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ENVIRONMENTAL DRIVERS OF PHYTOPLANKTON ABUNDANCE AND COMMUNITY SIZE COMPOSITION ACROSS THERMAL REGIMES IN THE U.S. NORTHEAST CONTINENTAL SHELF ECOSYSTEM

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BY

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ABSTRACT

Phytoplankton are a diverse group of photosynthetic microorganisms and are critical components of global biogeochemical processes. Rapid changes in the U.S. Northeast Shelf (NES), a region where multiple marine heatwaves have occurred and is warming faster than the global ocean, may have far-reaching effects on ecosystems and biogeochemical processes; this study seeks to describe how these changes impact the drivers of phytoplankton abundance and community size composition within this region. Environmental drivers were characterized using multivariate modeling via partial least squares regression (PLSR) and the importance of each predictor variable was determined via variable influence on projection (VIP) scores. To illustrate the rapidly changing conditions within the NES, trends of sea surface temperature, phytoplankton abundance, and community size composition were constructed via the Theil-Sen approach. Our analyses suggest spatial variation across thermal regimes determines environmental drivers of phytoplankton abundance and community size composition within the NES. Euphotic depth is the primary environmental driver across all size classes, however, the relative impact of other drivers varies across size classes. Predictably, size classes less suited to warmer conditions are more impacted by drivers associated with these conditions. The changing community size composition, distribution, and abundance may have negative implications for biogeochemical processes within the region as well as consequences to the marine carbon cycle and food web.

ACKNOWLEDGMENTS

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I would also like to take the time to acknowledge several projects and programs that enable contributions toward a greater understanding of ocean science by making their data open access, without which this body of work would not exist: The Ocean Colour Climate Change Initiative, the Global Ocean Physics Reanalysis from the Copernicus Marine Environmental Monitoring

Service, the Group for High Resolution Sea Surface Temperature, and Archiving, Validation, and Interpretation of Oceanographic Data.

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1. INTRODUCTION

Phytoplankton are a diverse assemblage of microscopic photoautotrophs grouped taxonomically by size, cell morphology, and pigment composition. They form the basis of the marine food web (Field et al. 1998), account for approximately half of global carbon fixation and oxygen production by photosynthesis (Field et al. 1998), and are a key link in the global carbon cycle (Mouw et al. 2016). Distribution and abundance of these organisms are linked to many dynamic processes and environmental drivers such as temperature variation, water column mixing, and nutrient availability (Winder and Sommer 2012).

However, climate variability can influence these processes leading to an alteration of phytoplankton community size structure (Mousing et al. 2014), bloom phenology (Edwards and Richardson 2004), and taxonomic composition (Winder and Sommer 2012). Abundance changes and distribution shifts have potential consequences not only for trophic efficiency but also for the biogeochemical cycles they play a critical role in (Falkowski 1994). Understanding how phytoplankton will respond to changing oceanographic conditions as a result of global climate change is an emerging field of study.

The U.S. Northeast Shelf (NES) is a region impacted by climate change, specifically rising sea surface temperatures. The NES (Fig. 1) spans from Cape Hatteras, North Carolina to Nova Scotia and is subdivided into the Gulf of Maine (GOM), Georges Bank (GB), and the Middle Atlantic Bight (MAB) (O'Reilly and Zetlin 1998). The NES is dominated by two major currents, the cooler and less saline southward flowing Labrador current and the warmer, more saline northward flowing Gulf Stream (Saba et al. 2015). This temperate western boundary ecosystem is one of the most productive shelf ecosystems in the world and supports substantial recreational and commercial fisheries (O'Reilly et al. 1987, Csandady 1990). Fisheries in this area rely on the region's high primary productivity which is strongly influenced by changes in temperature (Schofield et al. 2008).

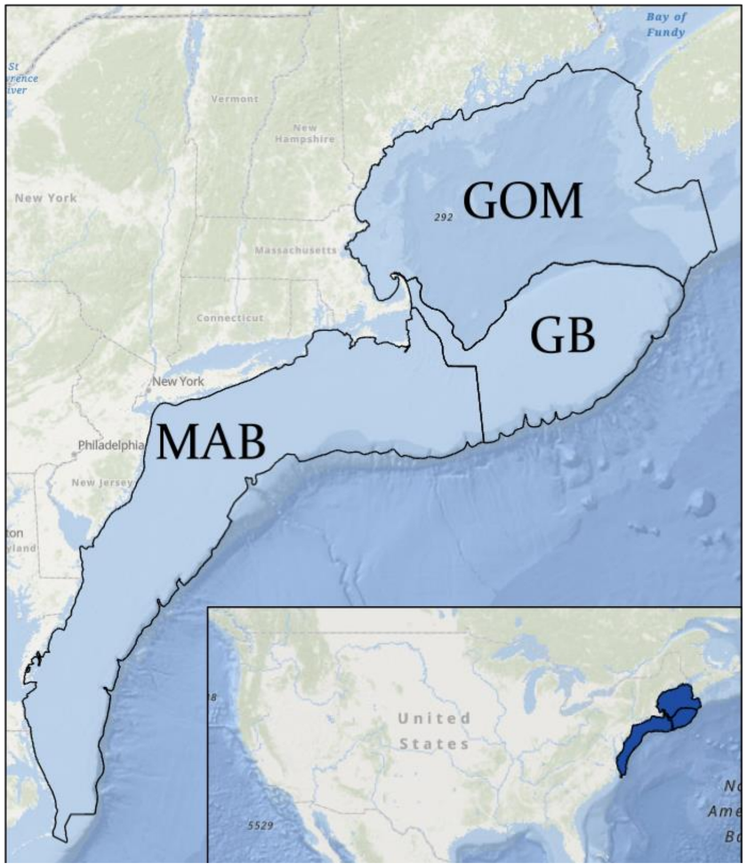

Figure 1. Map of study region displaying each subdivision: the Mid-Atlantic Bight (MAB), George's Bank (GB), and the Gulf of Maine (GoM).

The NES displays one of the strongest warming trends in the global ocean and the northernmost portion, the Gulf of Maine (GoM), has warmed 99% faster than the global ocean (Burrows et al. 2011, Pershing et al. 2015). Furthermore, the rate of warming in the southernmost portion, the Mid-Atlantic Bight (MAB), has rapidly accelerated from 0.026°C yr^{-1} ± 0.001 from 1977-2013 to 0.24°C yr^{-1} ± 0.03 from 2004-2012 (Forsyth et al. 2015). Additionally, the frequency and intensity of marine heatwaves in the region has increased over the past decades (Fig. 3). During the marine heatwave in 2012, surface waters 1-3°C warmer than average (Mills et al. 2013) with nearly identical temperature anomalies reported in 2016 (Pershing et al. 2018).

Temperature plays an important role in phytoplankton ecology. Beyond the role it plays in regulating and affecting metabolic rates (Brown et al. 2004), temperature also influences the size composition of phytoplankton communities (Mousing et al. 2014), specifically that small cells are associated with warmer, more stratified waters (Morán et al. 2009). Small cells are at an advantage in warm waters due to a smaller diffusion boundary layer and a smaller cell volume (Mousing et al. 2014). Decreasing cell size will have effects on sinking and carbon export production rates which has broad implications for the global carbon cycle (Hilligsøe et al. 2011). Additionally, enhanced stratification of the water column which negatively impacts vertical mixing and nutrient transport to surface waters which can lead to a decrease in total phytoplankton biomass (Cavole et al. 2016) and shift the phytoplankton community structure to dominance by smaller cells which ultimately impacts higher trophic levels of the marine food web.

While many studies have described the effect of increased sea surface temperature (SST) on phytoplankton abundance, community composition and distribution in the NES, little research has been conducted on how this warming trend affects phytoplankton environmental drivers. In the context of this research, environmental drivers are processes that influence phytoplankton abundance and community size composition. The goal of this project is to describe if different environmental drivers are more impactful during warming events and marine heatwaves as compared to the overall satellite record. Additionally, what impact does increased warming have on phytoplankton abundance and community size composition? Analysis of this region, specifically focusing on periods of rapid warming, has granted unique insight as to how the biological base of the ocean is changing and will continue to change given a projected increase in ocean temperature of 1-4°C by the end of the century (IPCC 2013).

2. SCIENTIFIC QUESTIONS

1. What are the environmental drivers of phytoplankton abundance and community size composition in the U.S. Northeast Continental Shelf?
2. What are the environmental drivers of phytoplankton abundance and community size composition in the U.S. Northeast Continental Shelf during warming events and marine heatwaves?
3. Are different environmental drivers dominant during warm periods and marine heatwaves as compared to the long-term trends over the satellite record?

3. METHODS

3.1. Data Sets

Table 1 contains a summary of data products and sources. Table 2 shows data products and usages.

3.1.1. Ocean Color Satellite Data

The beauty of remote sensing technology is that it lends the ability to analyze parameter variability and patterns over large spatial and temporal scales. Increasingly complex sensors and regional algorithm refinements have further strengthened the resulting data. Specifically, the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS), Medium Resolution Imaging Spectrometer (MERIS), Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua), Ocean and Land Color Instrument (OLCI), and Visible Infrared Imaging Radiometer Suite (VIIRS) have been globally merged by the Ocean Colour Climate Change Initiative (OC-CCI) to form monthly composites (OC-CCI version 5.0, Sathyendranath et al. 2019). By blending various satellite mission data, the OC-CCI provides chlorophyll concentration ([Chl]) and the diffuse attenuation coefficient (Kd(490)), which was used to calculate euphotic depth.

To enhance data quality and spatial resolution, recent work has focused on regional algorithm refinement and optimization for NES, particularly the retrieval of phytoplankton size class (PSC) (Hu et al. 2018, Moore and Brown 2020, and Turner et al. 2021). Recent advances have allowed for the retrieval of PSC via unique optical properties of each size class (Brewin et al. 2011, Bracher et al. 2017, Mouw et al. 2017). These methods have shown success at both the ocean basin (Hirata et al. 2011, Zhang et al. 2018) and regional scale (Hu et al. 2018, Sun et al. 2018, Turner et al. 2021). PSC was calculated following Turner et al. (2021) which found improvement in NES retrieval performance with the inclusion of SST. By leveraging an abundance-based algorithm, which takes advantage of the relationship between PSC and chlorophyll concentration, the biomass of each size class is calculated. PSC is divided into three classes: microplankton (>20 μm), nanoplankton (2–20 μm), and picoplankton (0.2–2 μm).

Table 1. Satellite Imagery, Derived and Reanalysis Products, and Sources

Parameter	Description	Source
SLA (m)	Sea level anomaly	AVISO https://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/gridded-sea-level-anomalies-mean-and-climatology/
[Chl] (mg/m^3)	Chlorophyll *a* concentration	OC-CCI https://www.oceancolour.org/
K_d(490) (m^{-1})	Diffuse attenuation coefficient at 490 nm	OC-CCI https://www.oceancolour.org/
Zeu (m)	Euphotic depth	OC-CCI https://www.oceancolour.org/
SST (°C)	Sea surface temperature	GHRSST https://www.ncei.noaa.gov/data/oceans/ghrsst/
S (PSU)	Sea surface salinity	GLORYS https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/
MLD (m^{-1})	Mixed layer depth	GLORYS https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/
Uo (m/s)	East-west current velocity	GLORYS https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030

Vo (m/s)	North-south current velocity	GLORYS https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/
[Micro] (mg/m^3)	Concentration microplankton	Turner et al. (2021)
[Nano] (mg/m^3)	Concentration nanoplankton	Turner et al. (2021)
[Pico] (mg/m^3)	Concentration picoplankton	Turner et al. (2021)

Note. AVISO = Archiving, Validation, and Interpretation of Oceanographic Data, GLORYS = Global Ocean Reanalysis and Simulations, GHRSST = Group for High Resolution Sea Surface Temperature, OC-CCI = Ocean Colour Climate Change Initiative

3.1.2. Physical Data

Satellite and blended products were used to characterize physical drivers including SST and sea level anomaly (SLA). SST measurements were obtained from the Group for High Resolution Sea Surface Temperature (GHRSST), which blends in situ sensors and satellite products. SLA data were obtained from the Segment Sol multi-missions d'Altimétrie, d'Orbitographie (SSALTO)/Data Unification and Altimeter Combination System (DUCAS) which is hosted by Archiving, Validation, and Interpretation of Oceanographic Data (AVISO) which provides monthly measurements with quarter-degree spatial resolution. SSALTO/DUCAS sources data from a variety of satellites including Jason-1, Jason-2, and Jason-3.

Some physical products require reanalysis to be retrieved including mixed layer depth (MLD). The MLD is the depth where the density compared to the density at 10 m corresponds to a decrease in temperature of 0.2°C and was retrieved from the Global Ocean Reanalysis and Simulation (GLORYS, Ferry et al. 2010). To minimize the uncertainty of modeled and reanalysis products, the GLORYS model utilizes multivariate data assimilation from both satellite and in situ observations and a bias correction on a 3-month window (Lellouche et al. 2018).

Table 2. Parameters and associated usage.

Parameter	Usage
[Chl], SST	Micro, Nano, Pico calculation
[Chl], MLD, S, SLA, SST, Uo, Vo, Zeu	Driver analysis
K_d(490)	Zeu calculation

3.2. Time Periods

In the context of this research, the satellite record is 1997-2019, the period for which all products necessary were available, when analysis was initiated. For the NES, a shift in thermal conditions was identified in 2010 and the trend has continued for all subsequent years. To best capture temporal variation in drivers, analyses were conducted over the entire satellite record (1997-2019), baseline conditions (1997-2009), and the period exhibiting exceptional warming trends (2010-2019). Additionally, analyses were conducted on the two years with marine heatwaves (2012 and 2016).

3.3. Data Processing

Given that the ocean color and physical data exhibit a range of gridding, spatial resolution, and time scales, all data were processed into a 9 x 9 km grid guided by the procedures outlined in Mouw et al. (2019). Ocean color products were retrieved at the highest spatial resolution then spatially smoothed or regridded to 9 x 9 km via a quarter degree geometric mean. Next, reanalysis products were retrieved and/or calculated following the same procedures as ocean color products. Data were then temporally smoothed via a three-month moving average. Spline interpolation was employed to fill gaps of six months or less. Quality control was performed by removing outliers with standard deviations greater than 5 removed from the final data set. These procedures resulted in a 9 x 9 km grid at a monthly resolution from 1997 to 2019 for all satellite and reanalysis products.

3.4. Statistical Analysis

Environmental drivers were characterized using multivariate modeling via partial least squares regression (PLSR) and the importance of each predictor variable was determined via variable influence on projection (VIP) scores. For PLSR analysis, response variables are chlorophyll concentration (a proxy for abundance) and each PSC. Explanatory variables are euphotic depth, sea surface temperature, sea level anomalies, salinity, mixed layer depth, and north-south and east-west current velocity.

To illustrate the rapidly changing conditions within the NES, trends of sea surface temperature, phytoplankton abundance, and community size composition were constructed for each time period via the Theil-Sen approach. This nonparametric method estimates the slope of each pixel over time and is insensitive to outliers (Barton et al. 2014, Theil 1950). By combining these techniques, the complex dynamics governing phytoplankton abundance, distribution, and size class are described.

PLSR provides a quantitative, multivariate approach that can be used to analyze datasets with many predictor variables and provides a method to determine the relative importance of each predictor variable (Wold et al. 2001). This method results in principal components, regression coefficients that describe both the magnitude and direction of the correlation, and allows for collinearity between predictor variables. VIP scores provide a summary of the importance of predictor variables by quantifying the total contribution of a specific predictor variable to the principal component and for the purposes of this study results with a VIP score greater than 0.5 are considered significant (Wold et al. 2001).

Given that not all environmental drivers are statistically independent of each other and to prevent the chance of finding a significant correlation by chance when using PLSR, a bootstrap test was conducted on the total data set. Additional tests were conducted to assess the confidence in parameter importance, such as leave-one-predictor-out validation which is appropriate for large data sets (Martens and Martens 2000). This method repeats PLSR analysis $n + 1$ times, where n is the number of predictor variables being analyzed (Mouw et al. 2019). The first test runs with all predictor variables and then excludes a single predictor for each subsequent run.

To better understand the spatial variability of environmental drivers and community composition within the NES, data were analyzed over the subdivisions of the GOM, GB, and the MAB (Fig. 1). These methods were employed for each time period, with emphasis on the 2012 and 2016 marine heatwaves, to capture temporal variability.

4. RESULTS

4.1. Trends

Detailed results for sea surface trends (Fig. 2) are presented to the side. Chlorophyll concentration and PSC trends are provided graphically (Fig. 3) and geographically (Fig. 4, Fig. 5).

Over the satellite record, (Fig. 2a) SST displayed a positive trend across the NES. Baseline conditions exhibited decreasing SST across all regions. The highest rate of change occurred during the warming period (Fig. 2c), with all regions exhibiting a positive trend in SST. Specifically, MAB temperatures increased at a rate of 0.02°C yr^{-1} (as compared to -0.01°C yr^{-1} during baseline conditions), GB at a rate of 0.08°C yr^{-1} (baseline condition: -0.03°C yr^{-1}), and the GOM with a 0.1°C yr^{-1} increase (contrast to the baseline rate of -0.06°C yr^{-1}).

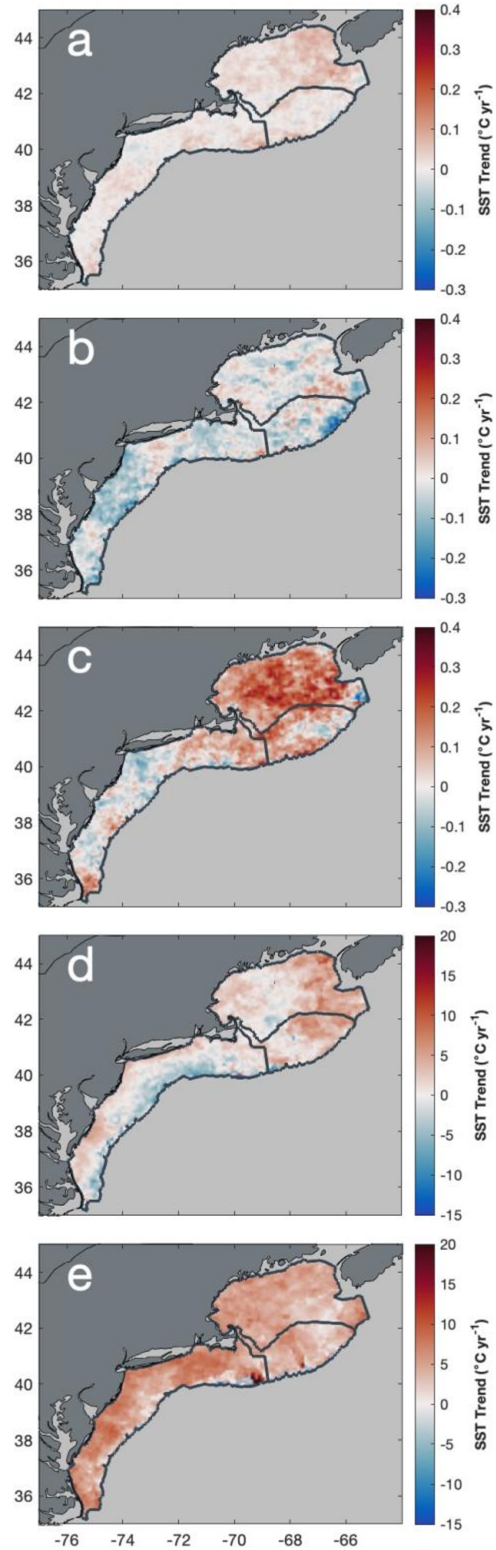

Figure 2. SST Trends over the satellite record (a), baseline conditions (b), warming conditions (c), and the 2012 (d) and 2016 (e) heatwaves.

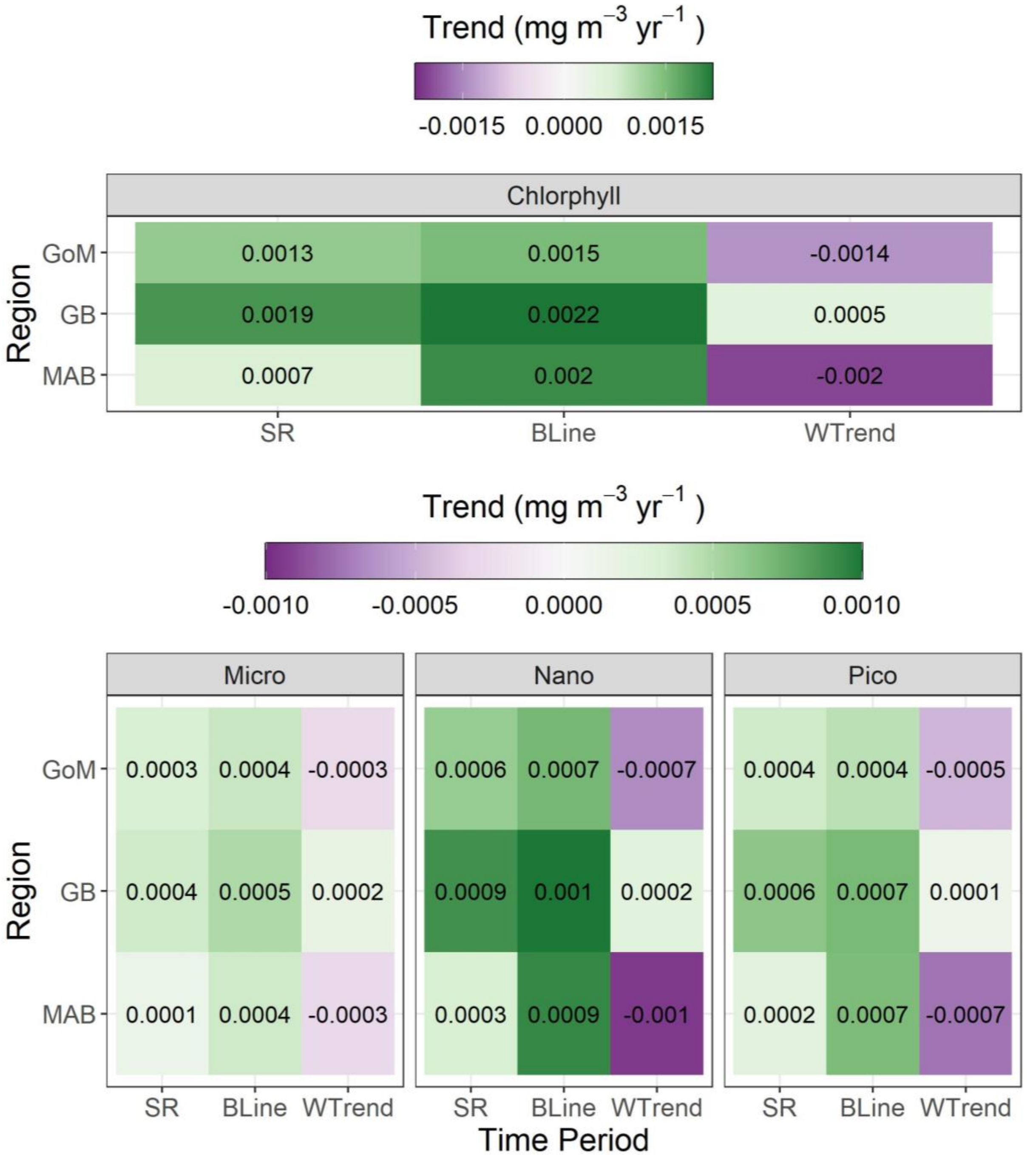

Figure 6. Least squares regression results for trends of chlorophyll concentration and size class concentration. Concentrations increase over the satellite record and baseline conditions. Generally, concentrations decrease during the identified warming trend (2009-2019). Additionally, nanoplankton exhibit the greatest range of trends. *Note*: Color bar ranges between chlorophyll and size class differ.

4.2. Partial Squares Least Regression

Regional and temporal differences and similarities are present in driver importance (Fig. 6). Some patterns are evident when considering drivers of abundance and size class across thermal regimes (Fig. 6). When considering the three regions, driver importance was similar in GB and GOM and different from the MAB.

Across all time periods and regions, euphotic depth was the most important determinant of phytoplankton abundance and size class composition. However, if we ask the most basic question "what governs phytoplankton abundance" the most basic answer is "light, nutrients, and grazing pressures". Given that our analysis does not consider the latter two categories, it is almost inevitable that euphotic depth is the single most important and unifying factor in driving overall abundance and size composition. Additionally, its calculation relies on the same metric ((Kd(490)) to quantify chlorophyll concentration.

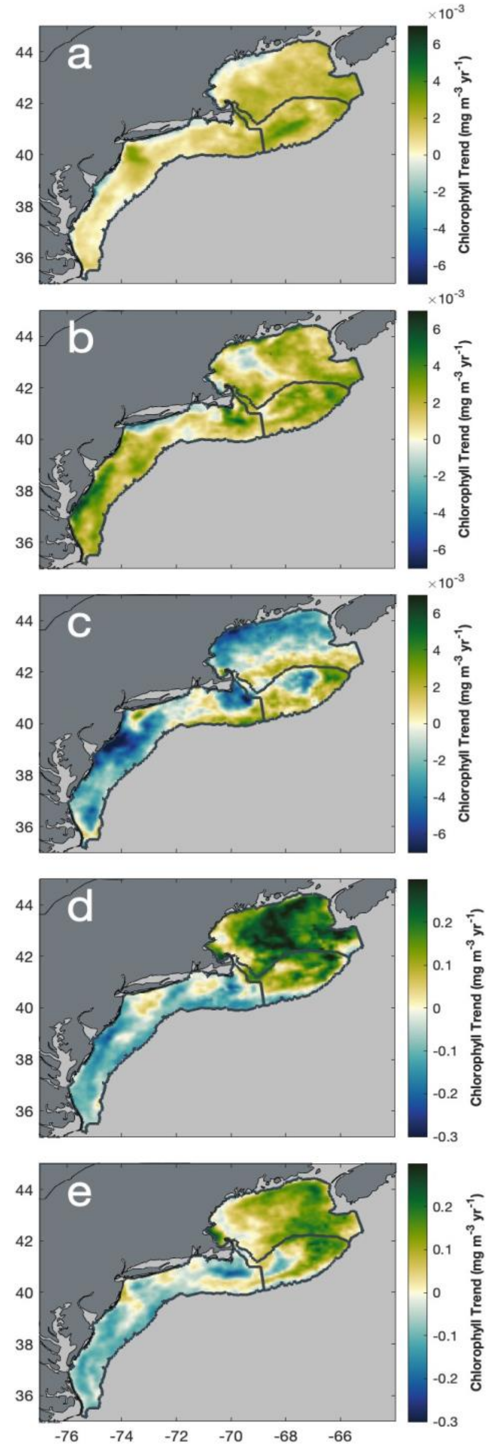

Figure 7. Chlorophyll increases over the satellite record (a), baseline conditions (b), and the 2012 (d) and 2016 (e) heatwaves. During extended warm conditions (2009-2019), chlorophyll generally decreases.

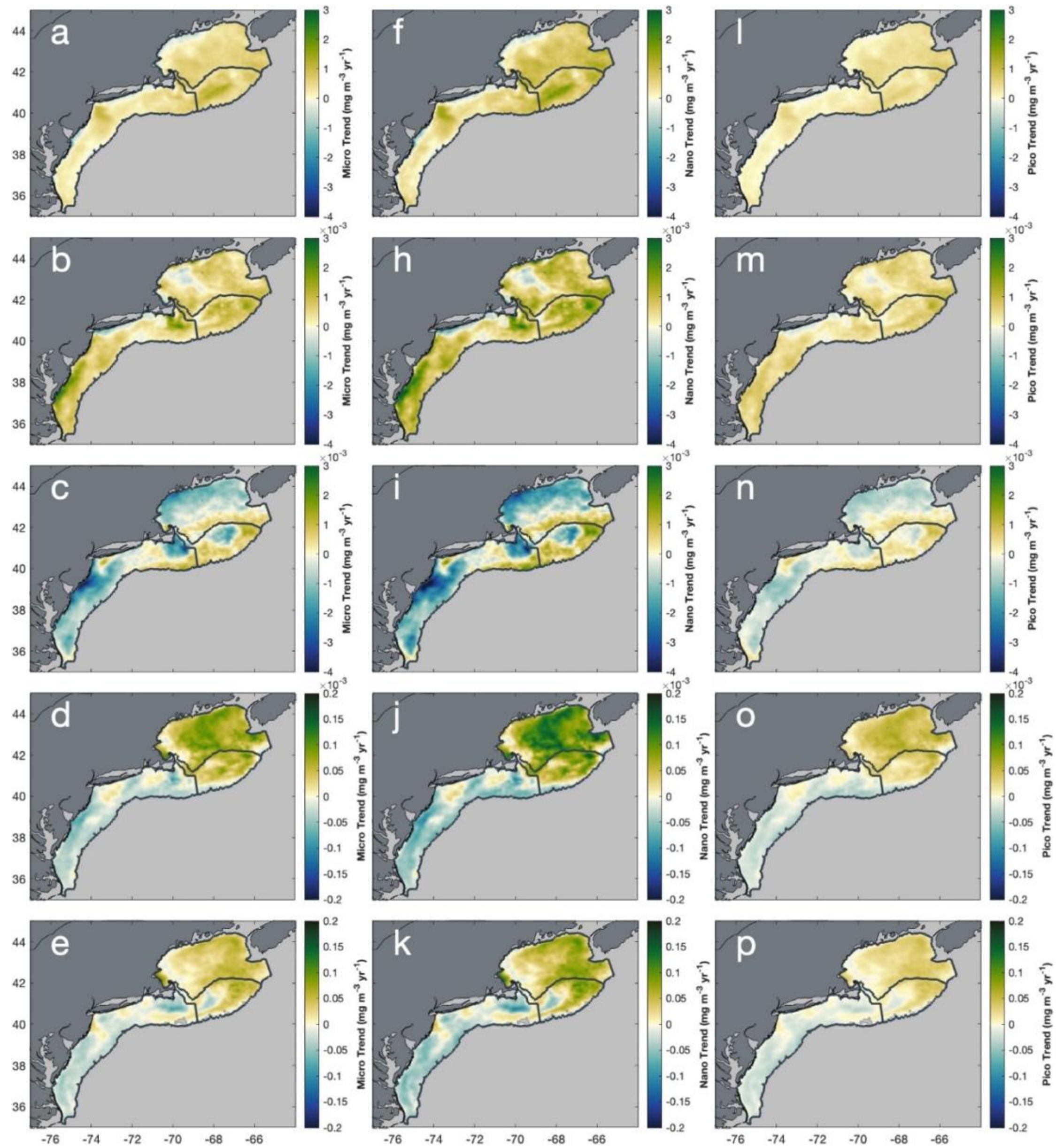

Figure 8. PSC size class trends vary over each time period. Rows correspond to time period following conventions in Figure 4. Moving left to right, columns correspond with microplankton, nanoplankton, and picoplankton respectively.

4.2.1. Chlorophyll

Regional and temporal differences of driver importance are present when considering phytoplankton abundance (Fig. 7). Across all time periods and regions, euphotic depth was the unifying, dominant driver of phytoplankton concentration, though, as previously stated, it is not calculated independently of chlorophyll, so this result is expected. For brevity, it will not be listed in detailed results.

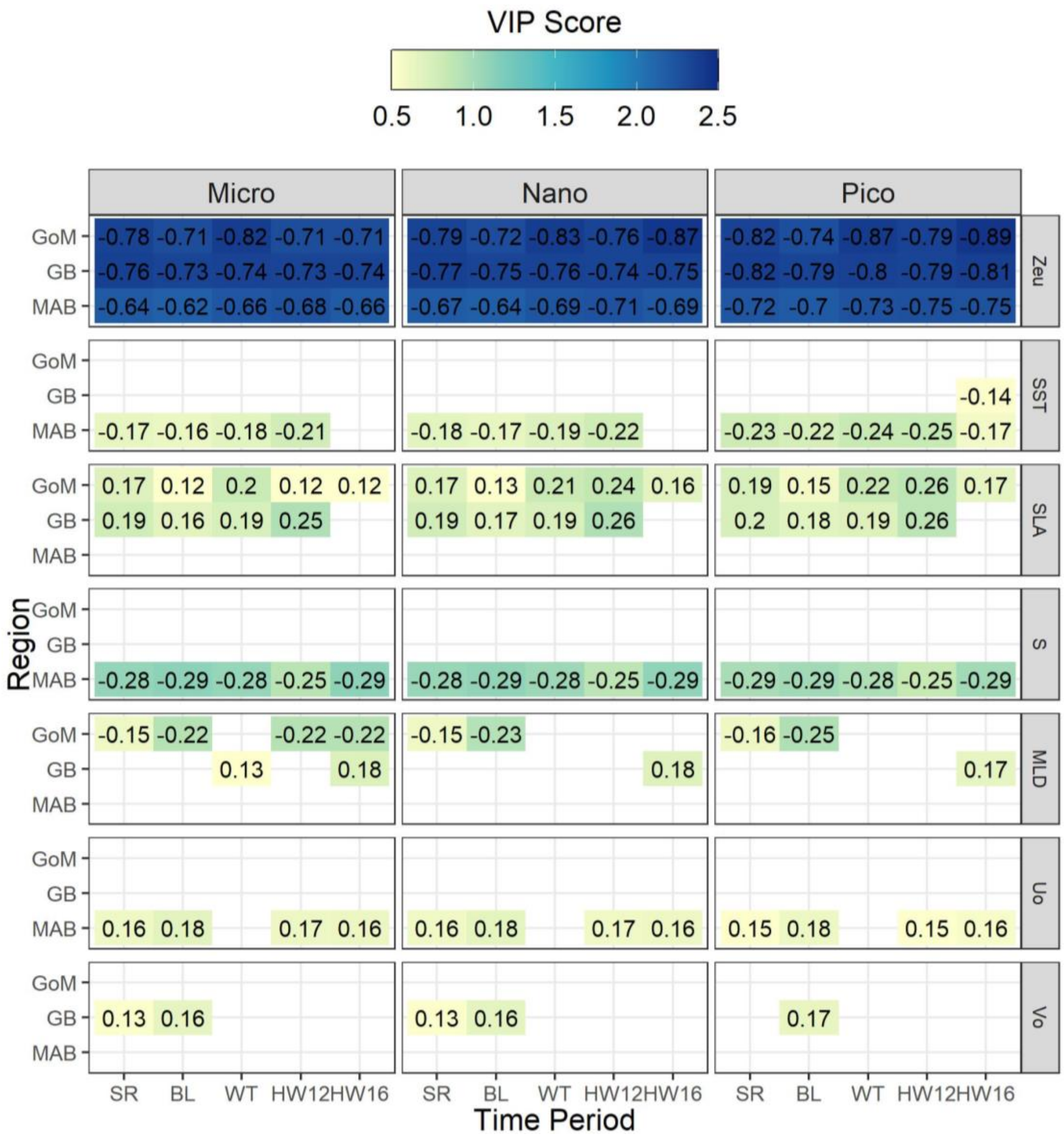

Figure 9. Full PSC results of PLSR analysis with only significant results shown. Fill color of each box corresponds to strength of VIP score, text indicates coefficient value, and absence of a box indicates the variable was not a significant driver. While euphotic depth is universally the strongest determinant across all thermal regimes, regions, and size classes, some variables are only drivers in specific regions (S and SST in the MAB). Generally, coefficient values are consistent across PSC, thermal regimes, and subregion except for MLD which switches signs between the GoM and GB (negative and positive respectively.

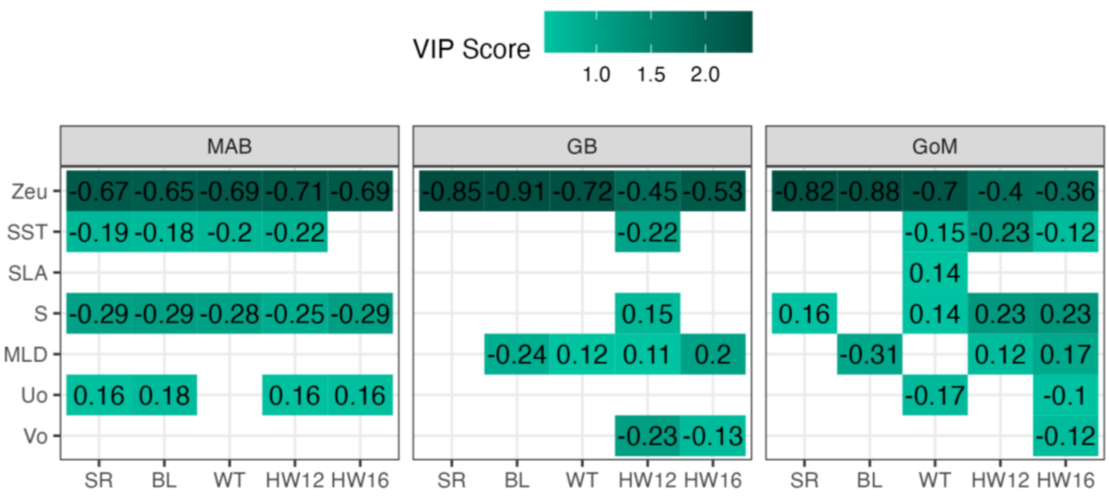

Figure 10. Results of PLSR analysis for chlorophyll concentration with fill color indicating strength of VIP score and text indicating coefficient values. A north (GoM and GB) and south (MAB) distinction in stability across thermal regimes is evident. In the MAB, drivers are generally consistent across all time periods, whereas drivers in GB and GoM are more dynamic across thermal regimes.

MAB: Salinity was a constant driver over all time periods. Over the satellite record and baseline conditions, the same drivers were significant (Zeu, SST, S, Uo). The warming trend is similar, with the exception of Uo no longer being significant. Drivers varied between the two heatwaves with euphotic depth, sea surface temperature, salinity, and east-west velocity dominant during 2012 and euphotic depth, salinity, and east-west velocity dominant during 2016.

GB: Over the satellite record, only euphotic depth drives phytoplankton abundance. The same drivers were present for both baseline conditions and the warming trend (Zeu, MLD). The 2012 heatwave exhibited more drivers (Zeu, SST, S, MLD, Vo) than the 2016 heatwave (Zeu, MLD, Vo) suggesting a more dynamic event in 2012.

GoM: Over the satellite record, salinity was a driver of phytoplankton abundance. During baseline conditions, mixed layer depth was a driver. Driver composition varies across time periods with increased sea surface temperature, specifically the warming trend (SST, SLA, S, Uo), 2012 Heatwave (SST, S, MLD), and 2016 Heatwave (SST, S, MLD, Uo, Vo).

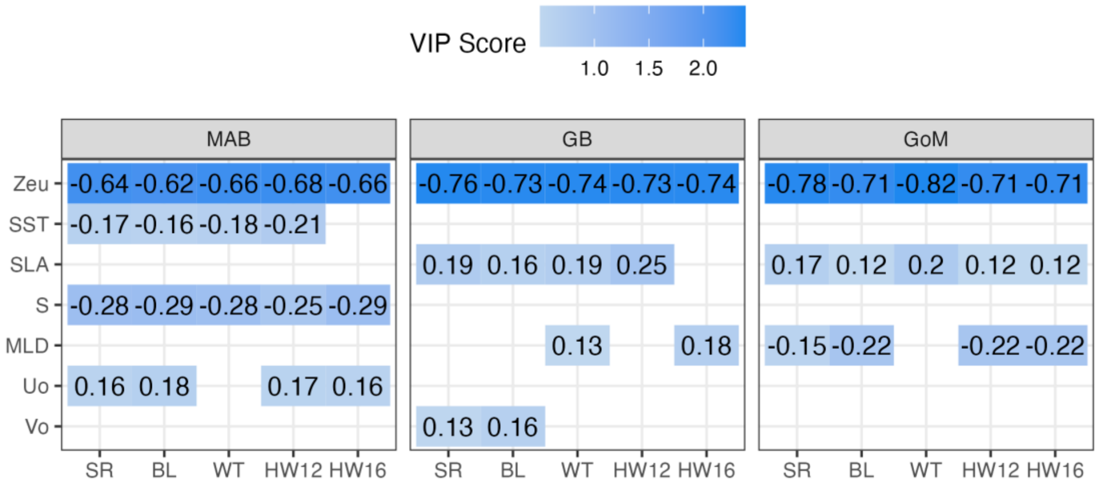

Figure 11. PLSR results for microplankton concentration. Here the north-distinction presents as drivers unique to the north (Vo in GB and SLA and MLD in GB and the GoM. SST, S, and Uo are only drivers in the MAB.

4.2.2. Microplankton

For all regions and time periods, euphotic depth is the unifying driver of microplankton concentration (Fig. 8).

MAB: Across all time periods, salinity drove concentration. Sea surface temperature drove microplankton concentration during all time periods except for the 2016 heatwave. East-west velocity was a driver during every time period except for the warming trend.

GB: For all time periods except for the heatwave in 2016, sea level anomalies with positive coefficients drove microplankton concentration. The mixed layer depth with positive coefficients was a driver during the warming period and the 2016 marine heatwave. North-south current velocity with a positive coefficient was impactful over the satellite record and during baseline conditions.

GOM: Sea level anomalies with positive coefficients were significant drivers over all time periods. Across all time periods except for the warming trend, mixed layer depth with negative coefficients were significant drivers of microplankton concentrations.

4.2.3. Nanoplankton

For all regions and time periods, euphotic depth is the unifying driver of nanoplankton concentration (Fig. 9).

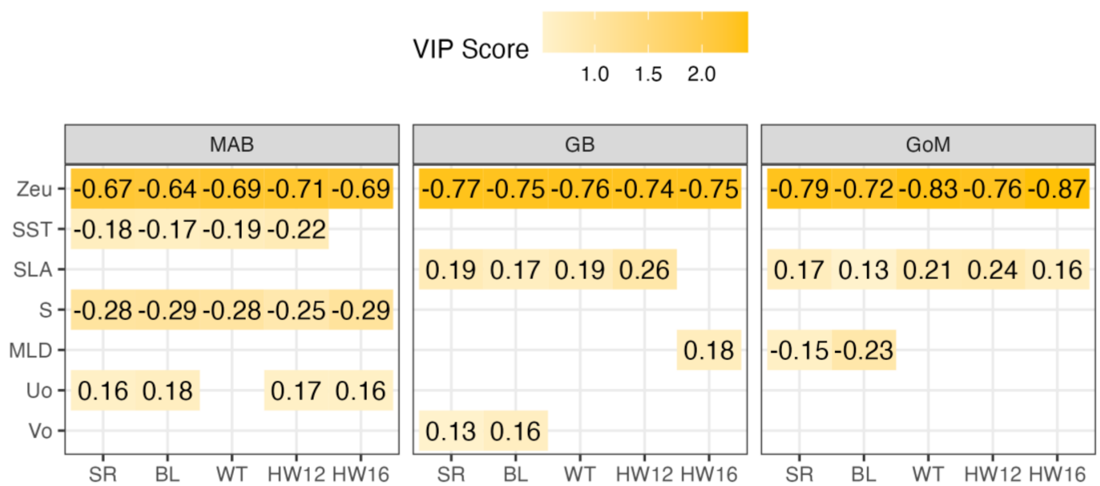

Figure 12. PLSR results for nanoplankton showing a similar pattern of drivers across regions as microplankton: SST, S, Uo in south and SLA, MLD, Vo in north.

MAB: Sea surface temperature, salinity, and east-west current velocity were drivers in all time periods except the 2012 marine heatwave. East-west current velocity was a driver during all time periods except for the warming period.

GB: Sea level anomalies were significant drivers during every time period except for the 2016 marine heatwave. North-south current velocities were significant drivers over the satellite record and during baseline conditions. Mixed layer depth was a significant driver only during the 2016 marine heatwave.

GOM: Sea level anomalies were significant drivers across all time periods. Mixed layer depth was a significant driver only over the satellite record and baseline conditions.

4.2.4. Picoplankton

For all regions and time periods, euphotic depth is the unifying driver of picoplankton abundance (Fig. 10).

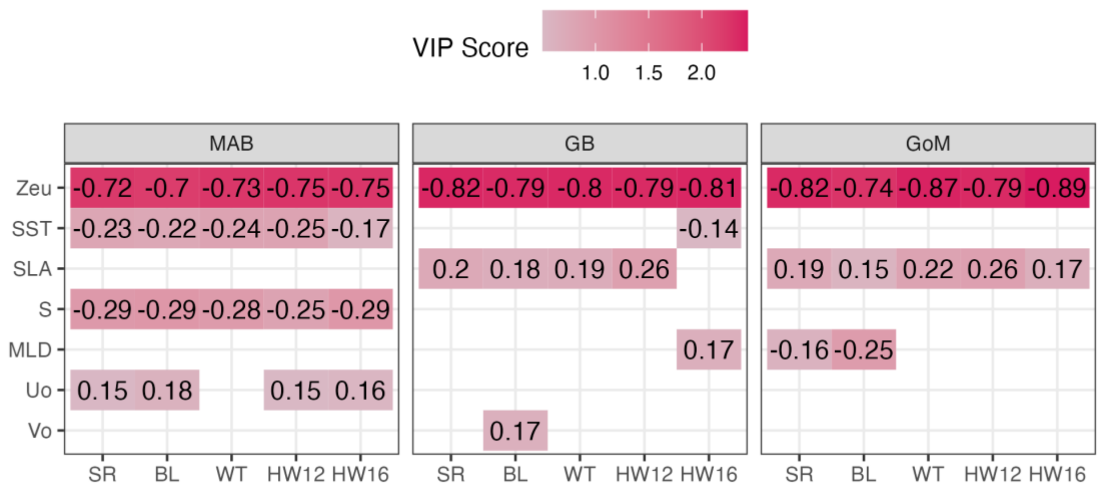

Figure 10. PLSR results for picoplankton, again displaying north-south divergence.

MAB: Picoplankton abundance was driven by sea surface temperature, salinity, and east-west current velocity during all time periods except for the warming period. During the warming period, sea surface temperature and salinity were significant drivers.

GB: Across all time periods, abundance was driven by sea level anomalies. Unique drivers were north-south current velocity during baseline conditions and mixed layer depth during the 2016 marine heatwave.

GOM: Sea level anomaly was a significant driver over all time periods. Mixed layer depth was a driver over the satellite record and during baseline conditions.

5. DISCUSSION

The goal of this study was to describe the environmental drivers of phytoplankton abundance and community size composition across a variety of spatial and temporal scales and determine if variations in drivers existed across those scales. This was accomplished by performing PLSR analysis on ocean color imagery and physical reanalysis products to determine VIP scores of each environmental variable on chlorophyll concentration and phytoplankton size class. From this analysis, it was determined that environmental drivers vary across spatial and temporal scales with respect to abundance and size metrics. Additionally, drivers during periods of increased sea surface temperature (warming trend and marine heatwaves), with few exceptions, were distinct from baseline conditions. These results suggest not only that distinct thermal regimes are evident over the satellite record, but that phytoplankton abundance and community composition response differ over these regimes.

5.1. Rising Temperatures and Phytoplankton: The Bigger Picture

Consistent with other studies, SST is increasing over the total study period across the NES, with an increased rate of warming identified in 2010. The magnitude of change increases along a northward gradient with the GOM displaying the greatest rate of change. When present as a significant driver, SST has a uniformly negative impact on overall chlorophyll concentration, as well as size class concentration. Additionally, temperatures within the NES, specifically in the northern reaches, are rapidly warming at a rate not only faster than the global ocean (Pershing et al. 2015, Saba et al. 2015). While these findings are consistent with previous studies, it is important to note that attempting to isolate singular or few variables as independent drivers of phytoplankton variability are notoriously difficult (Zang et al. 2021) given the complexity of physical and biogeochemical interactions and variable interdependence. While the methodology accounts for this, it is still worth pausing to address the nuances of warming environments and how it relates to larger ecosystem function.

In a vacuum, increased temperatures have a positive effect on phytoplankton growth rate (Eppley 1972), with smaller cells becoming more dominant due to physiological advantages (Mousing et al. 2014). However, this is an untenable view of the role temperature plays. As temperatures increase, the water column becomes more stratified and therefore becomes a constraint on nutrient flux to the surface. Additionally, warmer waters have increased rates of evaporation leading to more and more saline surface water, which in turn further increases overall stratification. Thus, it becomes imperative to further investigate the linkages and correlations between significant environmental variables and the mechanisms controlling phytoplankton abundance and size distribution. Therefore, we consider our findings as pieces of a larger, more dynamic picture.

5.2. Spatiotemporal Variability in Drivers

A main goal of this study was to ascertain if and how environmental drivers varied across thermal regimes. Our results suggest variation in drivers across thermal regimes with specific patterns evident on the regional scale.

Certain drivers are only present in specific regions of the NES during explicit thermal regimes, further highlighting the benefit of high-resolution data.

For example, SST is almost always a driver of chlorophyll concentration and size class abundance in the MAB overall thermal regimes but is only present as a driver in GB and the GOM during the warming trend or marine heatwaves. In reference to our above comments about the intrinsic links between drivers, S is only an environmental driver in the MAB when SST is concurrently significant and is not a driver across any other region. However, this is not surprising given the influence of the warm, saline Gulf Stream on this particular region. Another driver that is only significant in the MAB is east-west current velocity which has a positive correlation with abundance and across size classes.

Another regional distinction occurs with SLA which is only a driver in GB and the GOM. Indicative of a deep nutricline based on its positive coefficient (Mouw et al. 2019), other studies have identified a relationship between SLA and phytoplankton abundance within the same region (Schollaert et al. 2004). Additionally, MLD is a significant driver only in the northern regions and often presents concurrently with SLA. Overall while there is some cross-regional similarity among significant environmental drivers, there is also a clear north-south distinction in grouped drivers likely as a result of the two major current dynamics as the Gulf Stream peels away from the study region before encountering GB and the GOM while conversely little impact from the Labrador Current is observed in the MAB.

5.3. One Size Fits All: Drivers across Size Classes

Results indicate that no one environmental driver is unique to any given size class. Rather it is the relative strength of the driver that may vary across size classes (Fig. 10). No variation is present in Zeu which, as previously stated, is the dominant driver regardless of any scale. SST impacts microplankton and nanoplankton to a greater degree than picoplankton. Given that picoplankton are generally better suited to warmer environments, it follows that those size groups less suited to warmer environments are more affected by increasing temperatures. Following other drivers that influence water column stability, S follows the same pattern as SST, with microplankton and nanophytoplankton more strongly influenced than picophytoplankton. Both SST and S are increasing, presumably leading to a more stratified and therefore nutrient poor environment (due to constrained nutrient flux), which disproportionately impacts larger cells that require more nutrients due to their physiology. These findings are consistent with Pastor et al. (2013) which identified nutrient advection, particularly vertical, to govern abundance.

5.4. Phytoplankton and Heatwaves

In 2012 and 2016, nanoplankton displayed both the greatest increases (GB and the GoM) and decreases (MAB) in concentration, with microplankton displaying a similar, but slightly more subdued trend. This is consistent with other studies which describe a shift of temperate phytoplankton in the context of increasing sea surface temperatures, specifically marine heatwaves (Neukermans et al. 2018). These findings are also supported by Thomas et al.

2012, which identified an increase in phytoplankton diversity as a result of increased temperatures in the northern NES.

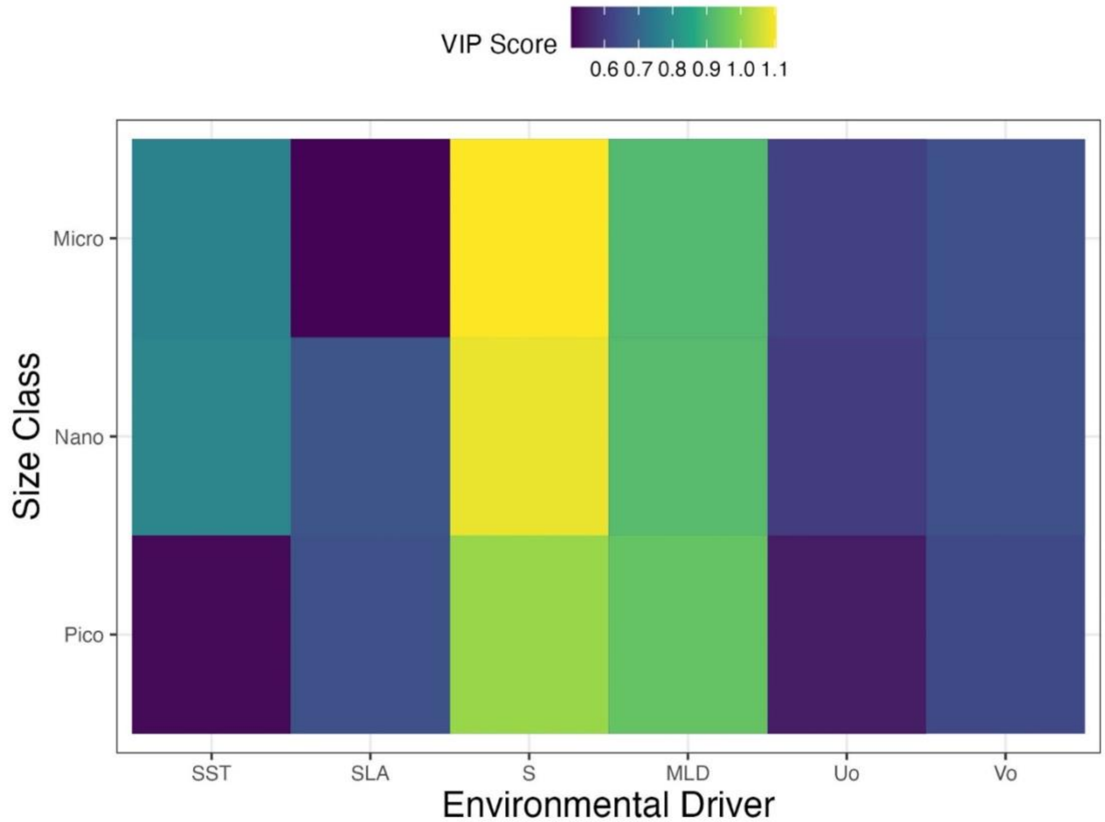

Figure 11. Over the NES across all time periods when considering strength of drivers across size classes, microplankton and nanoplankton are usually

During warming conditions and marine heatwaves, chlorophyll and size class concentrations decreased in the MAB and increased in GB and the GoM. Put another way, there is a clear correlation between SST and PSC when moving northward. Interestingly, SST, with one notable exception, only is a driver of PSCs in the MAB (Fig. 11). Therefore, even though a correlation is present it is not a direct causation of changes to overall phytoplankton concentrations. One way of interpreting this is to consider the role SST plays on growth rate rather than abundance. Soulie et al. (2022) found that during a simulated heatwave, overall concentration steadily declined while the growth rate steeply increased. Furthermore, consistent anomalous increased temperatures can severely constrain nutrient fluxes, both to and from the surface (Gupta et al. 2020). The lack of a uniform result (i.e. concentrations all increasing or decreasing regardless of region) highlights how spatially and systemically complex this region is. Beyond overall abundance and distribution, recent research has also focused on the impact of marine heatwaves on bloom phrenology (Friedland et al. 2023). Under these conditions, stratification can linger past the summer thus restricting the nutrient replenishment that occurs later in the year via increased mixing from storms. Consequently, a delayed bloom would result in a trophic mismatch for the ecosystem (Asch et al. 2019).

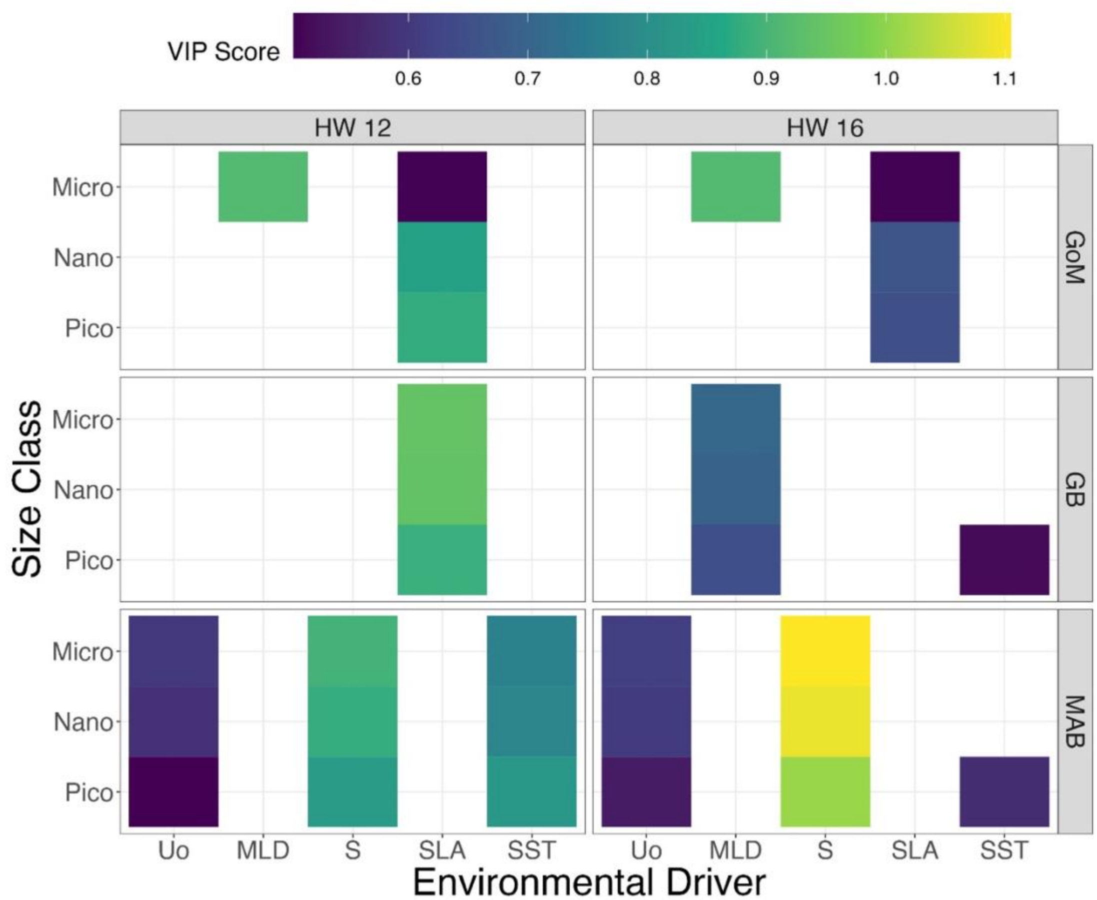

Figure 12. Relative strength of drivers on size classes during each heatwave varied over spatial scales and between each heatwave.

6. CONCLUSION

Our analyses suggest spatial variation across thermal regimes determines environmental drivers of phytoplankton abundance and community size composition within the NES. Euphotic depth is the primary environmental driver across all size classes, however, the relative impact of other drivers varies across size classes. Predictably, size classes less suited to warmer conditions are more impacted by drivers associated with these conditions. The changing community size composition, distribution, and abundance may have negative implications for biogeochemical processes within the region as well as consequences to the marine carbon cycle and food web.

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