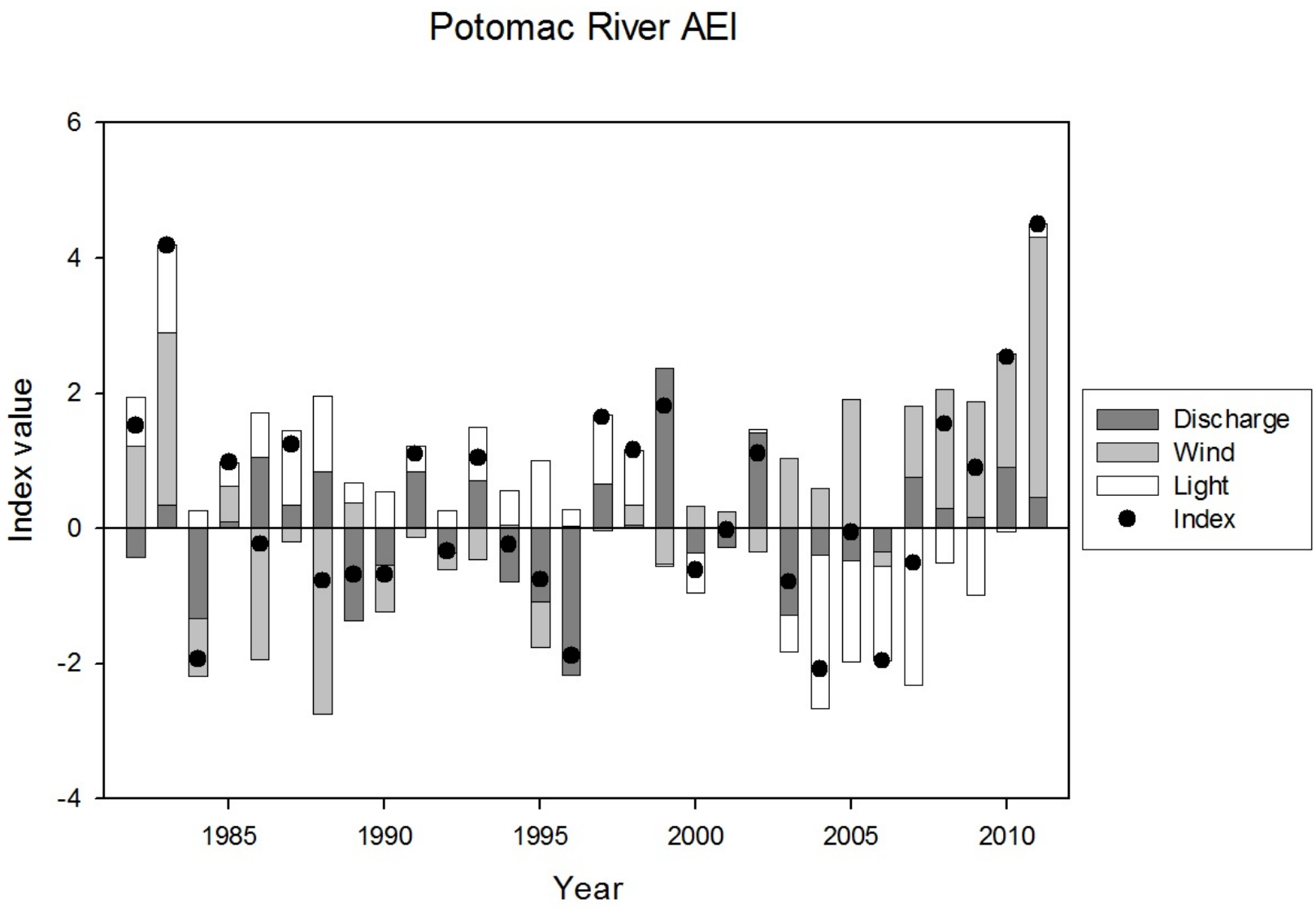


Figure 5. A breakdown of the contributions of each term to AEI values for each year for the tidal fresh Potomac River Estuary. The bars represent the summation of each term in the index and the point is the calculated AEI in that year.

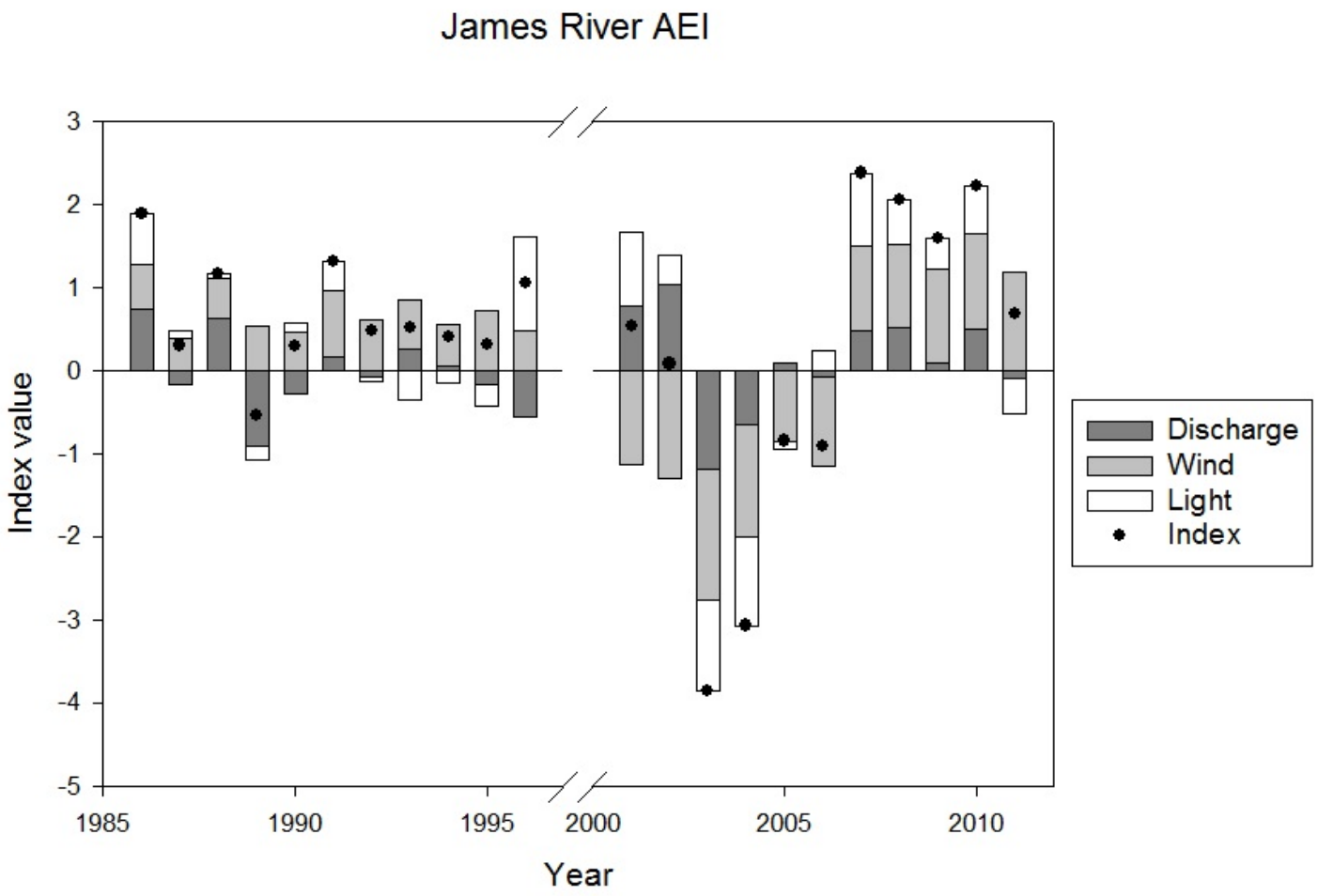


Figure 6. A breakdown of the contributions of each term to AEI values for each year for the tidal fresh James River Estuary. The bars represent the summation of each term in the index and the point is the calculated AEI in that year.

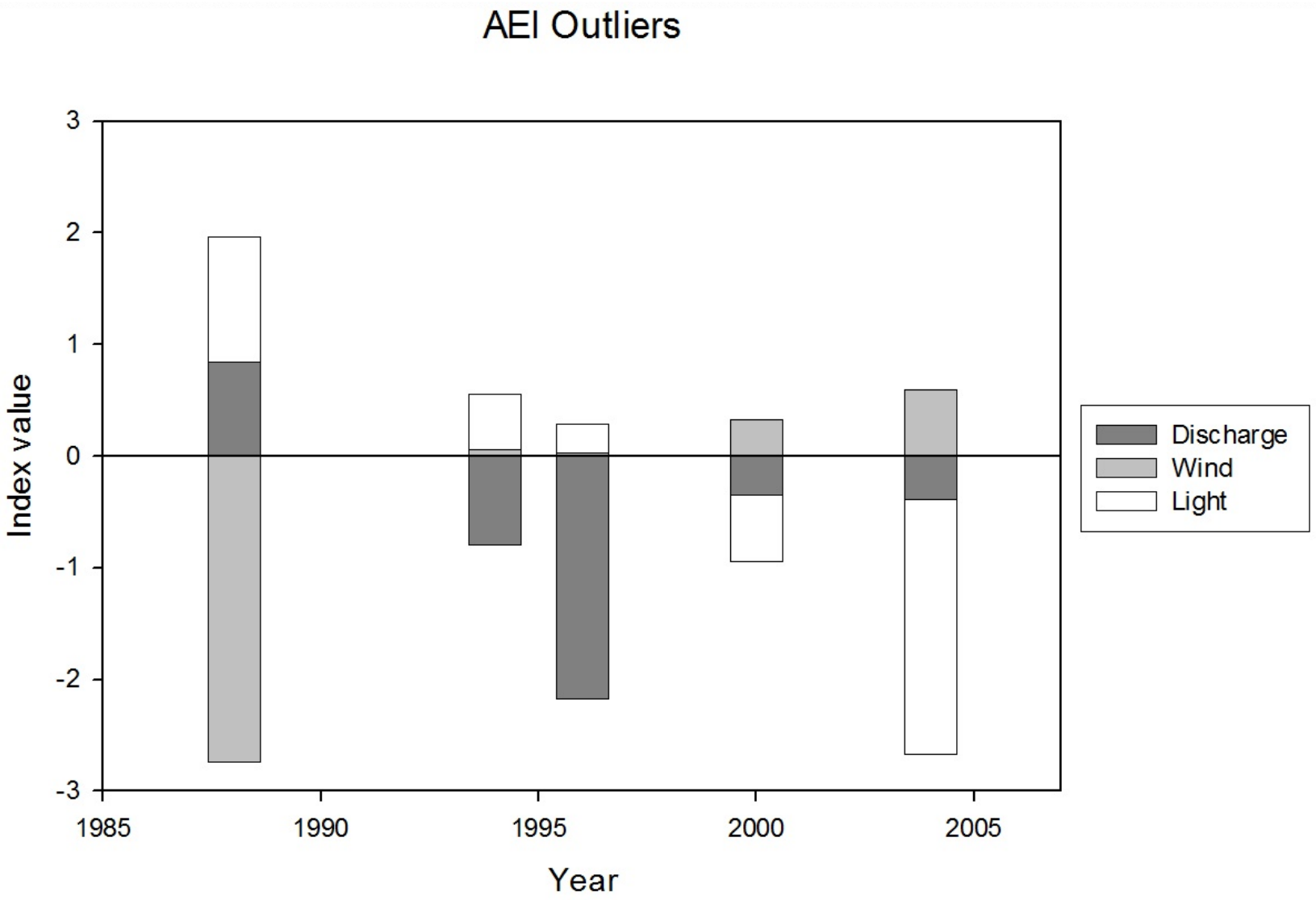


Figure 7. A breakdown of the contributions of each term in those years with a low AEI value but high *M. aeruginosa* abundances for the tidal fresh Potomac River Estuary.

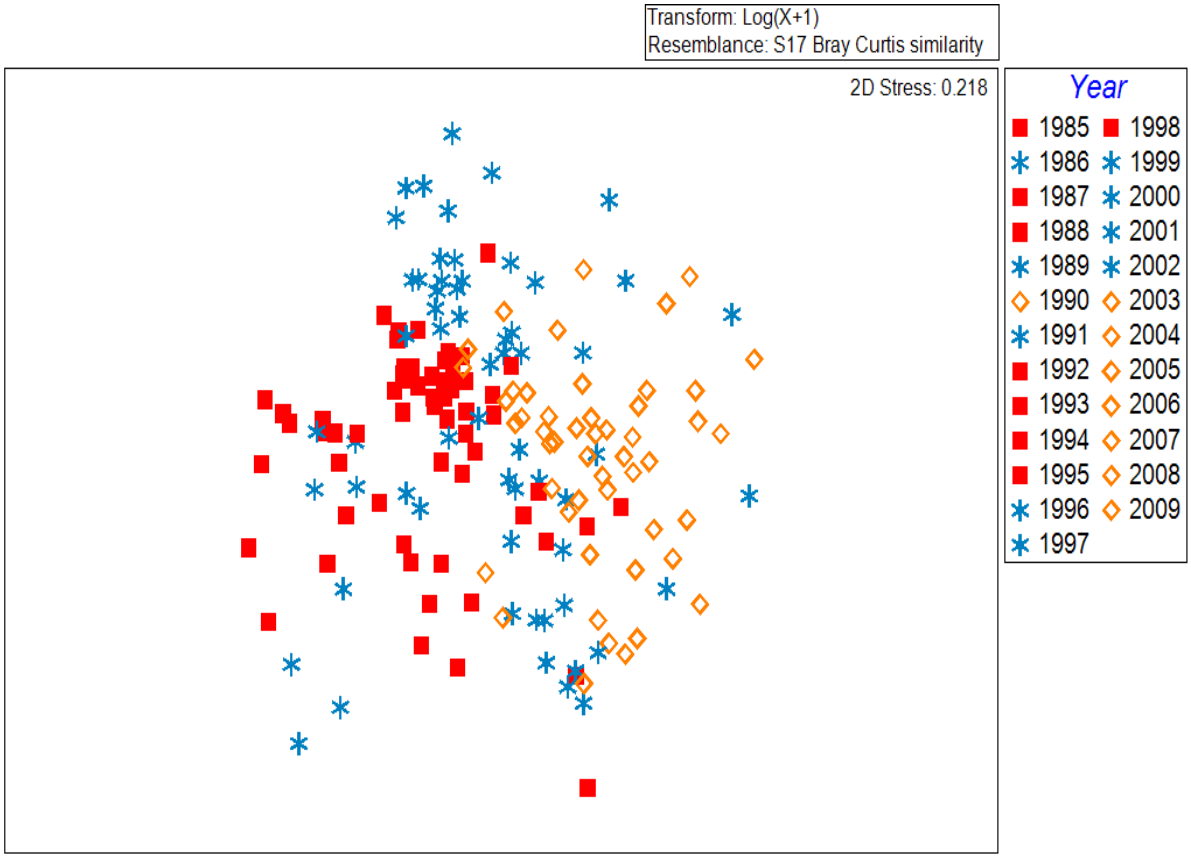


Figure 8. Non-metric multi-dimensional scaling plot (nMDS) of phytoplankton community assemblage. Years of high *M. aeruginosa* abundance are in red squares, mid-range *M. aeruginosa* abundance in blue stars and lower *M. aeruginosa* abundance years in orange diamonds. With high, mid and low abundances represented as the top, mid, and bottom third of those years with *M. aeruginosa* present.

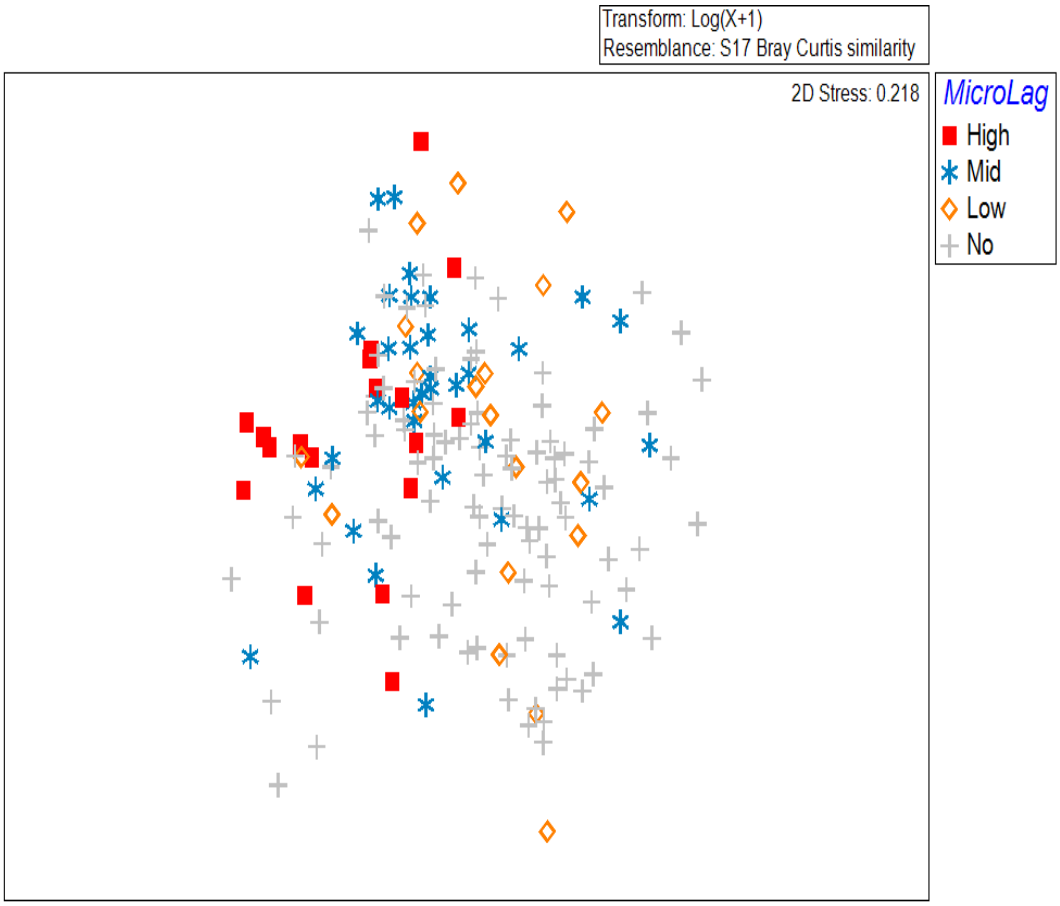


Figure 9. Non-metric multi-dimensional scaling (nMDS) plot of phytoplankton community assemblage representing a one-sampling-time step lag of *M. aeruginosa* abundance. Each point represents the community similarity one-sampling-time before high (red square), mid-range (blue stars), low (orange diamonds) or no (gray plus) *M. aeruginosa* abundance.

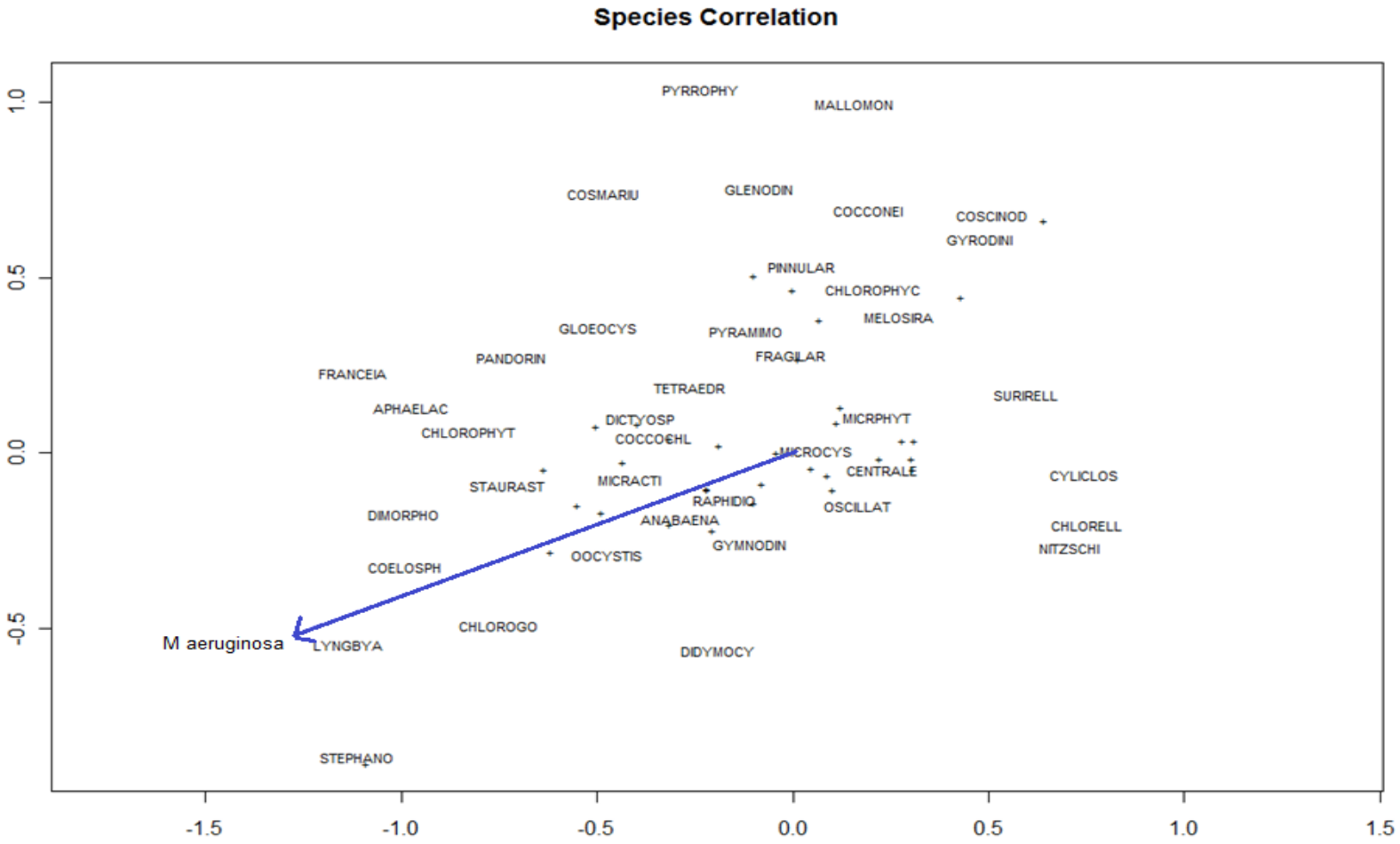


Figure 10. Redundancy analysis (RDA) of phytoplankton species as correlated with increasing *M. aeruginosa* abundances, represented by the blue arrow.

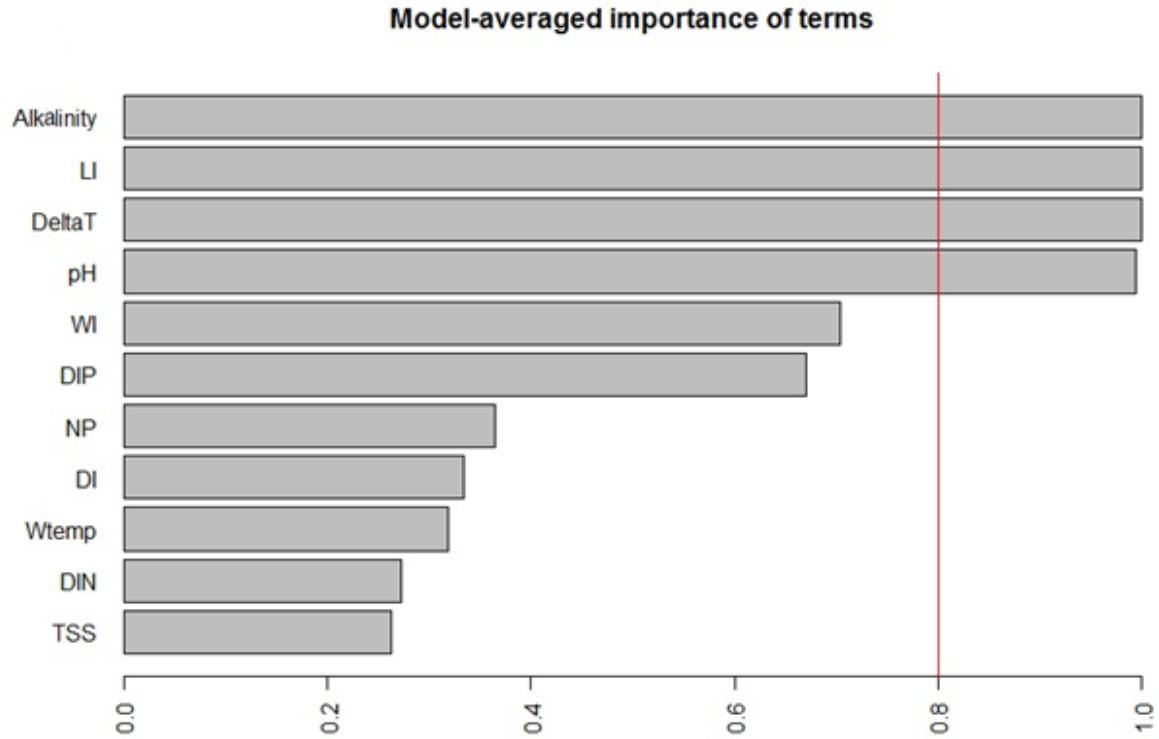


Figure 11. Plot of terms most influential in determining variance in reported *M. aeruginosa* abundances as determined by number of occurrence in top 100 models from all possible subset model selection and ranking.

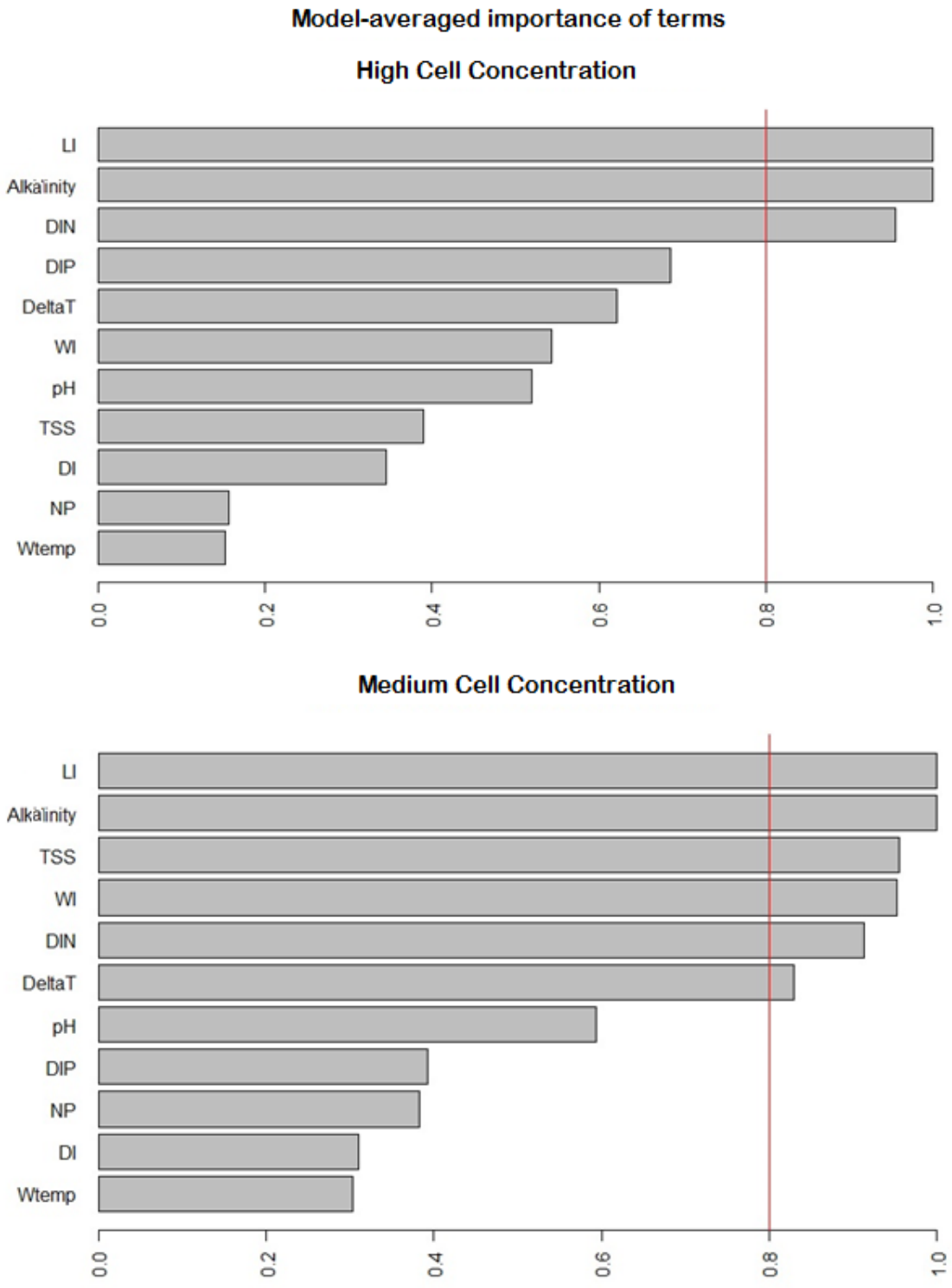


Figure 12. Model averaged importance of terms for binary logistic regression at high and medium cell concentration cutoffs as determined by number of occurrence in top 100 models from all possible subset model selection and ranking.

References

Anderson, C.R., M. R. P. Sapiano, M. B. K. Prasad, W. Long, PJ Tango, CW Brown, R. Murtugudde. 2010. Predicting potentially toxigenic Pseudo-nitzschia blooms in the Chesapeake Bay. Journal of Marine Systems, 83: 127-140.

Borja, A., D.M. Dauer R. Díaz , R.J. Llansó, I. Muxika , J.G. Rodríguez, L. Schaffner. 2008. Assessing estuarine benthic quality conditions in Chesapeake Bay: A comparison of three indices. Ecological indicators, 8: 395-403

Burnham, K. P., & Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer.

Calcagno, V. 2010. glmulti: GLM model selection and multimodel inference made easy. R package version 0.6-3.

Carvalho, L., C.A. Miller (nee Ferguson), E.M. Scott, G.A. Codd, P.S. Davies, A.N. Tyler. 2001. Cyanobacterial blooms: Statistical models describing risk factors for national-scale lake assessment and lake management. Science of The Total Environment, 409(24): 5353-5358

Gastrich, M.D. and C.E. Wazniak. 2002. A Brown Tide Bloom Index based on the potential harmful effects of the brown tide alga, Aureococcusano phagefferens. Aquatic Ecosystem Health & Management, 5(4):435–441

Imai, H, K Chang, M Kusaba, S Nakano. 2009. Temperature-dependent dominance of Microcystis (Cyanophyceae) species : M. aeuginosa and M wesenbergii. Journal of Plankton Research, 31(2): 171-178.

Jeong, K.S. F. Recknagel, G.J. Joo. Prediction and Elucidation of Population Dynamics of the Blue-green Algae Microcystis aeruginosa and the Diatom Stephanodiscus hantzschii in the Nakdong River-Reservoir System (South Korea) by a Recurrent Artificial Neural Network. Ecological Informatics (book) pg 255-273

Krogmann, D.W., R. Butalla, J. Sprinkle. 1986. Blooms of Cyanobacteria on the Potomac River. Plant Physiol. 80, 667-671

Kruk, C, VLM Huszar, E THM Peeters, S Bonilla, L Costa, M Lurling, CS Reynolds, M Scheffer. A morphological classification capturing functional variation in phytoplankton. Freshwater Biology, 55: 614-627.

Lacouture, R., J. Johnson, C. Buchanan, H. Marshall. 2006. Phytoplankton index of biotic integrity for Chesapeake Bay and its tidal tributaries. Estuaries and Coasts, 29(4), 598–616.

Lewitus, A.J., D.L. White, R.GTymowski, M.E. Geesey, S.N Ymel , and P.A. Noble. 2005. Adapting the CHEMTAX Taxonomic Composition Method for Assessing Phytoplankton in Southeastern U.S. Estuaries. Estuaries. 28(1): 160-172

Lewitus, A.J., R.A. Horner, D.A. Caron, E. Garcia-Mendoza, B.M. Hickey, M. Hunter, D.D. Huppert, R.M. Kudela, G.W. Langlois, J.L. Largier, E.J. Lessard, R. RaLonde, J.E. Rensel, P.G. Strutton, V.L. Trainer, J.F. Tweddle. 2012 Harmful algal blooms along the North American west coast region: History, trends, causes, and impacts. Harmful Algae, 19: 133-159

Lane, JQ, PT Raimondi, RM Kudela. 2009. Development of a logistic regression model for the prediction of toxigenic Pseudo-nitzschia blooms in Monterey Bay, California. Marine Ecology Progress series, 383: 37-51

Marshall, H. G., L. Burchardt, R.V. Lacouture. 2005. A review of phytoplankton composition within Chesapeake Bay and its tidal estuaries. Journal of plankton research. 27(11), 1083-1102

Marshall, H. G., R.V. Lacouture, C. Buchanan, J.M. Johnson. 2006. Phytoplankton assemblages associated with water quality and salinity regions in Chesapeake Bay, USA. Estuarine, Coastal and Shelf Science, 69(1-2), 10–18.

Paerl, H.W., R.S. Fulton 3rd, P.H.Moisander, J. Dyble. 2001. Harmful Freshwater algal blooms, with an emphasis on cyanobacteria. Scientific World Journal. 1:76-113.

Pinto, R., J. Patrício, A. Baeta, B.D. Fath, J.M. Neto, J.C. Marques. 2009. Review and evaluation of estuarine biotic indices to assess benthic condition. Ecological indicators, 9: 1-25.

Recknagel F., M French, P Harkonen, K Yabunaka. 1997. Artificial neural network approach for modelling and prediction of algal blooms. Ecological Modelling, 96(1-3): 11-28

R Development Core Team. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing 3-900051-07-0; 2011.URL http://www.R-project.org/.

Rost, AL, CH Fritsen, CJ Davis. 2011. Distribution of freshwater diatoms Didymosphenia geminate in steams in the Sierra Nevada, USA, in relation to water chemistry and bedrock geology. Hydrobiologia, 655: 157-167

Sellner, KG, G.J. Douchette G.J. Kirkpatrick. 2003. Harmful algal blooms: causes, impacts, and detection. Journal of industrial microbiological biotechnology, 30: 383-406

Stumpf RP, T.T. Wynne, D.B. Baker, G.L. Fahnenstiel. 2012. Interannual Variability of Cyanobacterial Blooms in Lake Erie. PLoS ONE 7(8): e42444.doi:10.1371/journal.pone.0042444

Sullivan, MP. 1987.Hydrometeorological data and its usefulness in the study of algae blooms in the Potomac River. Department of Environmental Programs: Metropolitan Washington Council of Governments.

Wei, B., N. Sugiura, T. Maekawa. Use of artificial neural network in the prediction of algal blooms. Water Research 35(8): 2022-2028

Wicks, R.J., P.G. Thiel. 1990. Environmental factors affecting the production of peptide toxins in floating scums of the cyanobacterium Microcystis aeruginosa in a hypertrophic African reservoir. Environmental Science & Technology 24,1413–1418.

Williams M., B.Longstaff, C. Buchanan, R.Llansód, W. Dennison. 2009. Development and evaluation of a spatially-explicit index of Chesapeake Bay health. Marine pollution Bulletin. 59: 14- 25

Wynne, T.T., R.P. Stumpf, M.C. Tomlinson, D.J. Schwab, G.Y. Watabayashi, J.D. Christensen. 2001. Estimating cyanobacterial bloom transport by coupling remotely sensed imagery and a hydrodynamic model. Ecological Applications, 21(7), 2709–2721

Wynne T.T, R. P. Stumpf, M.C. Tomlinson, J.Dyble. 2010. Characterizing a cyanobacterial bloom in western Lake Erie using satellite imagery and meteorological data. Limnology and Oceanography, 55(5), 2025–2036.

Chapter 2: Long term trends in phytoplankton phenology and diversity in the Potomac River Estuary

INTRODUCTION

Coastal marine ecosystems provide vital ecological and socio-economic services and are at risk due to climate change (Harley et al. 2006; Worm et al. 2006). Plankton monitoring has been proposed as a sentinel to identify future changes in marine ecosystems due to phytoplankton's high sensitivity to environmental perturbations, and are thus used in the assessment of ecological conditions (Hays et al. 2005; Paerl et al. 2006). Not only are phytoplankton sensitive to environmental change, but functional diversity in phytoplankton populations is a primary driver of chemical and biological dynamics, therefore serving as a link between climate forcing and indirect impacts on aquatic biogeochemistry (Cloern and Jassby 2010; Cloern and Dufford 2005).

Phytoplankton blooms are important seasonal features in aquatic environments because of their impact on water quality (hypoxia, nutrient cycling) and food supply for consumer organisms (Hjermann et al. 2007; Smayda 1997; Winder and Cloern 2010). Much of the phytoplankton variability in the open ocean is generated by annual cycles of solar radiation and atmospheric heat input (Sverdrup 1953; Cushing 1959). In contrast, phytoplankton variability in estuaries is generated by many additional processes (Cloern 1996), often with multiple responses evidenced from similar environmental forcing. For example, pulses of freshwater flow can both remove phytoplankton from a system via advection (de Madariaga et al. 1992), or promote phytoplankton growth by delivering

land-derived nutrients (Paerl et al. 2009). The potential for detecting ecological responses to climate change therefore varies by location, and depends on the relative importance of many ecological drivers (Winder and Cloern 2010).

Estuaries are also typically more susceptible to human impacts than other marine ecosystems because of the close interaction between activities on land and adjacent estuarine receiving waters. While estuaries are normally very productive systems, there is still evidence of nutrient limitation (Nixon 1995), where increased productivity can result from large inputs of nutrients from agricultural and municipal wastewater sources (Cloern and Jassby 2008). While there has been a long history of research examining the effects of nutrients on coastal receiving waters, recent studies have highlighted the need to examine how these alterations interact with anthropogenic climate change (Duarte et al 2009).

Both phytoplankton growth and loss rates can be affected by climate change operating at global and regional scales. For example, atmospheric heat waves promote surface blooms in nutrient-rich estuaries by establishing strong thermal stratification (Cloern et al. 2005), and seasonal wind mixing triggers blooms in nutrient-poor bays by mixing high-nutrient bottom waters to the surface (Iverson et al. 1974). Changes in estuarine hydrodynamics may result from new patterns of river discharge quantity and timing, as well as fluctuations in sea level and other ocean properties (Najjar 2010). Short-term episodic climatic perturbations, such as heat-waves or floods, can lead to abrupt phytoplankton changes (Cloern et al. 2005; Wetz and Paerl 2008). Whereas long-term climate variability may induce alterations in the magnitude and position of phytoplankton blooms (McQuatters-Gollop et al. 2007; Borkman et al. 2009), and

changes in their composition and phenology or dates of occurrence within an annual cycle (Leterme et al. 2005; Wiltshire et al. 2008). It is expected that influences of climatic change on phytoplankton act both directly by affecting the availability of resources, and indirectly by altering the balance of metabolic processes in interacting populations (Winder et al 2012). It is worthwhile to ask whether we can extract signals of climate change from phytoplankton observations in estuaries despite all of these interacting processes. Nixon et al. (2009) presented successful efforts in this regard for Narragansett Bay, Rhode Island. Expanding and developing these approaches in other estuaries provides another indicator of global change to complement phenological networks on land (Menzel et al. 2006), Continuous Plankton Recorder surveys of the North Sea (Edwards & Richardson 2004), and satellite measures of chl-a across the global ocean (Behrenfeld et al. 2006) that have provided valuable response data to climate drivers.

The Potomac River estuary, one of the major tributaries of the Chesapeake Bay, is an example of an impacted estuary with a variety of watershed-based pressures, such as urban/-suburban land use, livestock production, and row crop agricultural non-point sources of pollution. The Potomac is characterized by a strong salinity gradient along its length; from tidal freshwater conditions in Washington, DC, through oligohaline and mesohaline conditions where it meets the Chesapeake Bay. This sub-estuary of the Chesapeake Bay has been the subject of water quality research for over one hundred years, including the more recent efforts of the Chesapeake Bay Program (CBP) that coordinates monitoring and restoration efforts in Maryland and Virginia. Through this monitoring program, it is possible to retrospectively analyze phytoplankton phenology

and community and use resulting patterns to forecast future changes due to climate change. Most research and analysis of phytoplankton community dynamics and phenology has been done in the main stem of Chesapeake Bay, with less focus on its tributaries (Marshall et al 2005, Marshall et al 2006, Marshall and Nesius 1996).

Phytoplankton production, species composition, and phenology in the main stem of the Chesapeake Bay generally follow predictable seasonal patterns dictated primarily by river discharge, light, and temperature (Malone et al., 1996; Marshall and Nesius, 1996), with the annual spring bloom timing and extent governed by Susquehanna river discharge (Harding, 1994). During the relatively low-light, cold, and turbulent winter/early spring period, centric diatoms dominate the flora (Sellner, 1987). As nutrients delivered by the spring flow are exhausted from the surface waters and the spring diatom bloom sinks, remineralization and wind-induced mixing replenishes summer surface waters to support primary productivity. Summer blooms are typically more diverse and comprised of a mixture of picoplankton, small centric diatoms, and flagellates (Malone et al., 1986; Malone, 1992).

While this pattern typifies the main stem of the Chesapeake Bay, the Potomac River estuary is the largest tributary by surface area and is subject to its own environmental forcing and phytoplankton community dynamics. An emphasis on understanding the drivers of species composition is important for the Potomac because of the large environmental gradient that gives rise to multiple phytoplankton communities comprised of very different taxa. In a global context, Winder et al. (2012) report possible responses to climate change of phytoplankton communities that include advances in the bloom timing of functional plankton groups, changes in bloom magnitudes during

seasonal peaks in abundance, and overarching differences in total phytoplankton biomass dependent on species composition. The diverse community assemblages in the Potomac, structured according to spatial, temporal, and climatic forcings, offers an opportunity to explore these responses at the ecosystem scale.

Najjar et al. (2010) suggested that climate change has the potential to alter Chesapeake Bay phytoplankton dynamics through changes in precipitation and the intensity and frequency of storms. High winter and spring precipitation will likely increase spring nutrient loading, leading to higher planktonic production. This contrasts with the summer period, where future conditions may be more favorable for drought, interspersed with sporadic, high intensity storms and discharge events. Should intense storms pass over the area more frequently in the future, wind mixing of the water column could act to provide pulses of nutrients to surface waters. Higher temperatures will likely result in an earlier spring bloom, which could cause trophic de-coupling or changes to the spatial distributions of particular taxa. Higher temperatures can also affect metabolic processes. For example, it has been shown that planktonic respiration increases with temperature more rapidly than photosynthesis (Lomas et al. 2002, Harris and Brush 2012).

Climate change has been shown to alter phytoplankton species composition and diversity (Anderson et al 2002). The relationship between primary production and diversity is an active area of research in ecology. The classic work of Tilman et al (1997) would suggest that a community with higher diversity will have higher primary production. Tilman et al. (1997) experimentally varied plant species diversity, functional diversity, and functional composition in grassland plots. Resulting analyses identified

functional composition and functional diversity as the principal explanatory factors for the response variable of plant productivity. The diversity-productivity relationship was also supported by mathematical models looking at competitive interactions in communities containing various numbers of randomly chosen species (Tilman et al. 1997). When examining the diversity-productivity relationship, other researchers have concluded that a unimodel relationship is also common, with an increase in production at lower diversities followed by a decrease in production at very high diversities (Waide et al 1999, Grace 1999). In a comprehensive review Mittelbach et al. (2001) found that this hump-shaped relationship was also prevalent in aquatic systems, with maximum production at intermediate diversities. Tillman et al. (1997) also discusses differences in changes in species diversity versus functional diversity and the impacts they have on ecosystem processes, concluding that functional diversity can often be a sufficient measure for impact on ecosystem processes.

There are many consequences of the changes to phytoplankton dynamics that make it important to study the phenology and community composition of microbial populations in the past and into the future. One crucial element is the possible change of phytoplankton bloom timing, which could cause a separation of growth and grazing. During bloom periods, food limitation for grazers is suppressed. Because of this, phytoplankton seasonal patterns have important implications for the timing and efficiency of secondary production and, therefore, production at higher trophic levels (Cloern and Jassby 2008). There is also the question of what will happen over the next few years as large, legally mandated reduction in nitrogen inputs further change nutrient dynamics in the estuarine ecosystems subject to Total Maximum Daily Load regulations. Most studies

into phytoplankton dynamics and phenology use chlorophyll a (chl-a) as a proxy for biomass because it is a good predictor of primary production and the quantity of food available to consumers. However, the efficiency of production in food webs varies strongly with the species contributing to the chl-a stock (Cloern 1996). Therefore it is important to incorporate diversity changes into interpretation and understanding of phytoplankton phenological changes.

The broad research goal of understanding the relationships among biodiversity, phenology, and climate change can also be scaled to local and regional challenges specific to estuaries such as the tidal waters of the Potomac. Information on long term trends in phytoplankton is crucial to separate anthropogenic influences from natural variability and to identify the driving forces underlying phytoplankton variability. This enables a higher predictive ability and a more rational management of aquatic ecosystems (Paerl 2006; Smetacek and Cloern 2008; Borkman et al. 2009). Using the Potomac as a case study for investigating the changes in phytoplankton diversity and seasonal patterns also provides an example of how phenological studies in aquatic systems may begin to consider the effects of climate change on changing community composition.

The Potomac has been included in long term phytoplankton sampling and environmental monitoring records that have been coordinated by the Chesapeake Bay Program since 1985. To explore the effects of climate change on phytoplankton community dynamics, I targeted three main objectives. First, I documented changes in phytoplankton diversity and its relationship to primary production over time in an attempt to determine whether these aquatic microbial communities have a unimodal relationship as suggested by others (Mittelbach 2010), and whether this relationship has changed over

time. My second objective was to reveal the phenology of the phytoplankton community by tracking chl-a as an indicator of biomass and timing of bloom formation. Finally, I attempted to link diversity and phenology changes with regional and global climate change indicators to suggest a framework for determining how climate induced change to biodiversity might influence ecosystem primary productivity.

MATERIALS AND METHODS

Long Term Datasets

Data from the CBP Maryland Phytoplankton and Water Quality monitoring program collected between 1985 and 2011 for three sites in the Potomac were used to address the three objectives of this study. These three stations are located in the three major salinity zones of the estuary and are designated in Figure 1; a tidal fresh (TF) station (up to 0.5), a river-estuarine transition (RET) oligohaline station (0.5–5.0), and a lower estuary (LE) mesohaline station (.5.0–18). Phytoplankton identifications and abundances, as well as corresponding water quality data, were downloaded from the CBP data hub (http://www.chesapeakebay.net/data) for the three stations. Water quality data used in these analyses are summarized in Table 1. Chl-a values were reported as water column average to account for subsurface and mid depth phytoplankton abundances. Phytoplankton species identifications and abundances are reported through the CBP at the lowest possible taxonomic designation when possible. These taxonomic designations are often split into size classes to aid in conversion to biomass and carbon content estimates, resulting in duplicate entries related to size. For diversity analysis, the

phytoplankton community composition was compacted so that each taxonomic species had only one record per sampling time and location to eliminate error in counting a species twice. These phytoplankton were then assigned a taxonomic functional group according to those functional group designations used by the CBP Maryland monitoring program.

Three proxies of climate were used including, the climate index of North Atlantic Oscillation (NAO), precipitation patterns in the form of river discharge to the Potomac River estuary, and observed winter weather patterns delineated into wet and dry years. Data for monthly mean NAO index values were downloaded from the NOAA National Weather Service Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). The USGS National Water Information System (http://water.usgs.gov/) measures nutrients and computes average river discharge for the Potomac River at Little Falls, MD (Figure 1). Observed winter weather patterns have previously shown an impact on summer estuarine ecosystem responses for the Chesapeake Bay (Kimmel et al 2009). I used these same winter weather patterns as a large scale climate indicator variable for this study. Influential weather patterns were split into anomalous wet and dry climatic patterns and I used those pattern delineations for these analyses.

Diversity and Productivity Over Time

Analysis of the CBP time series was used to document trends in productivity and diversity at each station, as well as seasonal changes in community composition and functional groups. The primary production and chl-a long term data set was detrended by

removing seasonal patterns to look at the underlying trend in these variables over time. These analyses were performed with R version 3.0.0 (R development Core Team, 2001) using the R stats package time series function. This function creates a time series object that is then analyzed for and removes seasonal patterns from the data providing extracted periodic (annual) pattern, loess-smoothed (locally weighted scatterplot smoothing) time series trend, and the residuals of trend from the analysis.

Due to changes in sampling frequency over the time period of phytoplankton and water quality monitoring, the data were standardized for time series analysis. In those months with two sampling events, an average value was used. The detrending approach requires that every time point be represented in the dataset, therefore I chose to assign those months with no sampling event as zero. In the data set, most missing time points occurred in the winter months where previous sampling reported very low chl-a and primary production measurements. There was also a period of two years in which these data were not collected and those time points were removed for interpretation. I then compared diversity to primary production and chl-a trends over time. Diversity in this study is represented by species richness and was detrended for seasonal pattern as described for primary production and chl-a.

I used non-metric multi-dimensional scaling (MDS), an ordination technique, to investigate seasonal trends in community composition for each site in the Potomac. A Bray-Curtis similarity matrix was constructed from species abundance data normalized with a log transformation at each sampling time (Yoshioka 2008). An nMDS graph was then prepared by plotting the similarity matrix in space with the best 2D and 3D representations to investigate similarity patterns among communities over time (Clarke

1993). I used nMDS again to compare community composition at each site across seasons. All analyses were conducted using the PRIMER-E multivariate statistics package.

To look at changes in functional group diversity between seasons and over time, I plotted a percent stacked bar of functional group composition in the spring and summer. Community composition for a representative month in spring and summer, chosen by nMDS of seasonal community similarity, was used to show these diversity changes. Linear regression analyses were performed to evaluate the possibility of predicting primary production from available water quality data and diversity. Linear regressions were performed with R version 3.0.0 (R development Core Team, 2001) using the R stats package fitting linear models function. This function fits a linear model to those specified explanatory variables which are then eliminated based on significance until a best fit model is chosen.

Phytoplankton Phenology

The long term data set was analyzed to determine the months in which the maximum and minimum primary production (ugC/hour) and chl-a events occurred to look at phenological changes in these events. Depth integrated chl-a levels were used for the phenology analysis. I also examined primary production normalized to chl-a concentrations, generally defines as an assimilation ratio (ugC/hour/chl-a). Contour maps of each parameter over time were used to visualize changes in magnitude of maximum primary production and chl-a events. I also looked at phytoplankton taxonomic functional group phenology to expand this phenological treatment beyond an exclusive

focus on chl-a as a biomass proxy. The month of occurrence of the maximum and minimum abundance for each functional group was determined for each site. Again, contour maps of functional group abundance were analyzed to look at changes in magnitude of maximum abundance events.

Links to Climate Change

To explore the links between diversity and phenology changes and climate change, I used a combination of non-metric multi-dimensional scaling (MDS) and redundancy analysis (RDA) which show patterns in community composition and related environmental factors respectively. With Canoco (version 4.5), I used redundancy analysis to look at phytoplankton functional groups and the relationships to environmental variables at each sample site. RDA is a form of constrained ordination that examines how much of the variation in one set of variables explains the variation in another set of variables. It is the multivariate analog of simple linear regression (Leps and Smilauer 2003).

Additionally, I looked at three climate proxies and their impact on phytoplankton phenology and diversity. These three factors were chosen from the literature as representations of climate change that have been shown to effect system processes in the Chesapeake Bay. Lee et al. (2013) found that late winter spring NAO index values had a large impact on hypoxia in the Chesapeake Bay. I compared previous phenology observations for primary production, chl-a, and diversity from the Potomac to the reported NAO index. I also used nMDS plots to look for relationships between community composition and precipitation patterns. I created an nMDS ordination plot

for representative months in spring and summer for each salinity zone. These plots were then keyed so that different precipitation patterns were colored the same to look for similarities in community associated with precipitation. This color coordination was performed on river discharge as reported at Little Falls, MD for the same month as phytoplankton observations, as well as on a one and two month time lag to account for variations in distance to each sampling point from Little Falls. Color coordination was also performed for characteristic "wet or dry" years as reported by Kimmel et al (2009) for anomalous winter precipitation patterns shown to affect ecosystem responses in Chesapeake Bay.

RESULTS

In the Potomac River estuary, the three salinity regimes showed different patterns in changes in chl-a, primary production, and functional group composition over time. Figure 2 shows the time series analysis for primary production and chl-a at the TF station. At the TF station there was a decrease in both chl-a and primary production between 2007 and 2011. The large decrease in recent years was not as apparent at the RET or LE site (Figure 3 and 4). The TF station showed much more variability than the other two stations with the RET station being the most consistent over time. Chl-a and diversity trends over time pulled from the full time series analyses are shown in Figure 5, while primary production and diversity are represented in Figure 6. The RET station showed no relationship between diversity and chl-a or primary production.

Through the nMDS ordination plots differing patterns of community composition and seasonality in the Potomac River estuary were apparent in each estuarine zone. At the TF station, the summer community was distinctly different from the spring community (Figure 7). The winter months were not clearly associated with each other or spring and summer communities. The RET station, as seen in Figure 8, showed tight, separate summer and spring community groupings. The RET spring community was not as correlated as the TF spring community and showed a change in the timing of this community appearance. At the LE station, December through May showed 70 percent similarity, suggesting that winter species composition was more similar to the spring bloom community here than in other parts of the estuary (Figure 9). June through November assemblages also grouped together, with greater similarity between fall and summer communities than in the rest of the estuary. These assemblage groupings coincide with stratification patterns for the Chesapeake Bay, correlating in time with the start of thermal stratification in late spring and the breakdown of stratification in fall. Throughout the estuary the spring bloom community composition remained highly correlated with itself, although there was a shift in timing from March and April in the fresh waters to April and May in the lower, more saline estuary.

There were also shifts in functional group dominance within these highly similar seasonal patterns. While the major functional groups were present in each season, there were year to year differences in relative abundances of each. The TF station, Figure 10, displayed a shift from a mixture of diatoms and cyanophytes in the spring to a cyanophyte dominated community in the summer months. The spring community in the RET station as seen in Figure 11 showed much more functional diversity with a slight

dominance of diatoms. This higher diversity was maintained in the summer community, but with more cyanophyte dominance. Figure 12 shows the LE station functional groups had the most variable spring community with different species dominating in different years. The summer, however, showed a higher abundance of cyanophytes and diatoms.

Linear regression analyses were performed to look at the possibility of predicting primary production from available water quality data and diversity. The top two models for each station are reported in Table 2. Station TF has a strong relationship with environmental variables such as water temperature, secchi depth, and salinity. In the RET zone, these factors are also important but nutrients also play a role in determining primary production levels. Finally, the LE primary production responds to environmental forcing as well as diversity. Following the linear regression, phytoplankton diversity had very little impact on primary production, only appearing as a significant explanatory variable in the second mode, and only at the LE station.

The timing of maximum primary production and chl-a events was consistent for the tidal fresh Potomac, with a peak in the summer months (Figure 13). Minimum chl-a and primary production most often occurred from December through March. The magnitude of the chl-a levels, seen in the contour plot Figure 14, varied over time. Most chl-a peeks occurred in summer months (Figure 13) but the magnitude of these often varied (Figure 14). The RET station, Figure 15, showed a strong summer peak in chl-a and production, although there was a greater amount of variation around these peaks. High magnitudes of chl-a occurred in the spring and again in the summer with the summer magnitudes slightly higher (Figure 16). The timing of the minimum was more evenly distributed over the winter months for this part of the Potomac. The long term

phytoplankton monitoring RET station was not representative of all chl-a dynamics in the part of the river. Further down river from this station the timing of maximum and minimum chl-a shows a different pattern with high chl-a occurring in winter and early spring and low chl-a occurring in late fall (Figure 17). The RET station did not show the same consistent periods of high chl-a as found in the TF, but did have more variation in the timing of maximum and minimum events. The LE station was the most variable in terms of timing of surface maximum and minimum events (Figure 18). However, the LE station often experiences stratification and a subsurface chl-a maximum and depth integrated chl-a is important to consider.

In this case, the timing of maximum chl-a occurred in the early spring and the minimum most occurred in late summer and fall months (Figure 19). The timing of the minimum chl-a events also showed a possible cyclical pattern, with shifts from winter to late spring timing. There was a large mismatch between the peaks in chlorophyll and production, with times of maximum production having moderate chl-a levels. There were instances where peak production occurred in conjunction with the spring bloom events, but there were a similar number of peaks of maximum production in the summer months without corresponding maximum chl-a levels. To investigate this mismatch I looked at the assimilation ratio for the LE station. Times of low production per chl-a are observed in winter and early spring while high production per chl-a are observed in late spring and summer (Figure 20). Around the LE station, maximum chl-a levels were most often associated with the timing of the main stem spring bloom in April and May with a few observed maximum peaks in summer levels. This station showed a very large number of minimum production events in March directly before the seasonal spring

diatom bloom. Throughout the data set, minimum chl-a levels at the LE station, showed no discernible seasonal pattern (Figure 21).

To more specifically look at phenological changes of phytoplankton function groups over time, I determined the timing of the maximum and minimum abundance events and plotted contour maps for abundance data over the time period of the dataset. Two functional groups displayed a change over time in their phenology at two stations in the Potomac River estuary. In the TF station both cryptophytes and diatoms showed an earlier appearance of maximum abundances (Figure 22). Only cryptophytes showed a change in phenology at the LE station with an earlier appearance of maximum abundance (Figure 23). There was no change in phenology at the RET station with regards to minimum and maximum abundance.

Redundancy analysis was used to look at the relationship between phytoplankton functional groups and different environmental variables. A varying number of functional groups were present across the estuarine gradient (Table 3). Redundancy analysis showed chlorophytes were negatively correlated with water temperature in TF station (Figure 24) and with salinity in both the RET and LE stations (Figure 25, 26). Silicoflagellates only appeared in the LE station, Figure 24, and were correlated with salinity. Those functional groups that were highly correlated with water temperature tended to be associated with the spring bloom in the TF station, Figure 23, and with the summer community in the LE station.

Comparisons between the NAO and phenology observations for chl-a and primary production showed no relationship in the TF or RET stations. There was a negative

relationship between timing of minimum chl-a events and the NAO in the LE station (Figure 27). nMDS ordination plots showed no difference in community composition related to river discharge at any site at any time. There was also no relationship seen for community similarity based on winter climate pattern.

DISCUSSION

This study attempted to link diversity, productivity and phenology to environmental and climate forcing. In other ecosystems, it has been shown that diversity and primary production are correlated (Tilman et al. 1997, Mittelbach et al. 2001). However, for the Potomac River estuary, we did not see the expected relationship between increasing diversity and subsequent increases in primary production. The unimodal relationship between diversity and primary production often seen in other aquatic systems (Dodson et al. 2000, Guo & Berry 1998), with highest production at an intermediate diversity ranges, is also not apparent. However, this relationship has been found mainly on terrestrial ecosystems or for large macrofauna in aquatic systems. These types assemblages of organisms are very different than the sometimes extensively diverse phytoplankton community. Phytoplankton communities have a much larger species diversity than can be explained through ecological forcing. Hutchinson (1961) argued the paradox of having such high species diversity in one system given limited resources. This phenomenon implies the possibility of a threshold in diversity - where the diversity production relationship changes – that may not be a feature of other non-microbial assemblages.

Functional group diversity has also been used to describe a relationship with primary production in the place of species diversity (Tilman et al. 1997). However, in the Potomac this relationship is not explanatory because functional group richness remains steady through time. Because of these findings, the Potomac River estuary primary production may be controlled by other environmental factors that overshadow any impact diversity may have on production. A similar lack of correlation between diversity and productivity has also been reported in systems with confounding local and regional forcing (Cardinale et al 2004, Dodson et al 2000).

For the Potomac estuary, the gradient from a relatively small-in-volume and quick-in-flow, tidal fresh region, giving way to progressively larger, slower, and more saline water body has important implications for system processes and response to change. Like the work of Paerl (2009) describing the differing effects of nitrogen and phosphorus limitation along a similar freshwater to marine continuum, the Potomac river estuary is a crucial case study in understanding the impact of changing phytoplankton community, phenology and environmental drivers along a freshwater to marine environmental gradient. This study showed the tidal fresh Potomac exhibits a high connection to land-based forcing. Specifically, there has been a decrease in chl-a levels and primary production since 2007, most likely due to management strategies reducing nutrient loads to the river. This decrease can have dramatic effects on the system as a whole, as it represents a change in the phytoplankton community that can move through the food chain to affect higher trophic levels. A large influence of land-based environmental drivers is also promising for the future of environmental management of eutrophication in the fresh waters of the Potomac.

The lower Potomac estuary, however, is driven by more ocean and climate based forcing. Minimum chl-a phenology for this zone shows a strong relationship with the NAO. The NAO effects the strength and direction of westerly winds and storm tracks across the north eastern United States. When the index is high (NAO+), atmospheric pressure changes draw stronger south-westerly circulation with warmer associated wind and weather patterns. When the NAO index is low (NAO-), these winds are not present and colder northern weather patterns have a greater effect on the eastern seaboard. The large area and volume in this portion of the estuary provides a longer residence time, meaning that *in situ* hydrodynamics and biogeochemistry may have a greater influence on local system processes as opposed to watershed derived forcings. It follows that these lower estuarine waters should be the location to look for early signals of change within the system due to climate change. Changes in this area can have a large impact not only due to the stronger influence of climatic forcing but also because of its large volume and the effect on local ecosystem condition as a function of internal, possibly self-reinforcing dynamics.

While functional diversity does not play a role in primary production dynamics of the Potomac River estuary, the lack of an environmental gradient in diversity suggests that explanation for these documented changes should be looked for within the phytoplankton phenology, instead. Odum (1995) proposed a "maximum power principle" that describes self-organization of systems to maximize energy transformation. This concept of self-organization has been extensively cited as a structuring characteristic of ecosystems in both theoretical ecology and by community ecologists (eg. Weiher and Keddy 1999). However, few have empirically demonstrated the adaptation of ecosystems to maximize

production or other ecosystem goal functions based on changes in community assemblage. The changing phenology of functional groups in the Potomac provides a small piece of evidence that phytoplankton communities may be well adapted to self-organize in response to change.

While these changes may not impact the absolute magnitude of productivity in the Potomac and functional richness is maintained, proposed changes in successional timing and relative abundance of functional groups, due to climate change, could alter ecosystem processes through controls on secondary growth. Functional group change over time can have a large impact on the trophic ecology of aquatic systems, as some groups (cyanophytes and chlorphytes) are of poor nutritional quality, while others (diatoms and cryptophytes) can be of higher nutritional quality (Glibert et al. 2011). Dickman et al. (2008) found that these higher quality foods had the strongest effects on food chain efficiency. Transfer efficiency can also be effected by nutrient loading, where increases in nutrient loading results in larger phytoplankton taxa and shorter average food chains and there is a critical point above which further increases may lead to reductions in trophic efficiency (Kemp et al. 2001). While no overall change in chl-a phenology was found in this study, certain functional groups of phytoplankton did show a change over the data set, with two groups exhibiting changed phenology in the TF station and one in the LE station. These functional groups highlight the importance of looking beyond strict chl-a measurement as a proxy for whole system change. Using only chl-a as a proxy to examine phenology changes in the aquatic system limits the ability to assess ecosystem change in its early stages, when it is most important and influential.

My results suggest that the tidal fresh Potomac phytoplankton community is more impacted and controlled by land based factors. This portion of the estuary displayed very regular timing of maximum chl-a and primary production seasonal events. With a consistent chl-a phenology any disturbances to the system resulting in changes to this timing would have a larger effect than a more variable region. While showing no overall change in chl-a phenology, diatoms and cryptophytes did show a temporal constriction and shift of the timing of maximum abundance events to earlier in the year. These two high-quality foods now occur at different times than past years and therefore provide less opportunity for transfer of energy to higher trophic levels in this normally steady system.

Changes in phenology in the lower estuary, being more impacted by oceanic and climatic forcing, will have different impacts on ecosystem functioning than in the tidal fresh waters. The LE station displayed a large disconnect between the phenology of maximum production and maximum chl-a levels. This disconnect can alter interpretations of other studies that use chl-a as a proxy for community change and transfer to higher trophic levels. When looking at the timing of the chlorophyll-normalized production rates, a different relationship is apparent that points to changes in the assimilation efficiency of the phytoplankton cells contributing to the measured production. Because of the relationship between size and per chlorophyll-a concentrations (Niklas 1994), these changes could be due to shifting size spectra of the microbial community for this region of the Potomac. Changing environmental conditions can also alter size structure of the phytoplankton community as well as individual cells (Finkel et al 2010). However, many factors influence chl-a levels per cell and production rates and more research is necessary to determine if the observed disconnect between chl-

a levels and production rates is due to changes in size structure or other factors (Sathyendranath et al 2009; Felip & Catalan 2000).

Additionally, the lower estuary showed changes in the phenology of cryptophytes, here this functional group is also appearing earlier in the year. Changes in the trophic structure of the phytoplankton can have diverse effects on the aquatic system. Some studies suggest that mixotrophic flagellates, such as cryptophyes, can represent a link between the microbial loop and the micro and mesozooplankton however, on the basis of food size spectra such microzooplankton could function as competitors rather than as food for copepods (Stocker 2008, Ptacnik 2004). This diversion of energy through microzooplankton before entering the mesozooplakton can impact trophic efficiency. With a higher similarity and influence of oceanic and climatic forcing the main stem Chesapeake Bay may also be experiencing a functional group phenological shift, creating a large impact on Bay wide trophic efficiency transfer.

A key component of management decisions looks into the future and uses our understanding of estuarine processes to evaluate how potential changes could affect the system. This study provides a comprehensive look at phytoplankton diversity, phenology, and reaction to climate change along a freshwater to mesohaline continuum for the Potomac River estuary that can be applied to similar estuarine systems. I have found that some phytoplankton functional groups displayed changes in phenology that have not yet manifested into larger ecosystem processes, however, these changes should be monitored for more wide spread change.

Table 1. List of water quality and climate variables used in statistical and ordination analysis for the Potomac River Estuary.

Environmental Parameter	Unit	Abbreviations
Chlorophyll a	ug/L	Chl-a
Primary Production	ug/L/hour	Carbon
Salinity	SU	Salinity
Dissolved oxygen	mg/L	DO
Water temperature	Deg C	Wtemp
Total dissolved phosphorus	mg/L	TDP
Total dissolved nitrogen	mg/L	TDN
North Atlantic oscillation		NAO
River discharge	m^3/sec	Discharge
Winter weather pattern		Winter

Table 2. Results of regression analysis for linear regression predicting primary production from water quality parameters and diversity. Top two significant models shown with model fit, significance, and percent variance explained (adj r^2).

Station	**Model fit BIC**	**Significance p<0.10**	**% Variance explained Adj r^2**
TF	-62	All significant	0.306
Production = -0.216year + 0.236wtemp + 3.374secchi			
TF	-60	All significant	0.310
Production = -0.216year + 0.237wtemp + 3.266secchi + 2.232salinity			
RET	-44	All significant	0.243
Production = 0.580salinity +0.346wtemp +2.814TDN			
RET	-42	All significant	0.252
Production = 0.618salinity +0.490wtemp +2.881TDN +0.645DO			
LE	-18	All significant	0.167
Production = -0.200year - 2.295secchi - 2.666TDN + 0.136wtemp			
LE	-17	All significant	0.177
Production = -0.198year - 2.491secchi - 2.855TDN +0.140wtemp +0.215Diversity			

Table 3. List of taxonomic functional groups found in the Potomac River Estuary, their reference number and station where each group has been reported.

Reference Number	Taxonomic group	Stations Found
1	Diatom	TF, RET, and LE
2	Dinoflagellete	TF, RET, and LE
4	Silicoflagellate	LE
5	Cyanophyte	TF, RET, and LE
6	Euglenophyte	TF, RET, and LE
7	Chlorophyte	TF, RET, and LE
8	Cryptophyte	TF, RET, and LE
10	Chrysophyte	TF, RET, and LE
11	Haptophyte	LE
12	Parsinophyte	RET, and LE
13	Choaroflagellete	TF, and LE
14	Flagellate protozoa	TF, RET, and LE

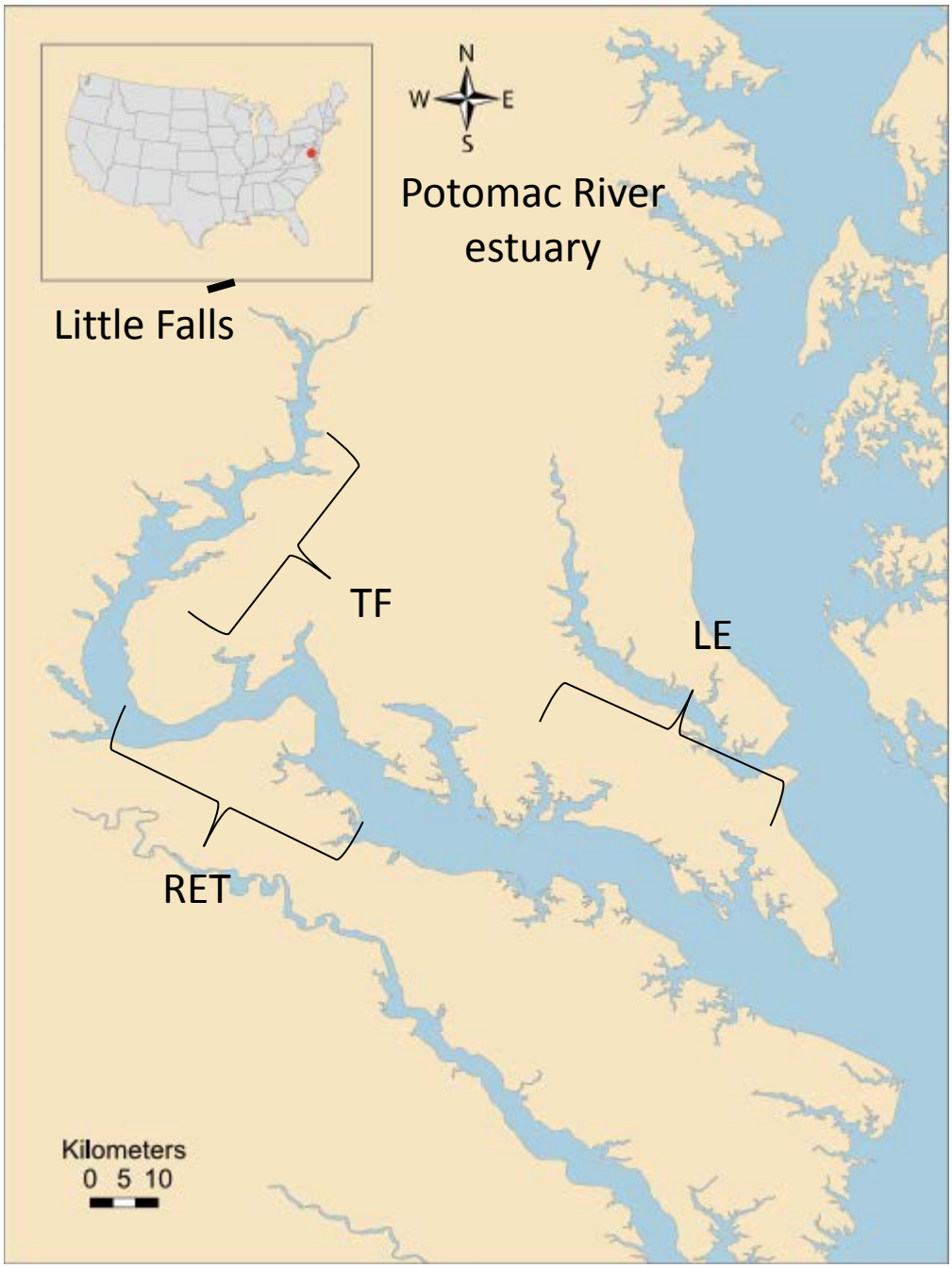


Figure 1. Potomac River estuary with salinity zones marked, TF, RET, and LE. River discharge measurement site Little Falls shown.

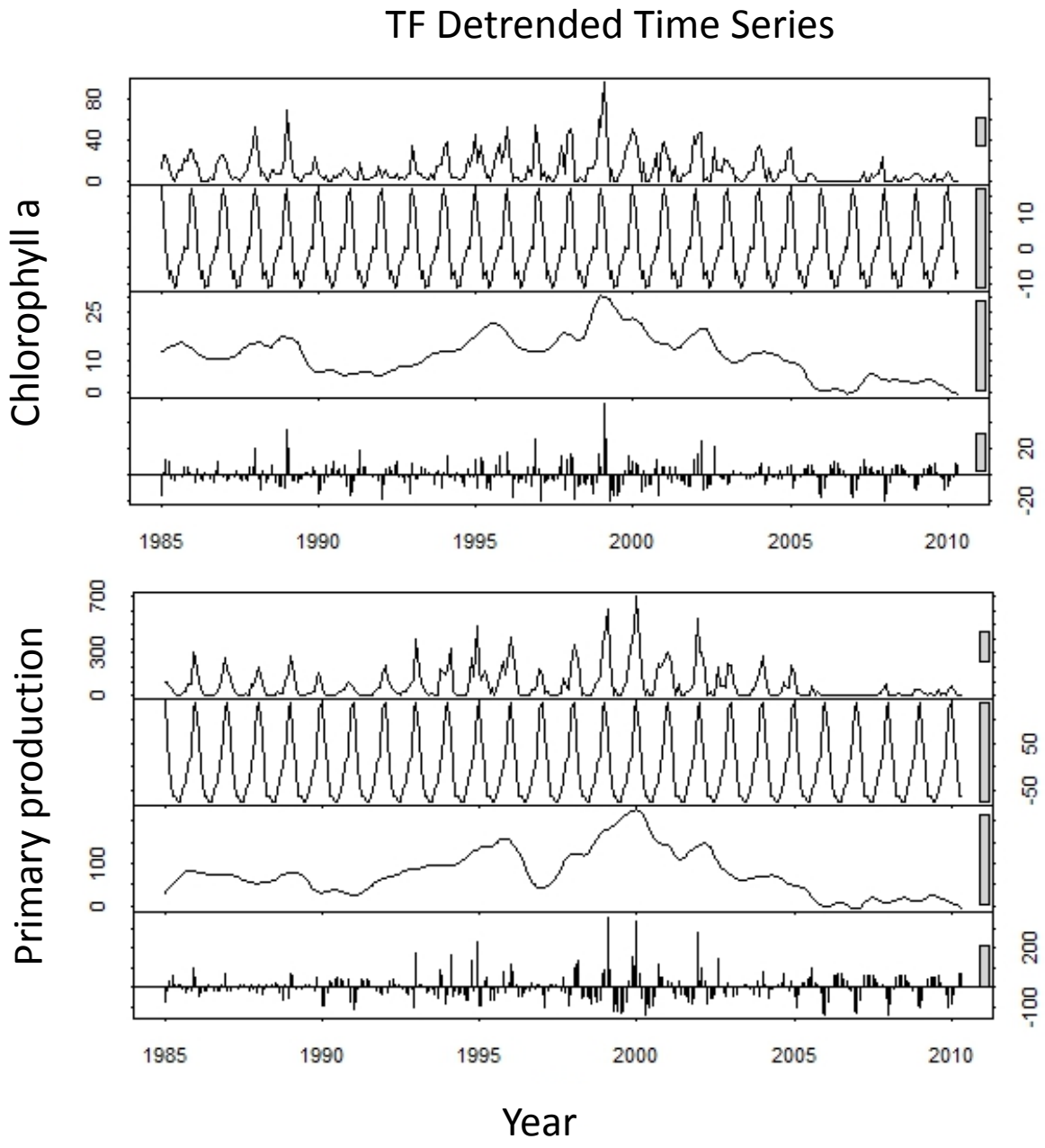


Figure 2. TF station chl-a and primary production time series over the years 1985-2011. From top to bottom, the graph shows raw time series, extracted periodic (annual) pattern, loess-smoothed time series trend, and the residuals of trend.

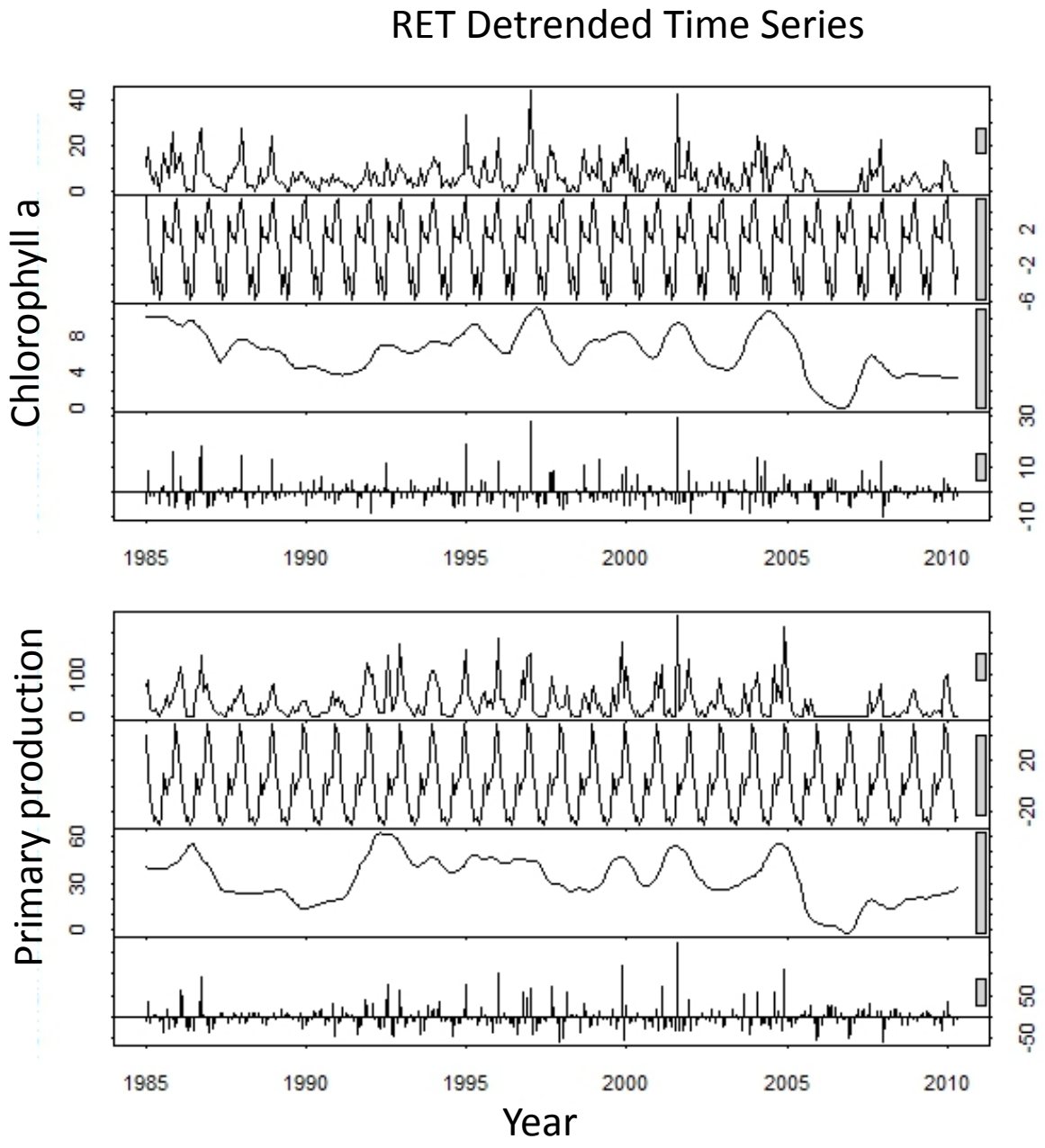


Figure 3. RET station chl-a and primary production time series over the years 1985-2011. From top to bottom, the graph shows raw time series, extracted periodic (annual) pattern, loess-smoothed time series trend, and the residuals of trend.

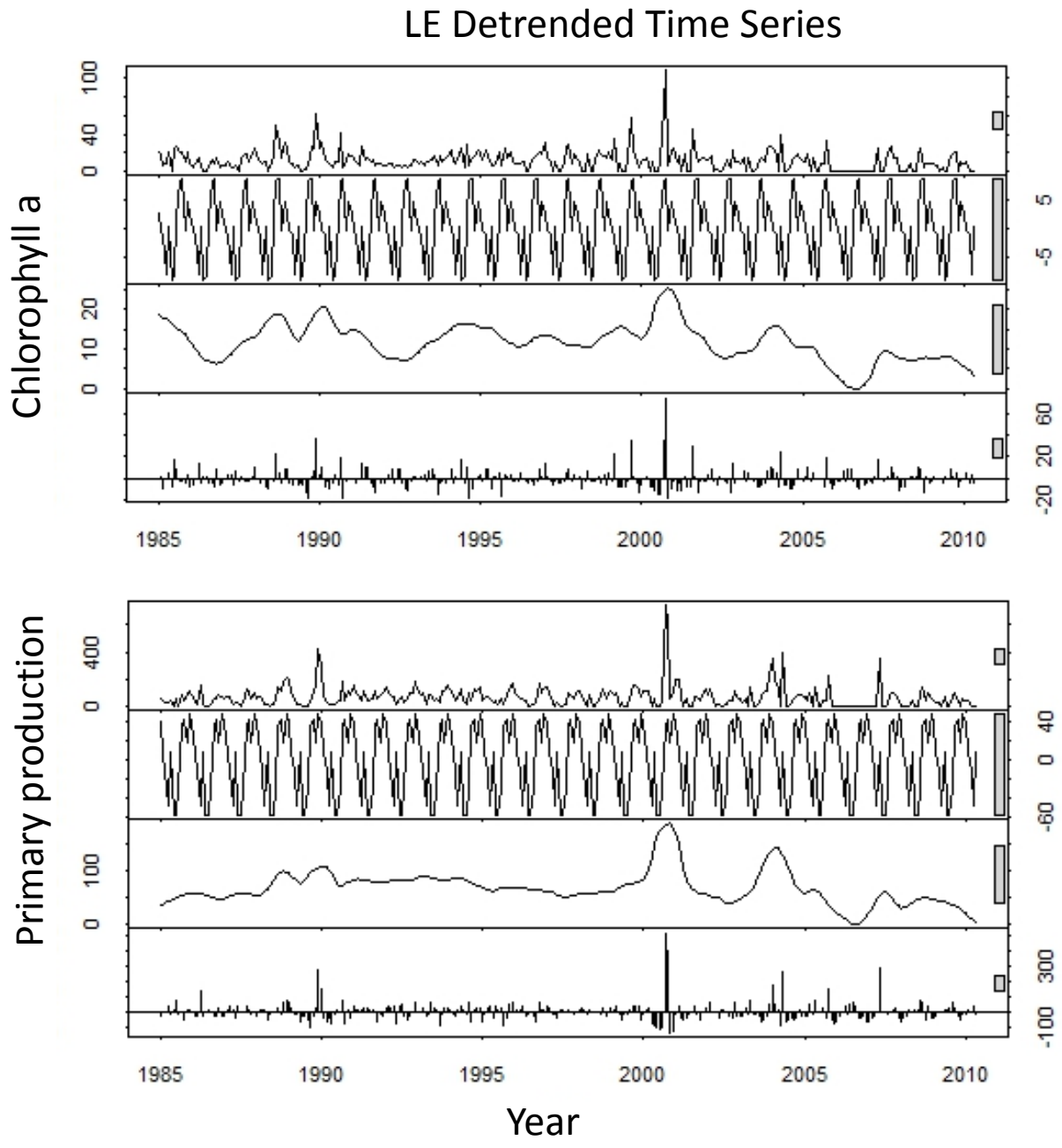


Figure 4. LE station chl-a and primary production time series analysis over the years 1985-2011. From top to bottom, the graph shows raw time series, extracted periodic (annual) pattern, loess-smoothed time series trend, and the residuals of trend.

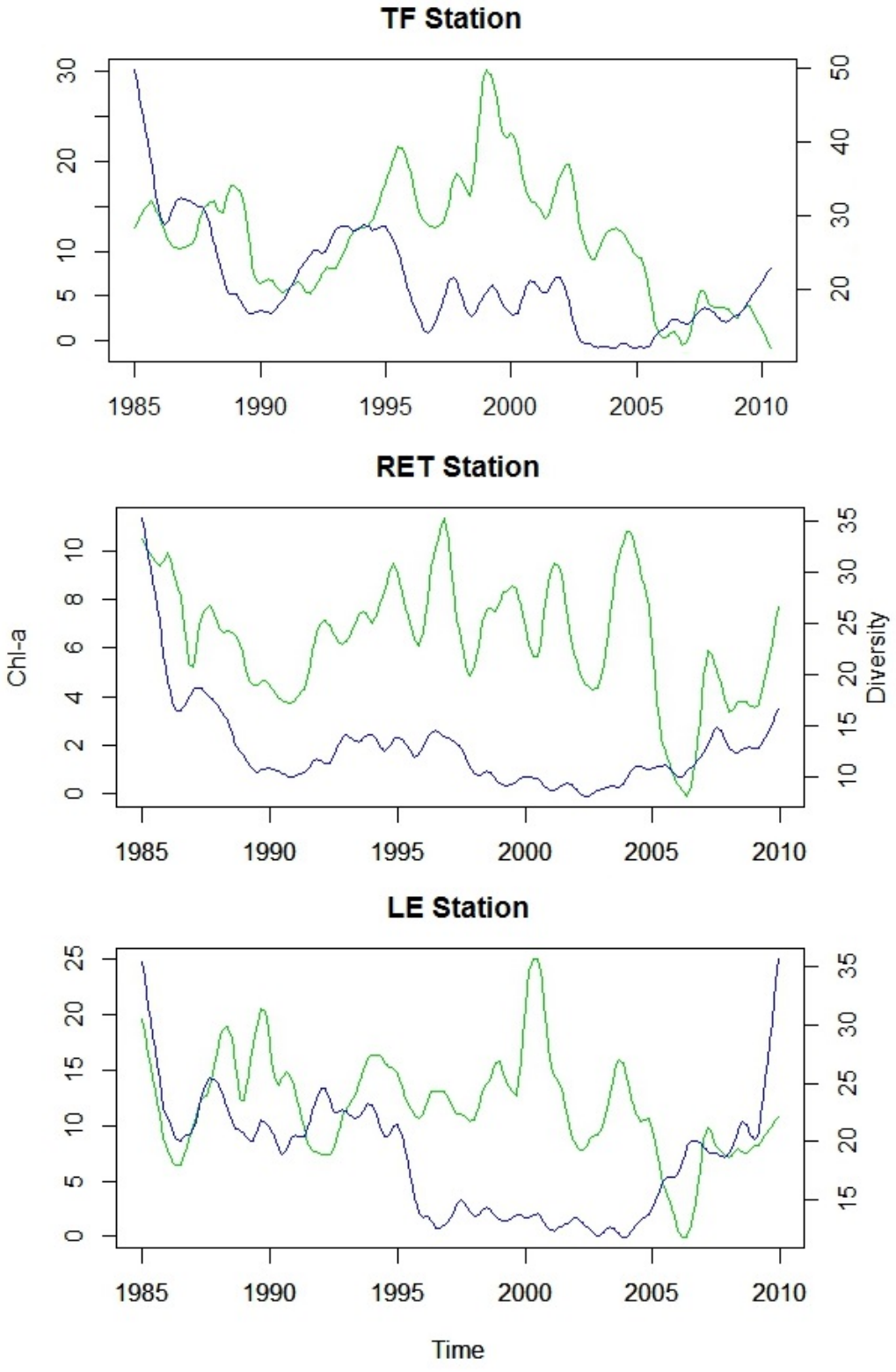


Figure 5. Chl-a (green line) and diversity (blue line) loess-smoothed trend over time for stations, TF, RET, and LE respectively from time series analysis.

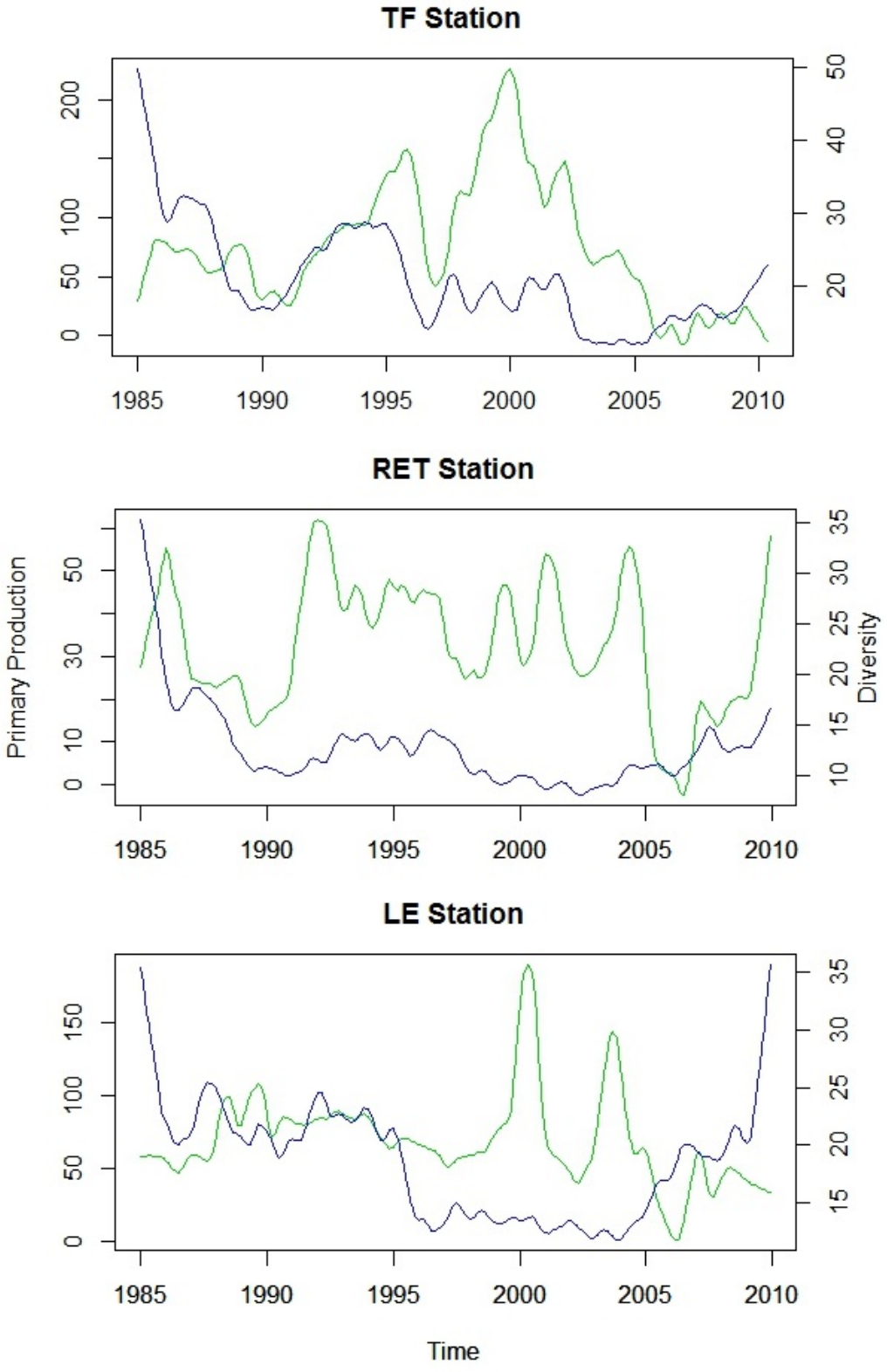


Figure 6. Primary production (green line) and diversity (blue line) loess-smoothed trend over time for stations, TF, RET, and LE respectively from time series analysis.

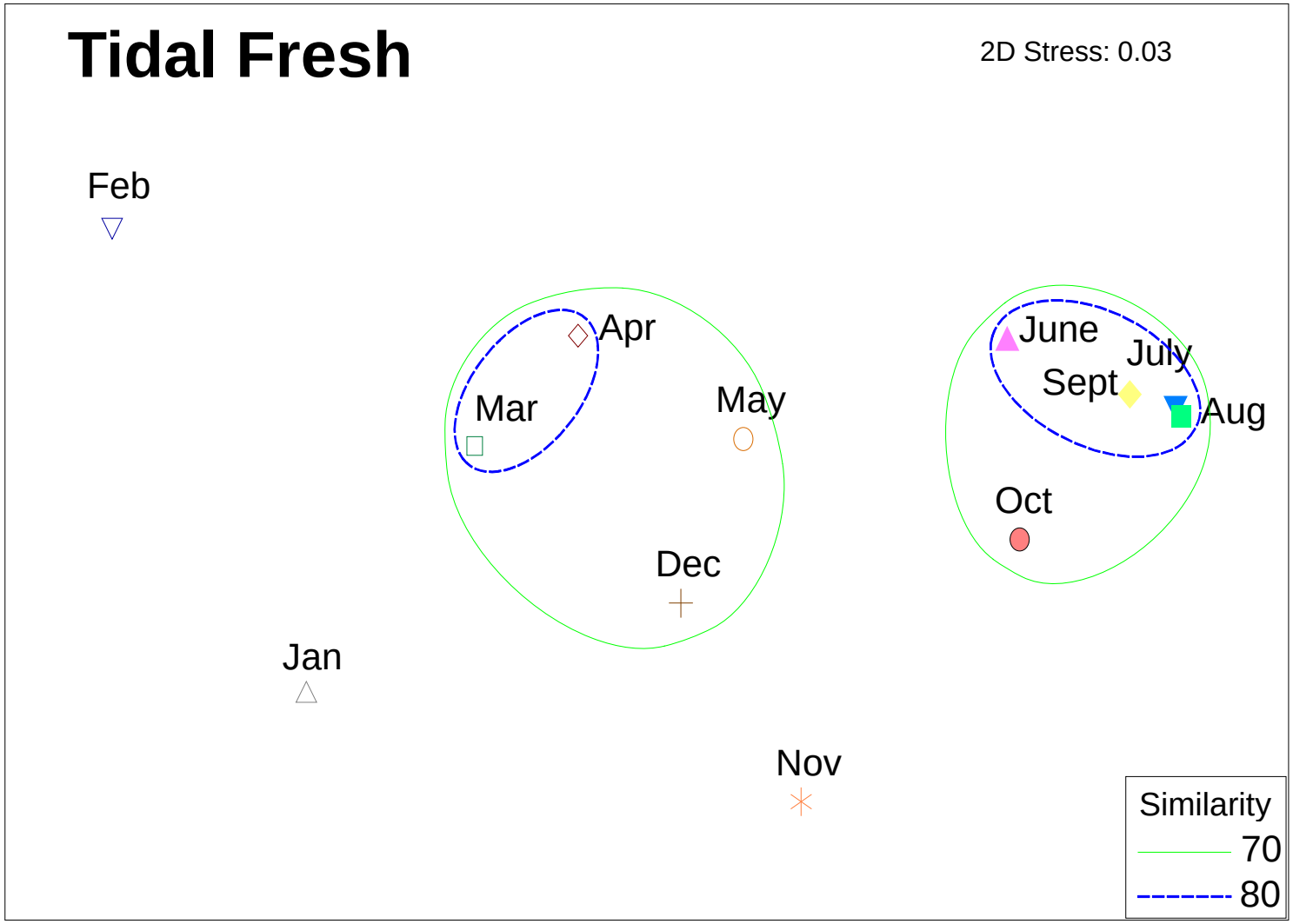


Figure 7. nMDS of average monthly community composition for TF station of the Potomac River. Colored lines represent percent similarity of community composition.

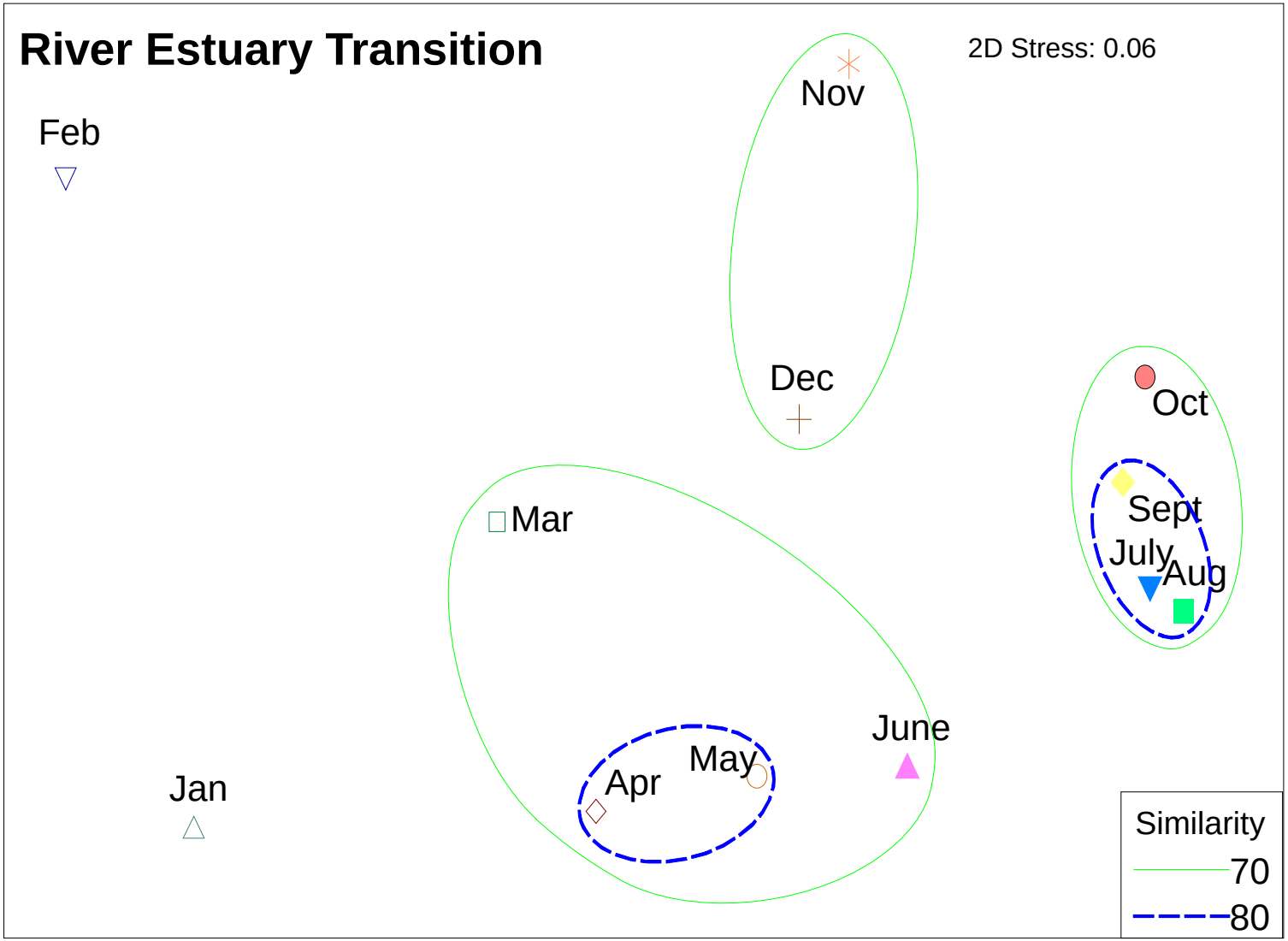


Figure 8. nMDS of average monthly community composition for RET station of the Potomac River. Colored lines represent percent similarity of community composition.

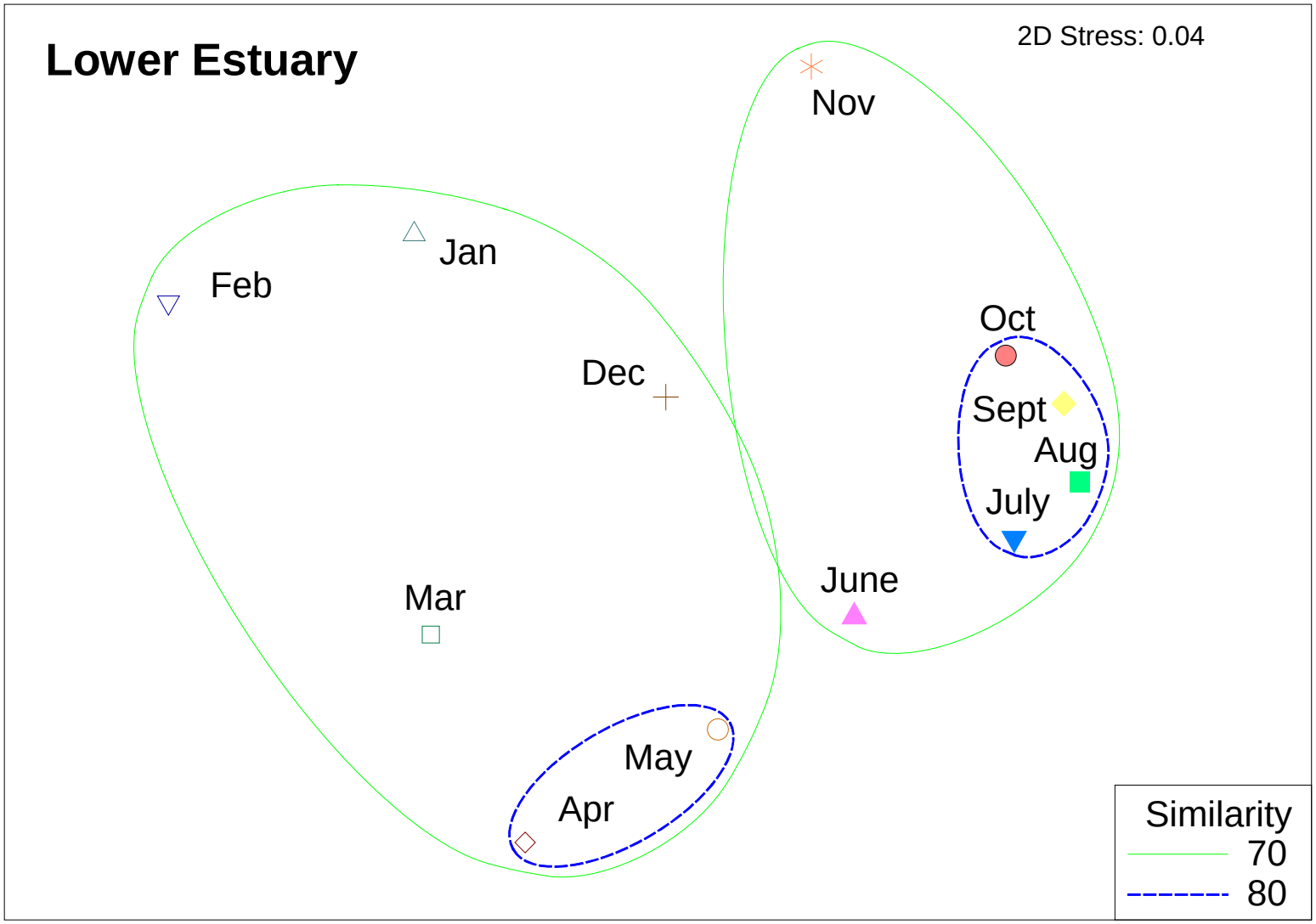


Figure 9. nMDS of average monthly community composition for LE station of the Potomac River. Colored lines represent percent similarity of community composition.

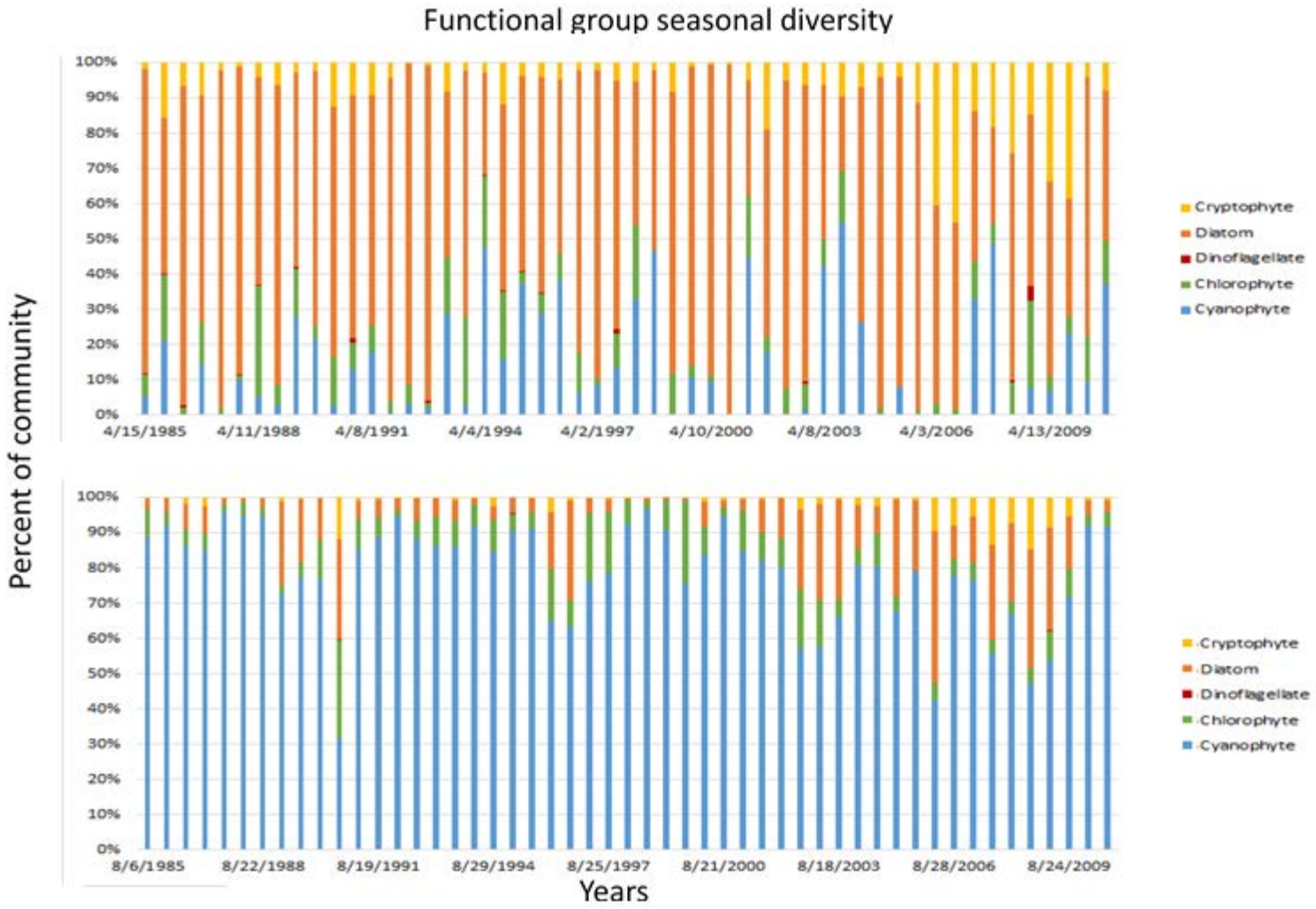


Figure 10. Stacked bar plot of functional group diversity for the TF station in representative spring month in the top (April) and summer month on bottom (August) over the years 1985-2011.

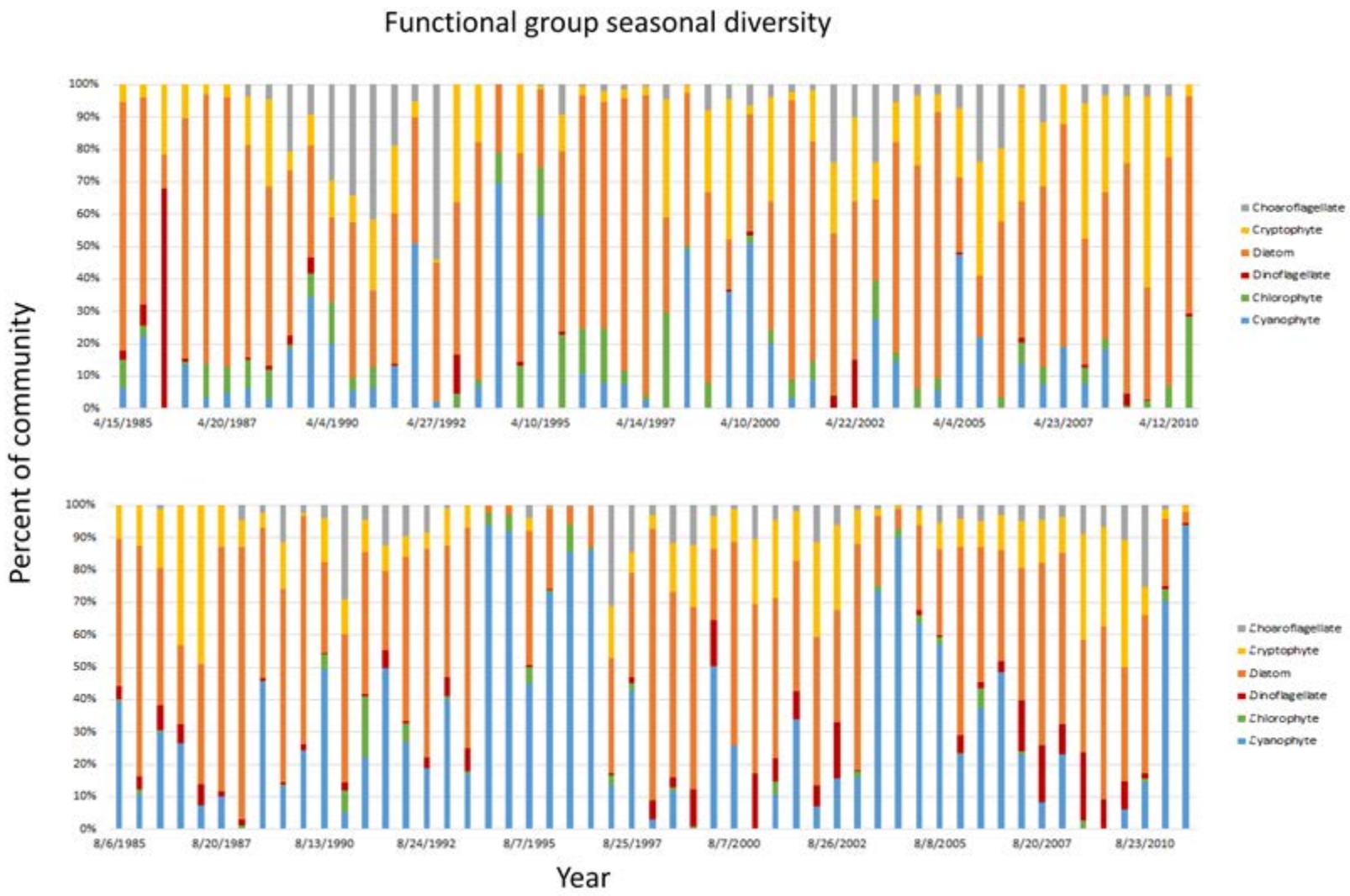


Figure 11. Stacked bar plot of functional group diversity for the RET station in representative spring month in the top (April) and summer month on bottom (August) over the years 1985-2011.

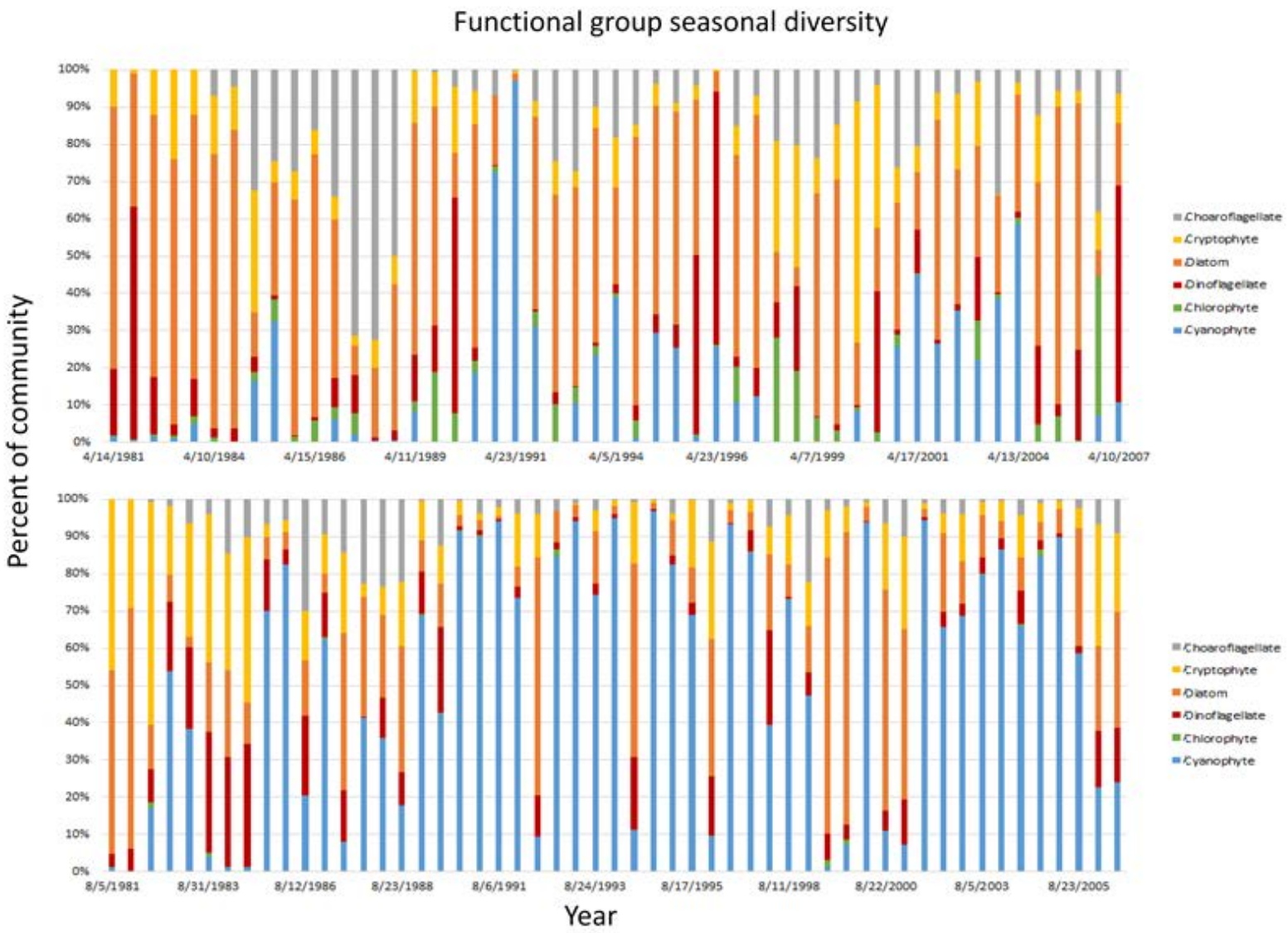


Figure 12. Stacked bar plot of functional group diversity for the LE station in representative spring month on top (April) and summer month on bottom (August) over the years 1985-2011.

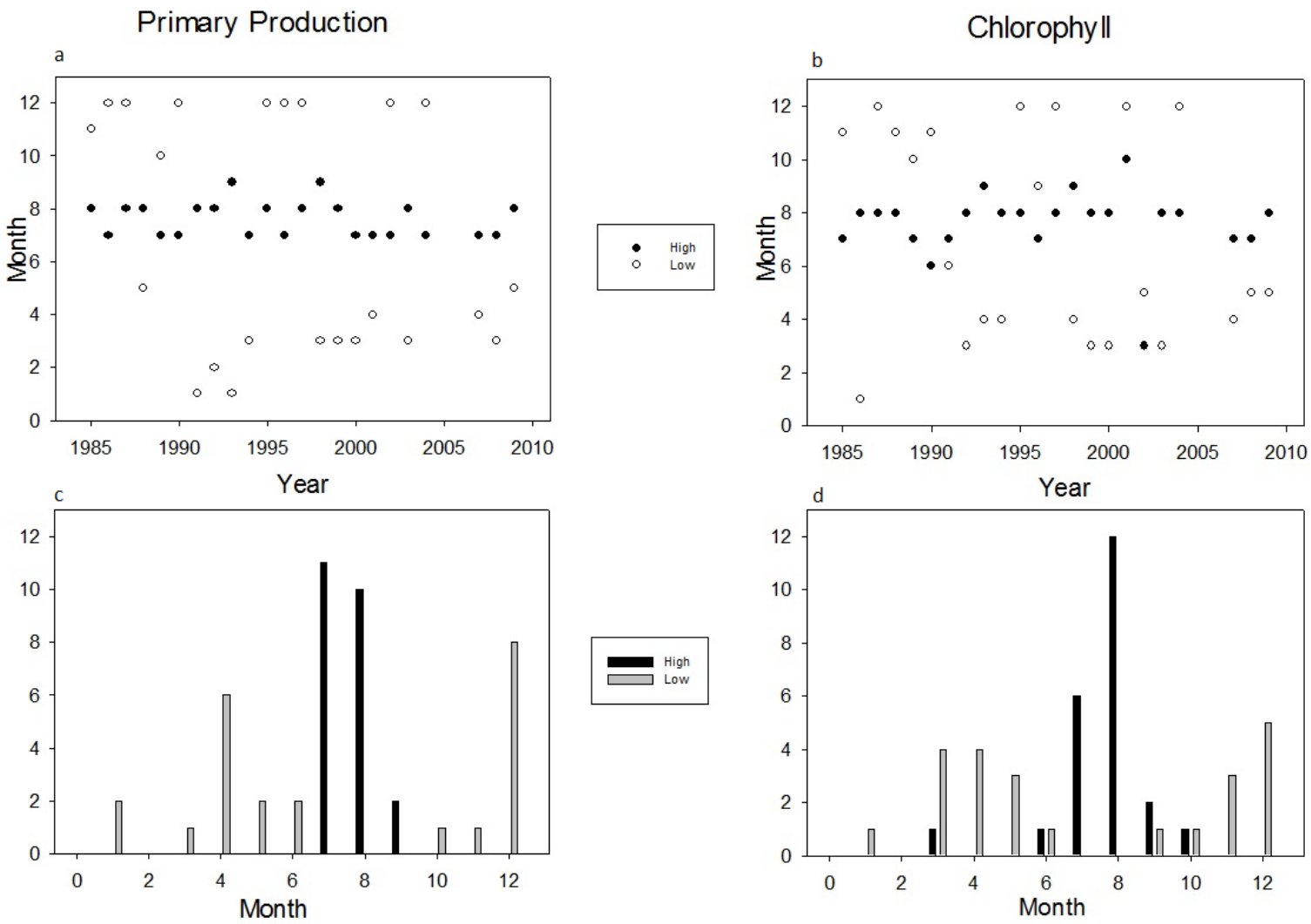


Figure 13. Phenology of TF station showing timing of high and low primary production and chl-a events over the years 1985-2011 in part a and b, respectively. Number of occurrences of high and low production and chl-a events in each month in part c and d.

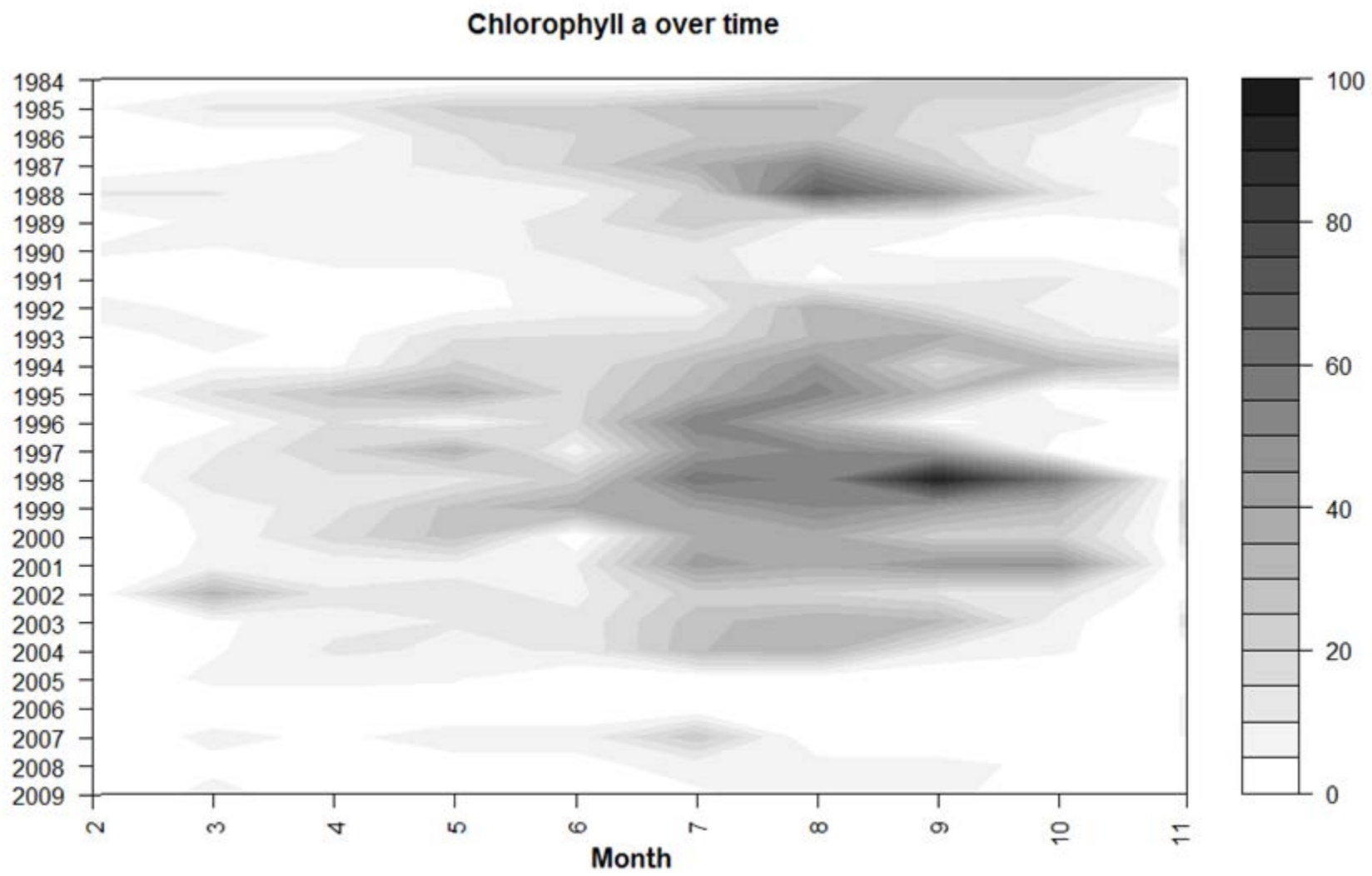


Figure 14. Contour plot of magnitude of observed chl-a levels at the TF station in each month over the years 1985-2009. Bar on the right represents color gradation of chl-a levels.

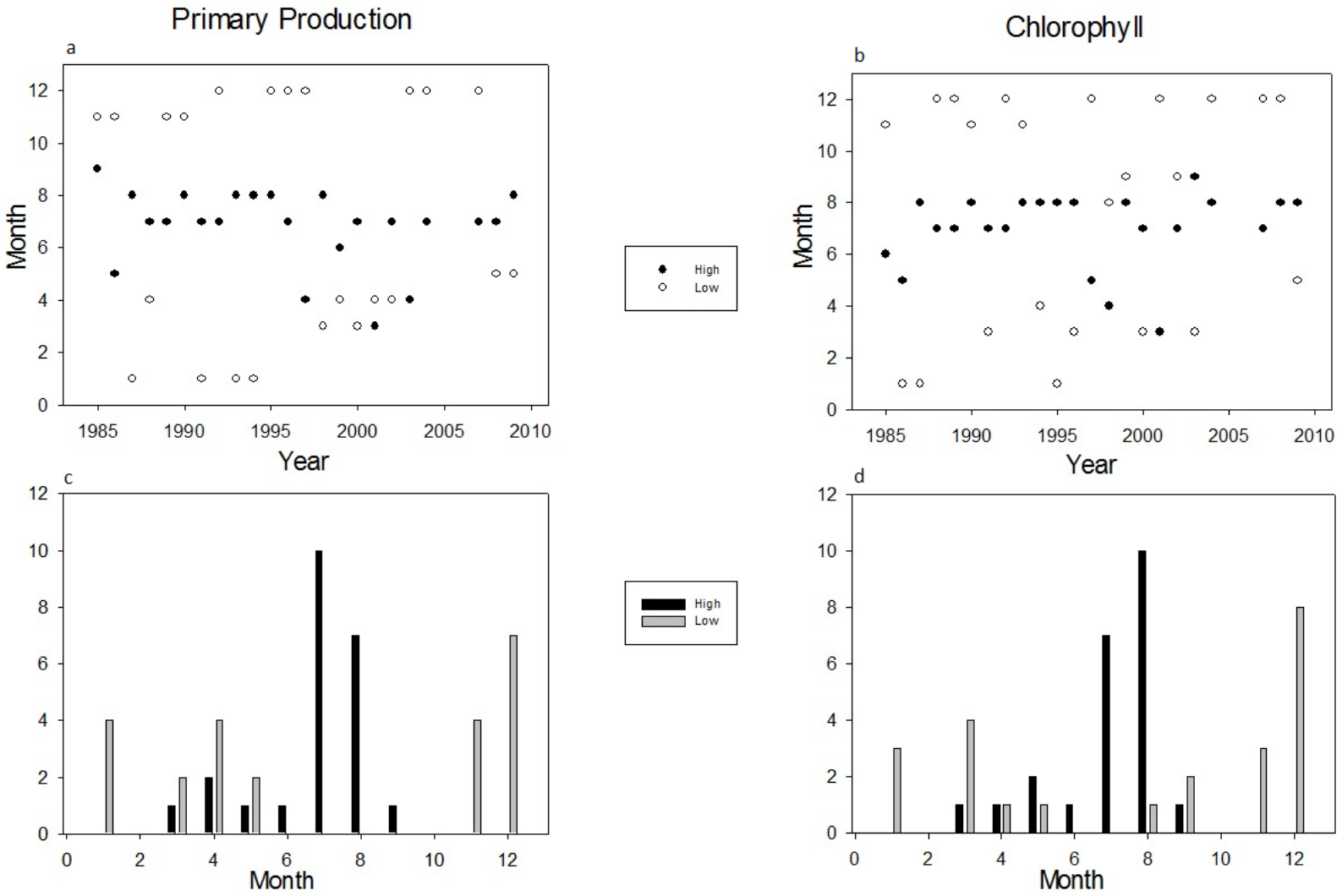


Figure 15. Phenology of RET station showing timing of high and low primary production and chl-a events over the years 1985-2011 in part a and b, respectively. Number of occurrences of high and low production and chl-a events in each month in part c and d.

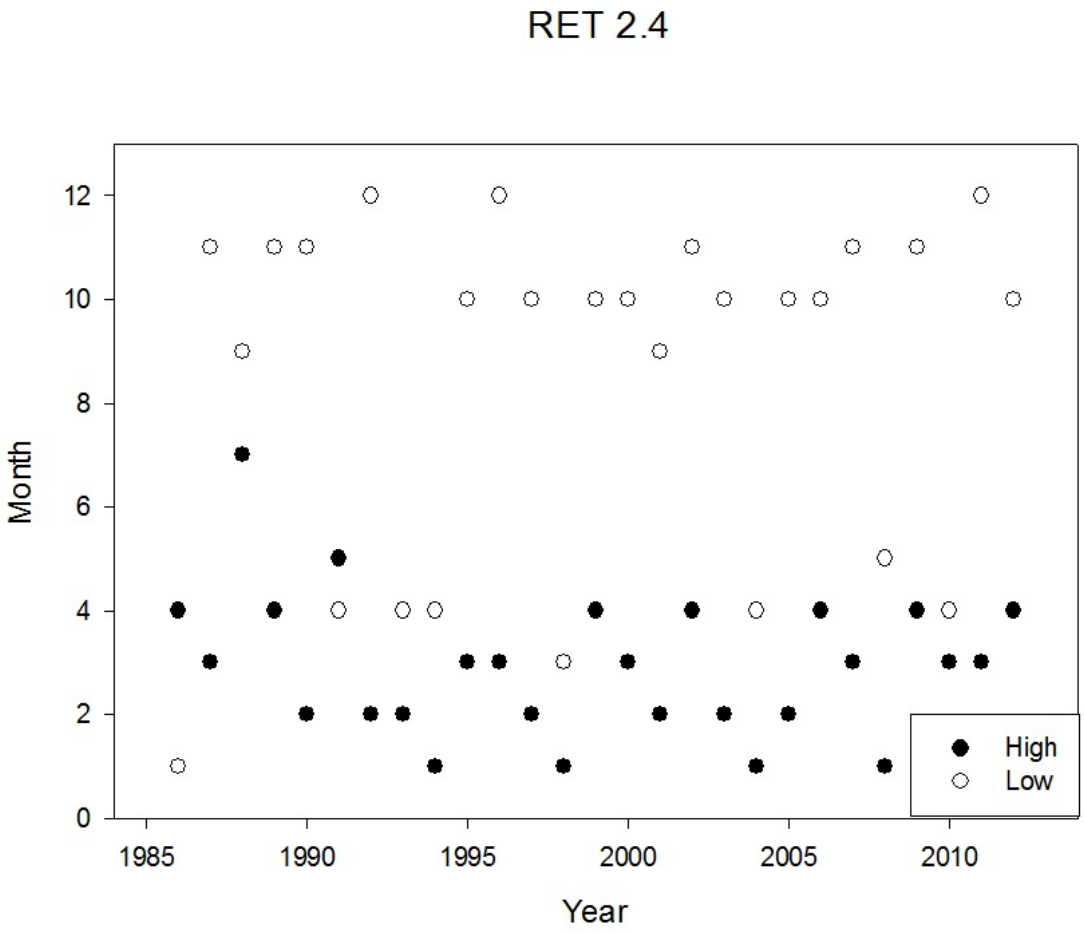


Figure 16. Timing of maximum and minimum chl-a events for the last RET station before the LE zone in the Potomac River estuary.

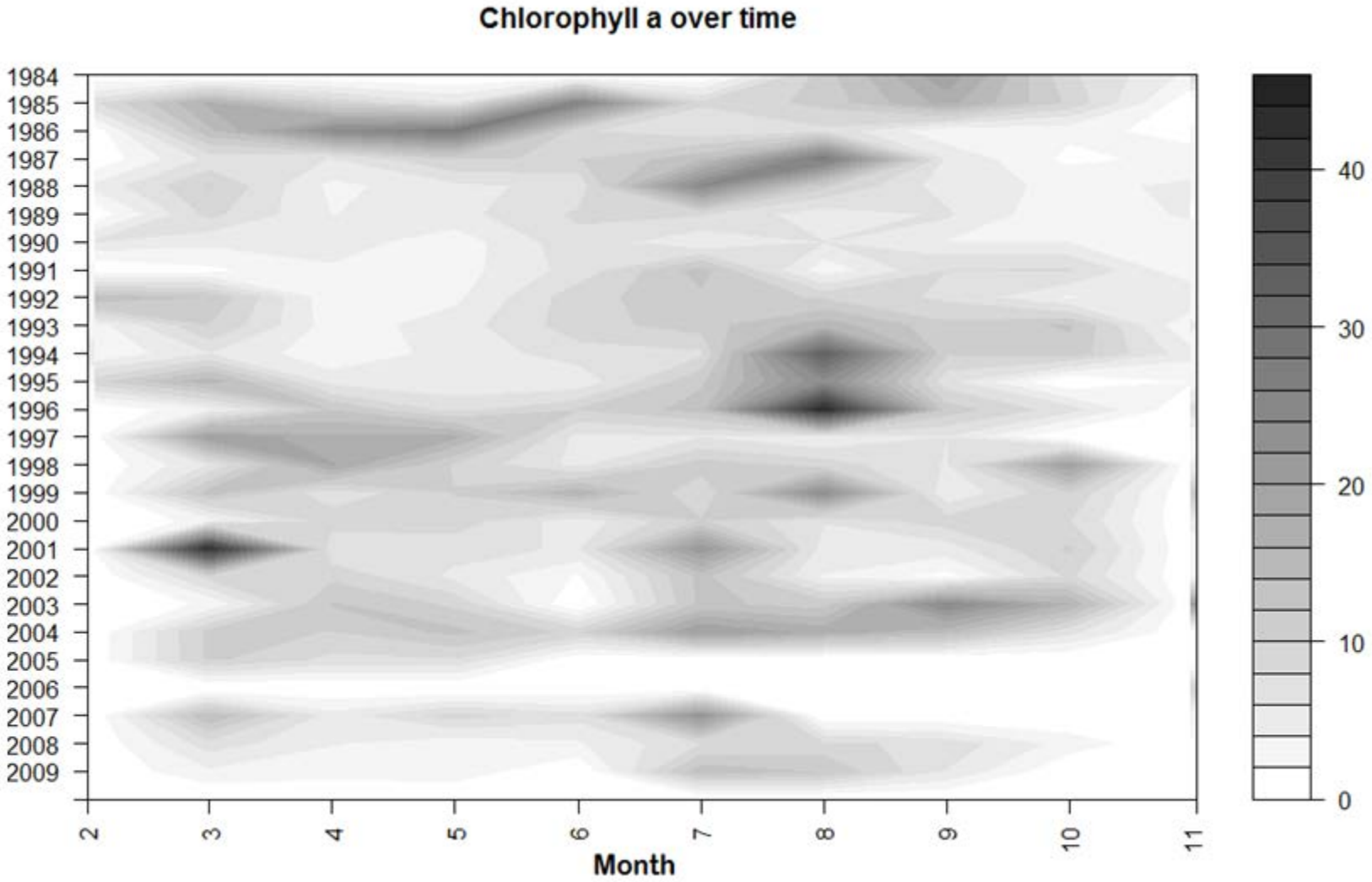


Figure 17. Contour plot of magnitude of observed chl-a levels at the RET station in each month over the years 1985-2009. Bar on the right represents color gradation of chl-a levels.

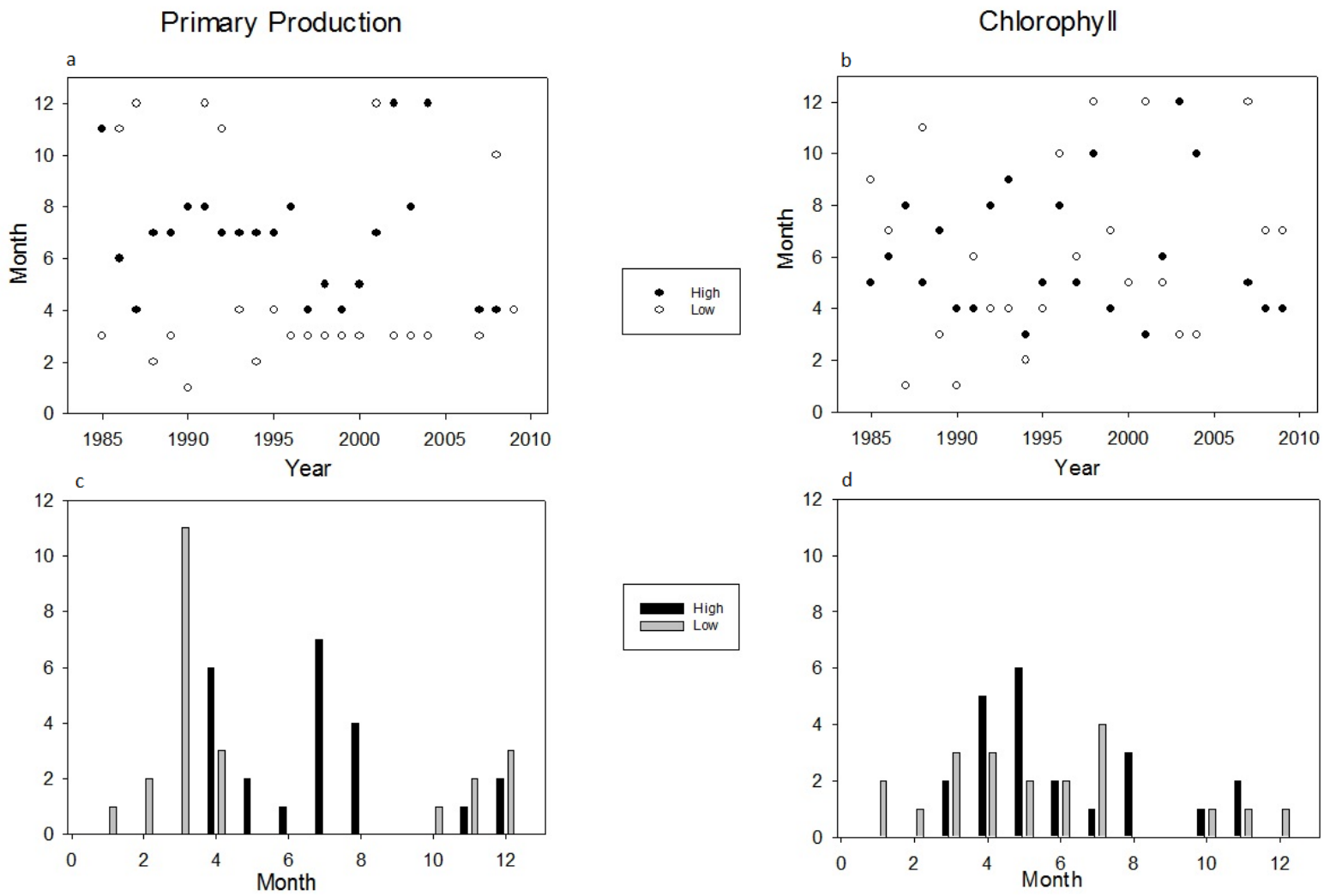


Figure 18. Phenology of LE station showing timing of high and low primary production and chl-a events over the years 1985-2011 in part a and b respectively. Number of occurrences of high and low production and chl-a events in each month in part c and d.

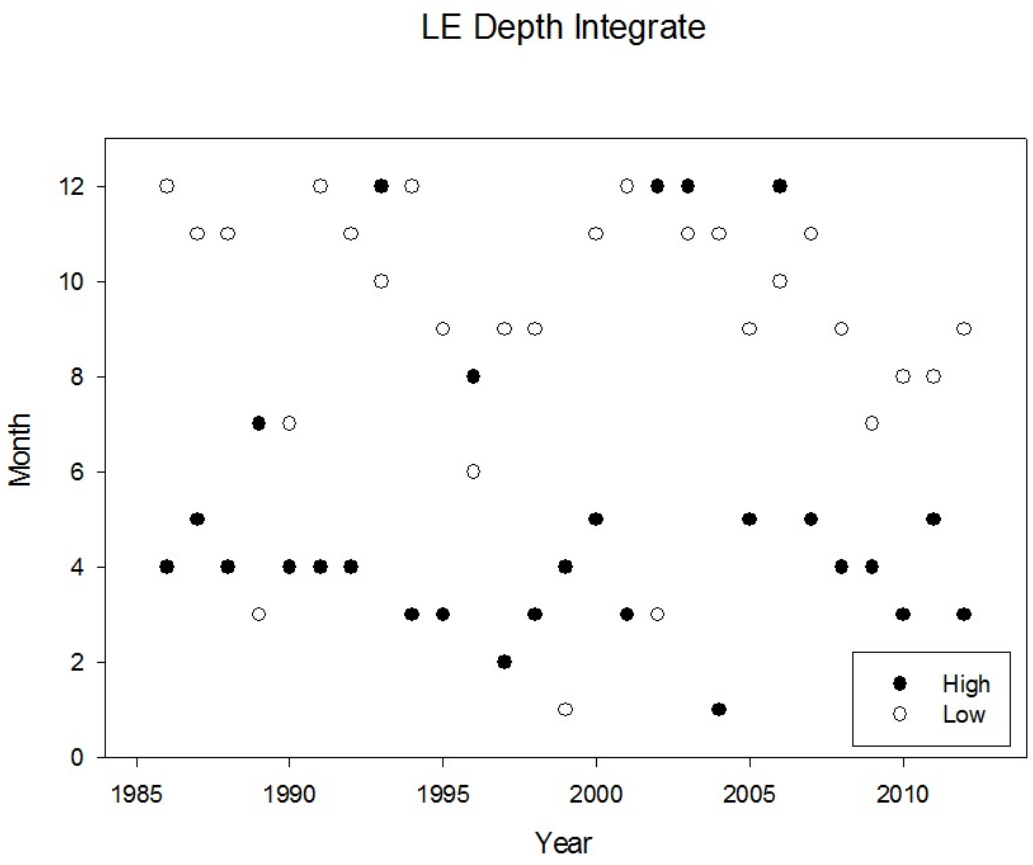


Figure 19. Timing of maximum and minimum chl-a events for depth integrated chl-a at the LE station.

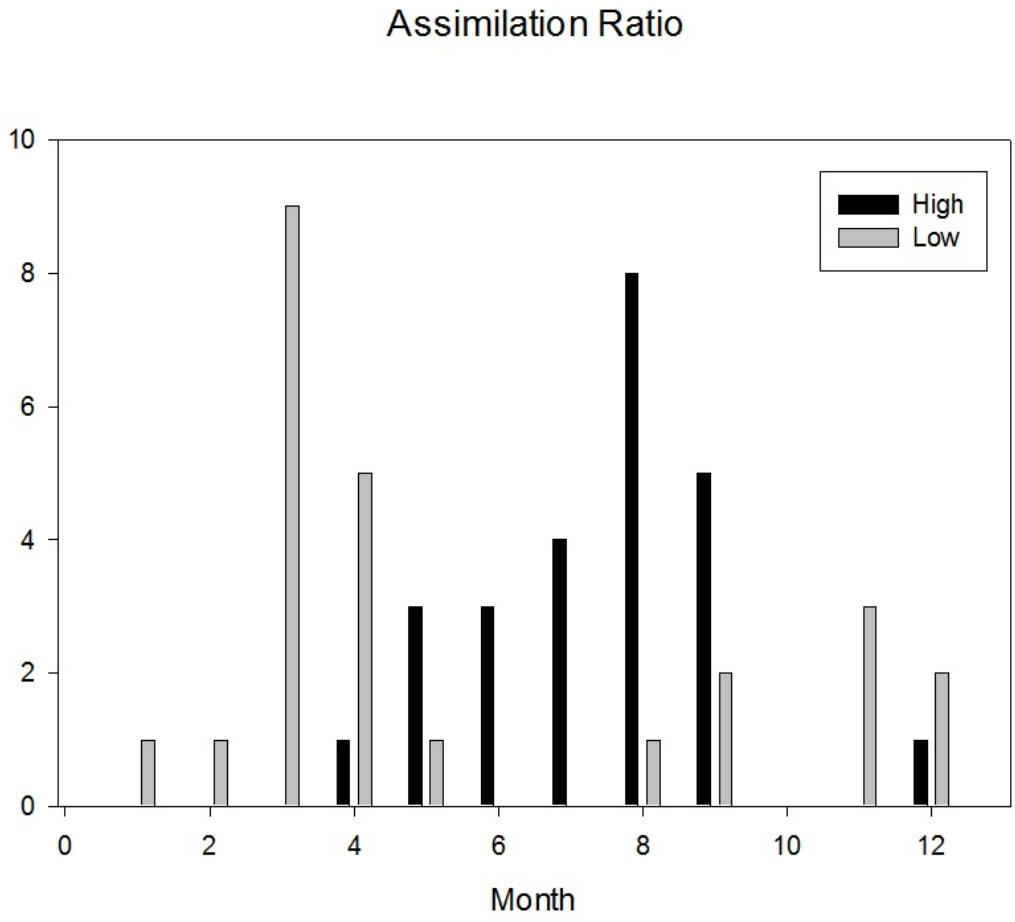


Figure 20. Count of occurrence of maximum and minimum chl-a corrected production reported as assimilation ratio events in each month for the LE zone.

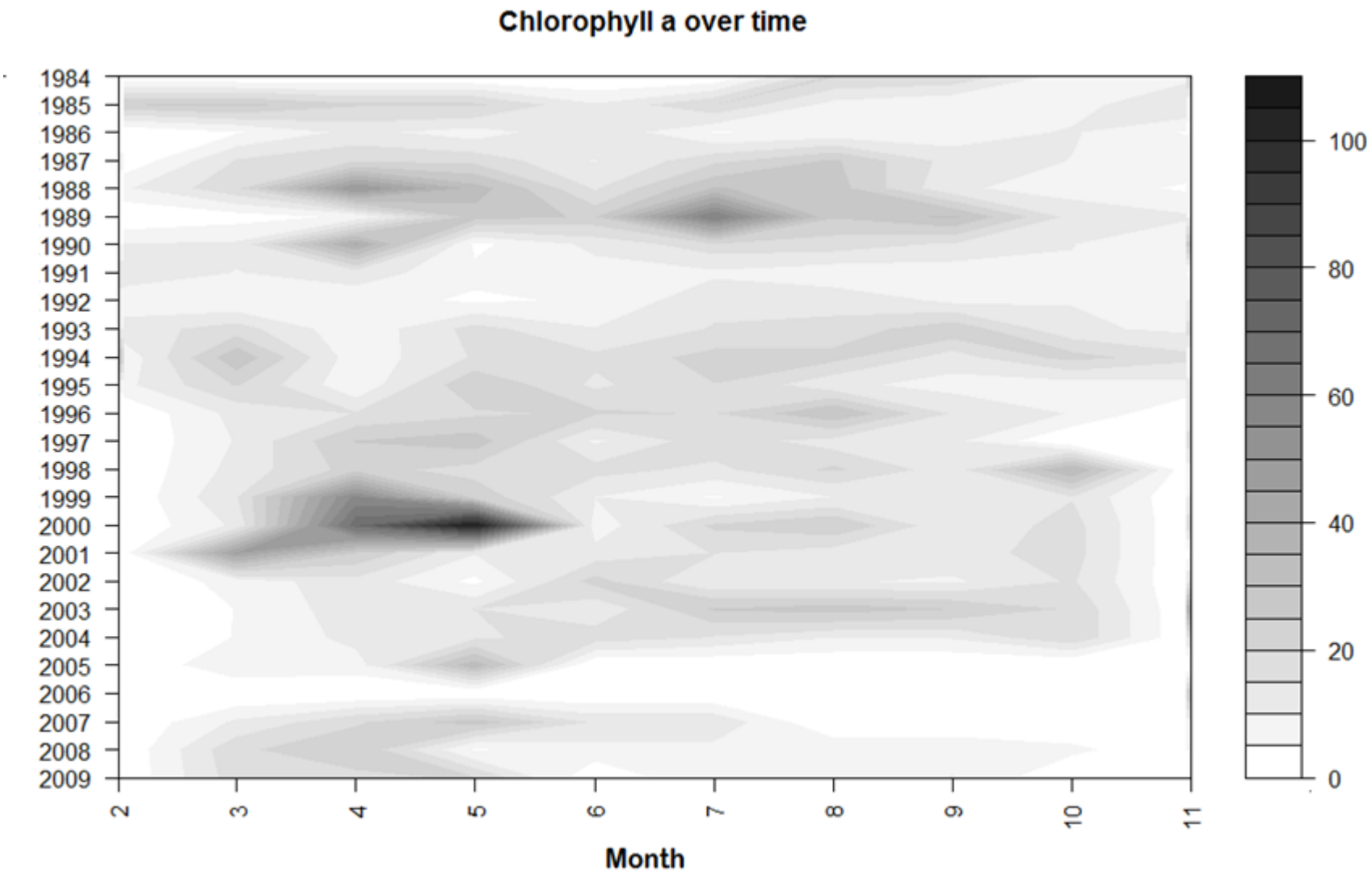
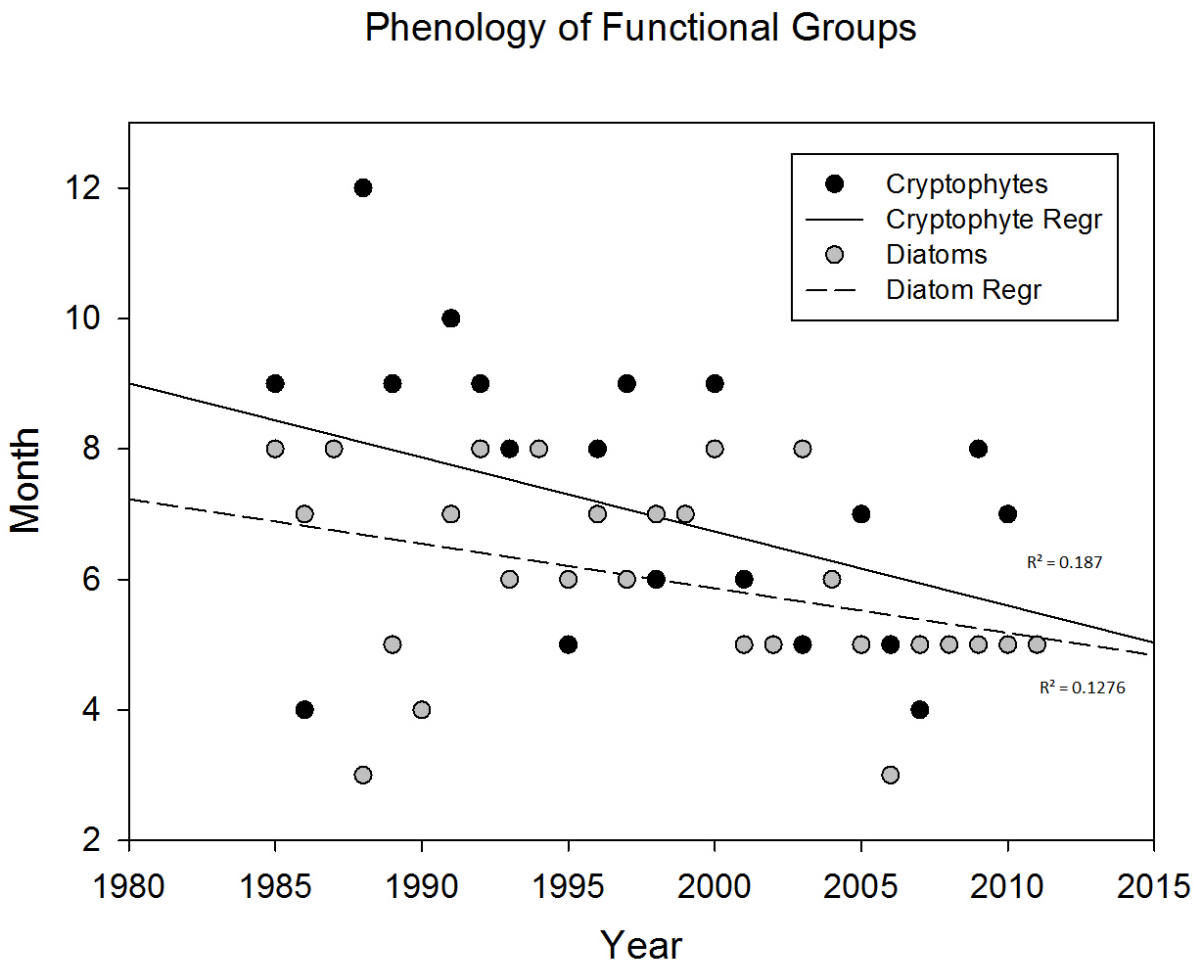
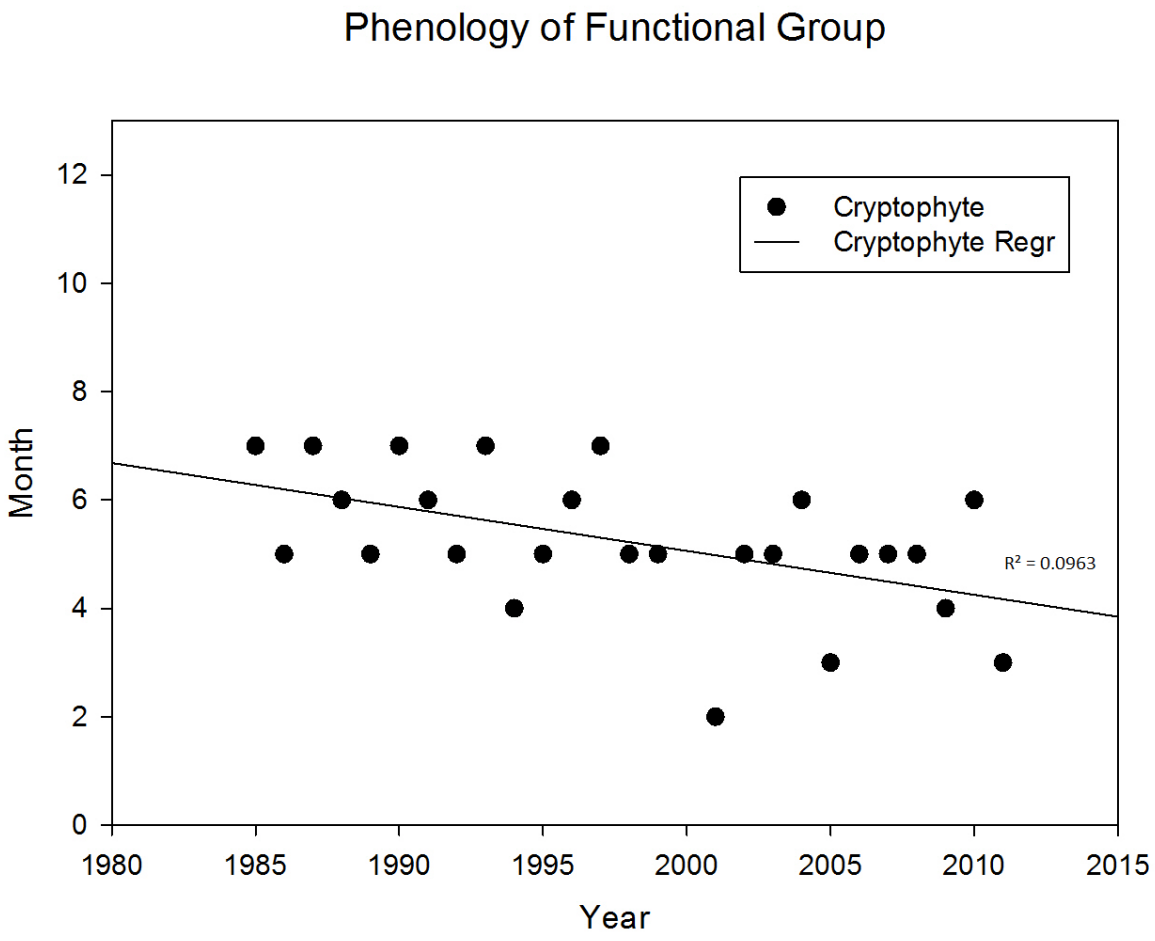


Figure 21. Contour plot of magnitude of observed chl-a levels at the LE station in each month over the years 1985-2009. Bar on the right represents color gradation of chl-a levels.


Phenology of Functional Groups
Cryptophytes
Cryptophyte Regr
Diatoms
Diatom Regr
R² = 0.187
R² = 0.1276
Month
Year
12
10
8
6
4
2
1980
1985
1990
1995
2000
2005
2010
2015


Phenology of Functional Group
Cryptophyte
Cryptophyte Regr
R² = 0.0963
Month
Year
0
2
4
6
8
10
12
1980
1985
1990
1995
2000
2005
2010
2015

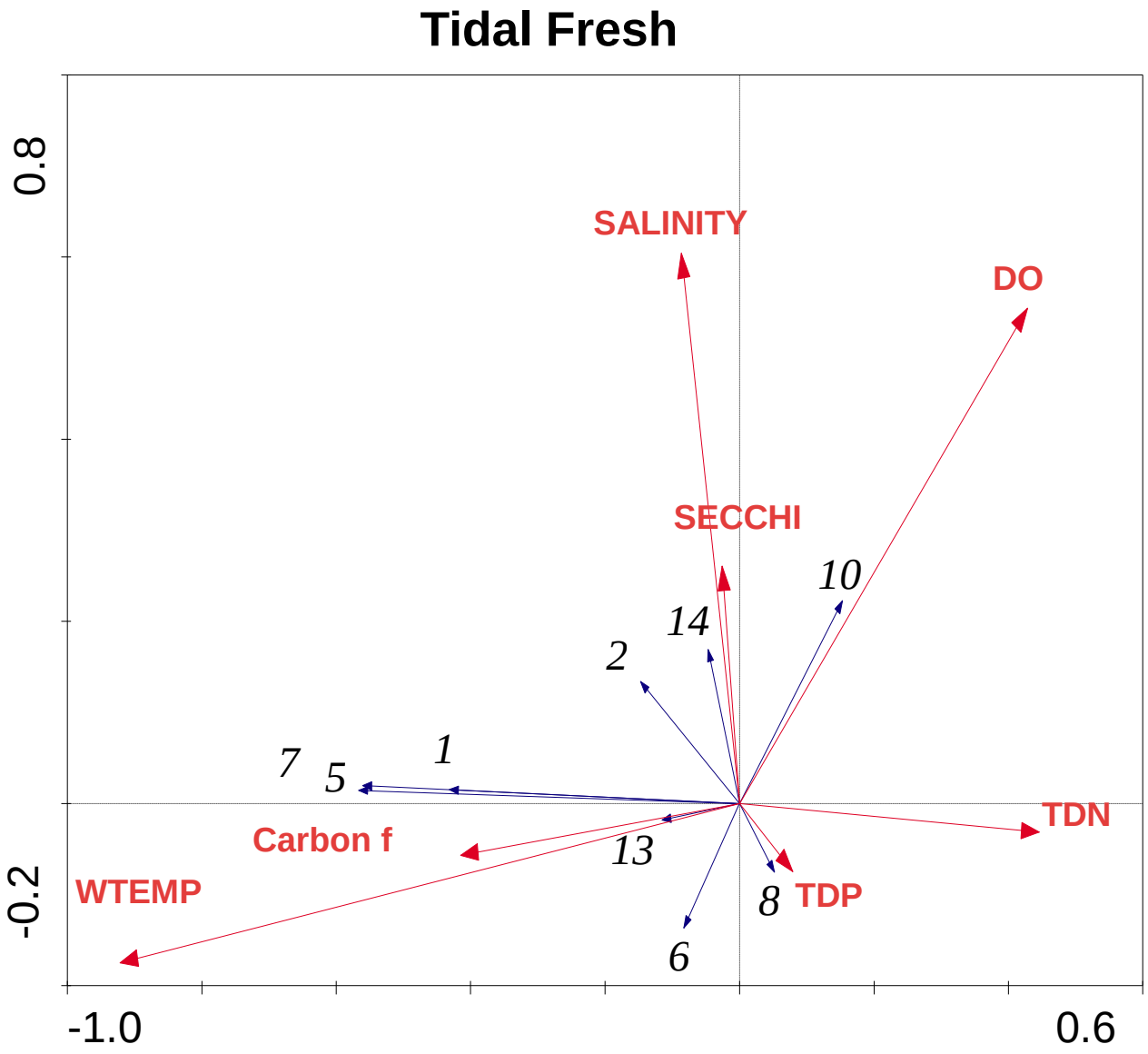


Figure 24. RDA ordination plot of TF station functional groups and correlations to significant environmental variables.

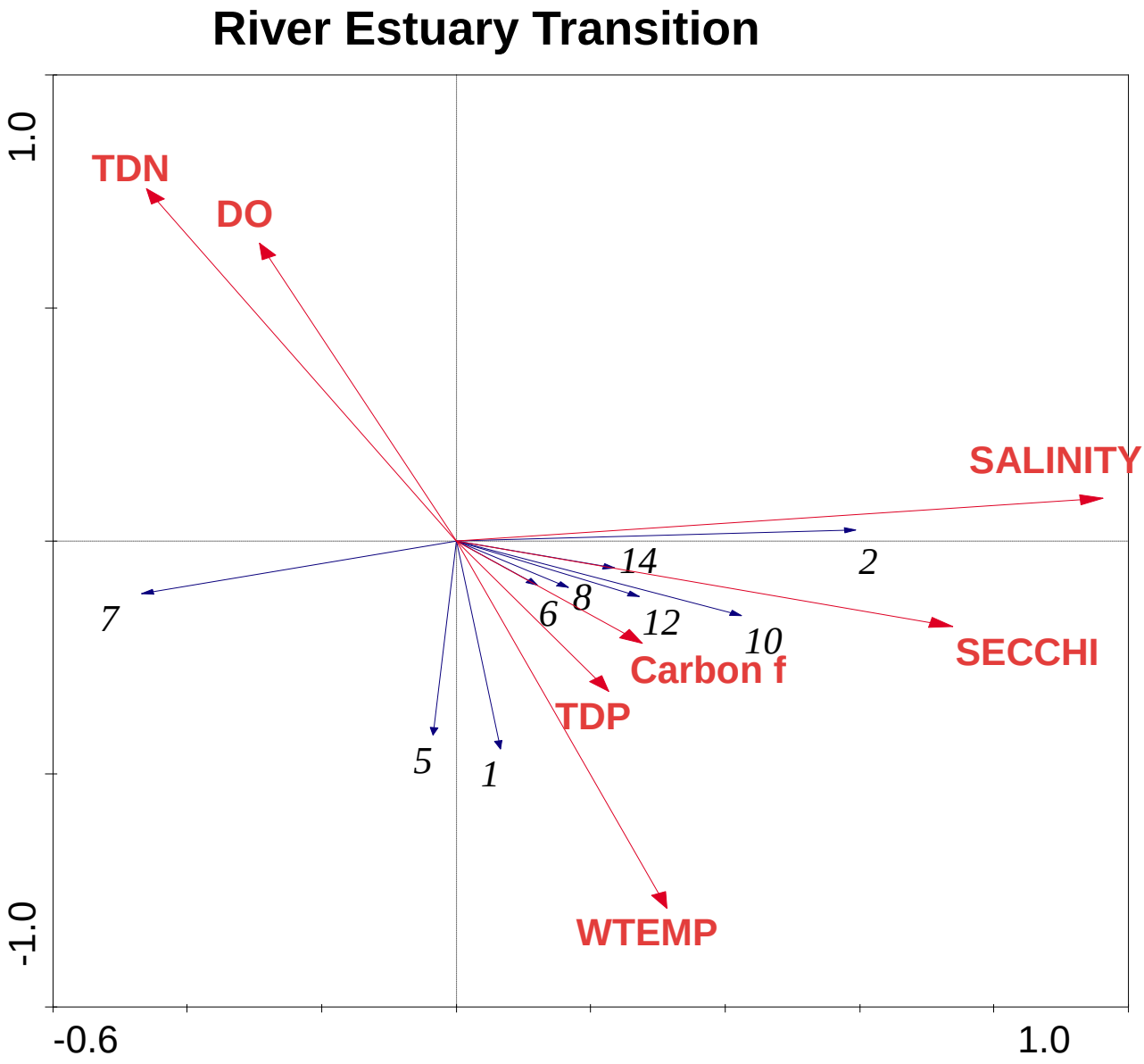


Figure 25. RDA ordination plot of RET station functional groups and correlations to significant environmental variables.

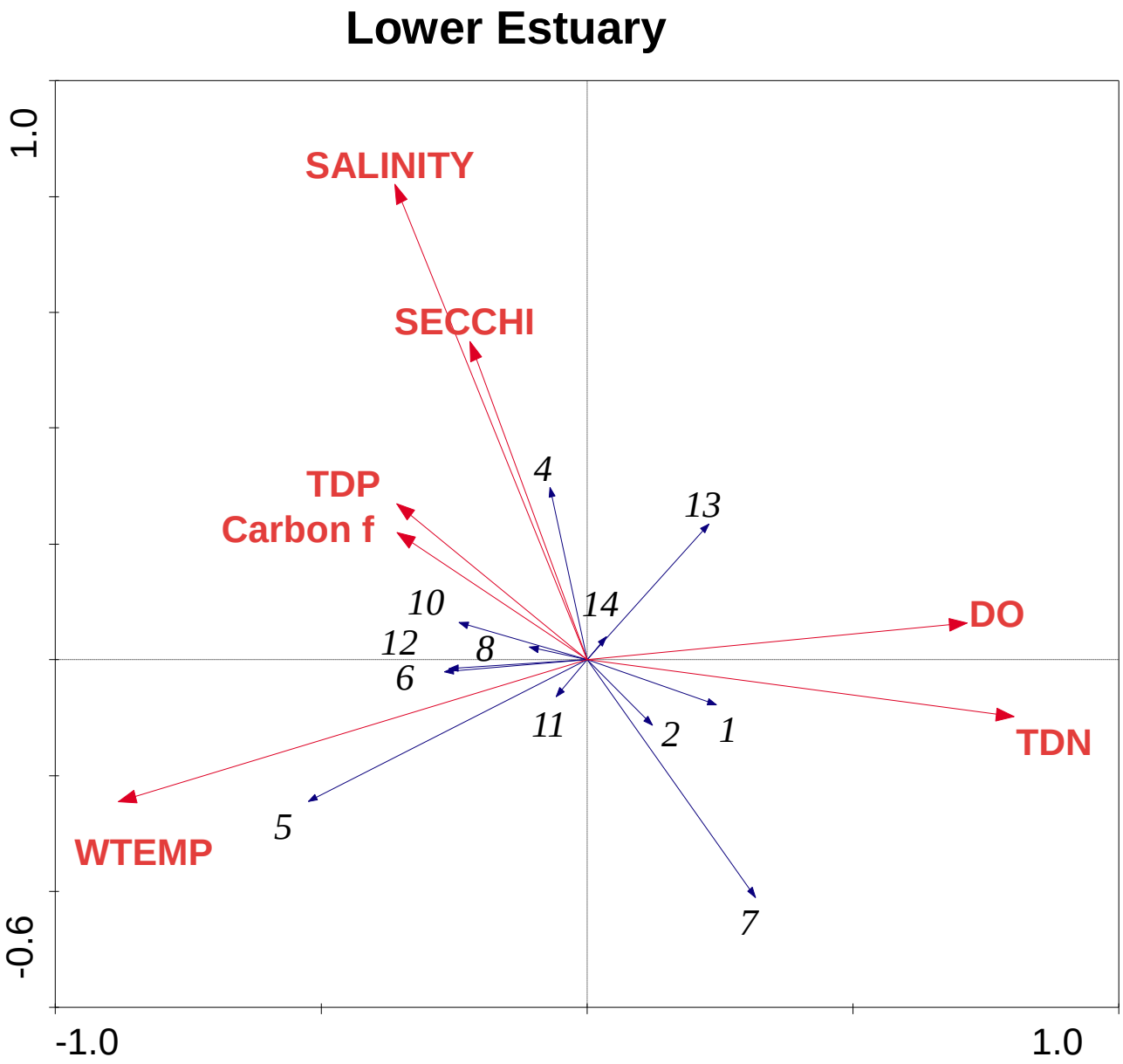


Figure 26. RDA ordination plot of LE station functional groups and correlations to significant environmental variables.

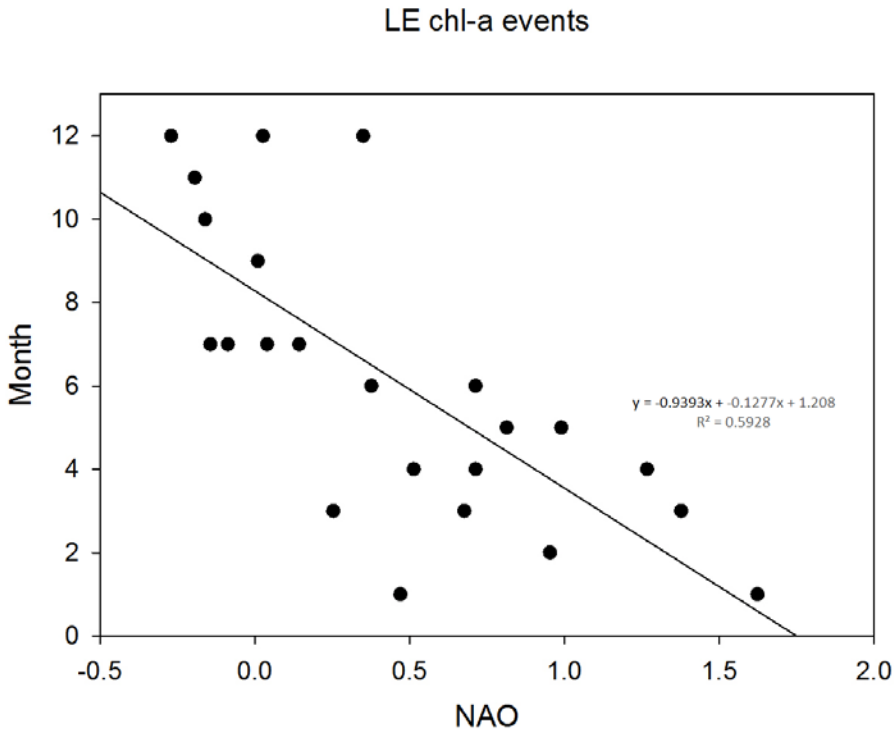


Figure 27. Linear relationship between NAO and minimum chl-a phenology in the LE station of the Potomac River Estuary, with equation and R^2 value.

References

Anderson, D.M., P.M. Glibert, J.M. Burkholder. 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries, 25(4): 704-726.

Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C. et al. 2006. Climate-driven trends in contemporary ocean productivity. Nature, 444, 752–755.

Borkman, D.G. and T. Smayda. 2009. Multidecadal (1959–1997) changes in Skeletonema abundance and seasonal bloom patterns in Narragansett Bay, Rhode Island, USA. Journal of Sea Research 61: 84–94.

Cardinale, B.J., A.R. Ives, P. Inchausti. 2004. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos, 104(3):437-450.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology, 18(1): 117-143.

Cloern, J.E. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. Reviews of Geophysics 34: 127–168.

Cloern, J.E., T.S. Schraga, C.B. Lopez, N. Knowles, R.G. Labiosa, and R. Dugdale. 2005. Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay. Geophysical Research Letters 32: LI4608.

Cloern, J.E., R. Dufford. 2005. Phytoplankton community ecology: principles applied in San Francisco Bay. Marine Ecology Progress Series, 285:11-28.

Cloern, J.E., A.D. Jassby. 2008. Complex seasonal patterns of primary producers at the land–sea interface. Ecology Letter, 11:1294-1303.

Cloern, J.E., A.D. Jassby. 2010. Patterns and Scales of Phytoplankton Variability in Estuarine–Coastal Ecosystems. Estuaries and Coasts. 33:230-241.

Cushing, D.H. 1959. The seasonal variation in oceanic production as a problem in population dynamics. Journal du Conseil International pour l'Exploration de la Mer 24: 455–464.

Dickman, E. M., Newell, J. M., González, M. J., & Vanni, M. J. (2008). Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proceedings of the National Academy of Sciences, 105(47), 18408-18412.

Dodson, S.I., S.E. Arnott, K.L. Cottingham. 2000. The Relationship in Lake Communities between Primary Productivity and Species Richness. Ecology 81:2662–2679.

Duarte, C.M., D.J. Conley, J. Carstensen, M. Sánchez-Camacho. 2009. Return to Neverland: Shifting Baselines Affect Eutrophication Restoration Targets. Estuaries and Coasts, 32:29-36.

Edwards, M. and A.J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884.

Felip, M., & Catalan, J. 2000. The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: decoupling in their spatial and temporal maxima. Journal of Plankton Research, 22(1), 91-106.

Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V., & Raven, J. A. 2010. Phytoplankton in a changing world: cell size and elemental stoichiometry. Journal of Plankton Research, 32(1), 119-137.

Glibert, P.M, D. Fullerton, J.M. Burkholder, J.C. Cornwell, T.M. Kana. 2011. Ecological Stoichiometry, Biogeochemical Cycling, Invasive Species, and Aquatic Food Webs: San Francisco Estuary and Comparative Systems. Reviews in Fisheries Science, 19(4): 358-417

Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. Perspectives in Plant Ecology, Evolution, and Systematics 2:1-28.

Guo, Q., and W. L. Berry. 1998. Species richness and biomass: dissection of the hump-shaped relationships. Ecology 79:2555-2559.

Harding, L.W. 1994. Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. Marine Ecology-Progress Series 104: 267-267.

Harley, C.D.G., A.R. Hughes, K.M. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thorner, et al. 2006. The impacts of climate change in coastal marine systems. Ecol. Lett., 9, 228–241.

Harris, L. A., M.J. Brush. 2012. Bridging the gap between empirical and mechanistic models of aquatic primary production with the metabolic theory of ecology: An example from estuarine ecosystems. Ecological Modelling, 233: 83-89.

Hays, G.C., A.J. Richardson, & C. Robinson. 2005. Climate change and marine plankton. Trends Ecol. Evol., 20, 337–344.

Hjermann, D., B. Bogstad, A.M. Eikeset, G. Ottersen, H. Gjøsæter, N.C. Stenseth. 2007. Food web dynamics affect Northeast Arctic cod recruitment. Proc. R. Soc. B, (274): 661–669.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist 95, 137-145.

Iverson, R.L., H.C. Curl Jr., H.B. O'Connors Jr., D. Kirk, and K. Zakar. 1974. Summer phytoplankton blooms in Auke Bay, Alaska, driven by wind mixing of the water column. Limnology and Oceanography 19: 271–278.

Kemp, W. M., M. T. Brooks, and R. R. Hood. 2001. Nutrient enrichment, habitat variability and trophic transfer efficiency in simple models of pelagic ecosystems. Marine Ecology Progress Series 223: 73-87.

Kimmel, D.G., W.D. Miller, L.W. Harding, E.D. Houde, M.R. Roman. 2009. Estuarine Ecosystem Response Captured Using a Synoptic Climatology. Estuaries and Coasts, 32:403-409.

Lee, Y.J, W.T. Boynton, M. Li, Y. Li. 2013. Role of Late Winter–Spring Wind Influencing Summer Hypoxia in Chesapeake Bay. Estuaries and Coasts, 1-14.

Lepš, J., & Šmilauer, P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press.

Leterme, S. C., M. Edwards, L. Seuront, M.J. Attrill, P.C. Reid, A.W.G. John. 2005. Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. Limnology and Oceanography, 50(4), 1244-1253.

Lomas, M.W., P.M. Glibert, F. Shiah, E.M. Smith. 2002. Microbial processes and temperature in Chesapeake Bay: current relationships and potential impacts of regional warming. Global Change Biology 8(1): 51-70.

de Madariaga, I., L. González-Azpiri, F. Villate, and E. Orive. 1992. Plankton responses to hydrological changes induced by freshets in a shallow mesotidal estuary. Estuarine, Coastal and Shelf Science 35: 425–434.

Malone, T.C. 1992. Effects of water column processes on dissolved oxygen, nutrients, phytoplankton and zooplankton. Oxygen dynamics in the Chesapeake Bay, 61-112.

Malone, T. C., W. M. Kemp, H. W. Ducklow, W. R. Boynton, and J. H. Tuttle. 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. Marine Ecology Progress Series, 32(2/3).

Malone, T.C., D.J. Conley, T.R. Fisher, P.M. Glibert, L.W. Harding, K.G. Sellner. 1996. Scales of nutrient-limited phytoplankton productivity in Chesapeake Bay. Estuaries, 19(2): 371-385.

Marshall, H.G., K.K. Nesius. 1996. Phytoplankton composition in relation to primary production in Chesapeake Bay. Marine Biology, 125:611-617.

Marshall, H.G., L. Burchardt, R. Lacuture. 2005. A review of phytoplankton composition within Chesapeake Bay and its tidal estuaries. Journal of Plankton Research, 27(11):1083-1102.

Marshall, H.G., R.V. Lacouture, C. Buchanan, J.M. Johnson. 2006. Phytoplankton assemblages associated with water quality and salinity regions in Chesapeake Bay, USA. Estuarine, Coastal and Shelf Science, 69:10-18.

McQuatters-Gollop, A., Raitsos, D. E., Edwards, M., Pradhan, Y., Mee, L. D., Lavender, S. J., & Attrill, M. J. 2007. A long-term chlorophyll data set reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient trends. Limnology and Oceanography, 52(2), 635.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A. & Ahas, R. 2006. European phenological response to climate change matches the warming pattern. Glob. Chang. Biol., 12, 1969–1976.

Mittelbach, G.G., C.F. Steiner, S.M. Scheiner, K.L. Gross, H.L. Reynolds, R.B. Waide, M.R. Willig, S.I. Dodson, L. Gough. 2001. What is the Observed Relationship between Species Richness and Productivity? Ecology, 82(9): 2381-2396.

Mittelbach, G.G. 2010. Understanding species richness–productivity relationships: the importance of meta-analyses. Ecology 91:2540–2544.

Najjar, R.G., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M. Kempf, R. Howarth, M.R. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardrop, R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. Estuarine, Coastal and Shelf Science 86:1–20.

Niklas, K. J. 1994. Plant allometry: the scaling of form and process. University of Chicago Press.

Nixon, S.W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia, 41:199-219.

Nixon, S.W., R.W. Fulweiler, B.A. Buckley, S.L. Granger, B.L. Nowicki, K.M. Henry. 2009. The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. Estuarine, Coastal and Shelf Science, 82:1-18.

Odum 1995: H.T.Odum 1995 'Self-Organization and Maximum Empower', in C.A.S.Hall (ed.) Maximum Power: The Ideas and Applications of H.T.Odum, Colorado University Press.

Paerl, H.W. 2006. Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations. Ecological Engineering, 26(1):40-54.

Paerl, H.W., L.M. Valdes, B.L. Peierls, J.E. Adolf, L.W. Harding, Jr. 2006. Anthropogenic and Climatic Influences on the Eutrophication of Large Estuarine Ecosystems. Limnology and Oceanography, 51(1): 448-462.

Paerl, H.W. 2009. Controlling Eutrophication along the Freshwater–Marine Continuum: Dual Nutrient (N and P) Reductions are Essential. Estuaries and Coasts, 32:593-601.

Ptacnik, R., Sommer, U., Hansen, T., & Martens, V. 2004. Effects of microzooplankton and mixotrophy in an experimental planktonic food web.*Limnology and oceanography*, *49*(4), 1435-1445.

R Development Core Team 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Sathyendranath, S., Stuart, V., Nair, A., Oka, K., Nakane, T., Bouman, H., Forget, M., Maass, H., Platt, T. 2009. Carbon-to-chlorophyll ratio and growth rate of phytoplankton in the sea. Mar. Ecol. Prog. Ser, 383, 73-84.

Sellner, K. G. 1987. Phytoplankton in Chesapeake Bay: Role in carbon, oxygen and nutrient dynamics.

Smayda, T.J. 2007. Reflections on the ballast water dispersal—harmful algal bloom paradigm. Harmful Algae, 6(4):601-622.

Smetacek, V. and J.E. Cloern. 2008. Perspective: On phytoplankton trends. Science 319: 1346–1348.

Stoecker, D. K., Thessen, A. E., & Gustafson, D. E. 2008. “Windows of opportunity” for dinoflagellate blooms: Reduced microzooplankton net growth coupled to eutrophication. Harmful Algae, 8(1), 158-166.

Sverdrup, H.U. 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil International pour l’Exploration de la Mer 18: 287–295.

Tilman, D., C. L. Lehman, K.T. Thompson. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Natl. Acad. Sci. USA, 94:1857–1861.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300-1302.

Waide, R. B., M. R. Willig, C. F Steiner, G. G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between primary productivity and species richness. Annual Review of Ecology and Systematics. 30:257-300.

Watson, S.B., E. McCauley, J.A. Downing. 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. Limnology and Oceanography, 42(3): 487-495.

Weiher, E., P. Keddy. 1999. Ecological Assembly Rules: Perspectives, Advances, Retreats. Cambridge University Press.

Wetz, M.S., H.W. Paerl. 2008. Estuarine phytoplankton responses to hurricanes and tropical storms with different characteristics (trajectory, rainfall, winds). Estuaries and Coasts 31(2): 419-429.

Wiltshire, K.H., A. Malzahn, W. Greve, K. Wirtz, S. Janisch, P. Mangelsdorf, B.F.J. Manly, M. Boersma. 2010. Resilience of North Sea phytoplankton spring blooms dynamics: an analysis of long term data at Helgoland Roads. Limnology and Oceanography 53: 1294-1302.

Winder, M., J.E. Cloern. 2010. The annual cycles of phytoplankton biomass. Phil. Trans. R. Soc. B, 365:3215-3266.

Winder, M., S.A. Berger, A. Lewandowska, N. Aberle, K. Lengfellner, U. Sommer, S. Diehl. 2012. Spring phenological responses of marine and freshwater plankton to changing temperature and light conditions. Mar. Biol. 159:2491-2501.

Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314, 787–790.

Yoshioka, P. M. 2008. Misidentification of the Bray-Curtis similarity index. Marine Ecology Progress Series, 368, 309-310.