Episodic physical forcing and the structure of phytoplankton communities in the coastal waters of New Jersey

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Abstract
The high variability in physical, biological, and chemical properties in coastal waters have limited our ability to sample the appropriate timescale and space scale to resolve physical forcing of the ecosystem. To improve our understanding, a multiplatform adaptive sampling program at the Long-term Ecosystem Observatory (LEO-15) off the coast of New Jersey examined the relationship between episodic summertime upwelling and downwelling events and the corresponding dynamics in bulk phytoplankton biomass and community structure. Inherent and apparent optical properties were concurrently measured to evaluate the use of optics to improve future sampling coverage in coastal regions. Results indicate peak chlorophyll biomass tracked the maximum density gradient and that increasing surface phytoplankton biomass was associated with decreasing stratification offshore over time. Diatoms dominated the study site; however, significant shifts in cyanobacteria and dinoflagellate communities were observed. Dinoflagellate and cyanobacteria communities responded inversely to episodic events, with cyanobacteria being favored during intense downwelling. Differences in phytoplankton absorption properties significantly changed the corresponding in water inherent optical properties, allowing for characterization of the community structure from measurements of above water hyperspectral reflectance.

Introduction
Coastal ecosystems are inherently complex at the land-water-atmosphere interfaces and our knowledge is limited by the ability to measure on the scales of relevant change. There is a long history in physical oceanography of fine-scale measurements (i.e., temperature, salinity, and acoustics), chiefly
attributed to early development and advances in instrumentation. In the same environment, biologists have not enjoyed this larger perspective and have, with the exception of fluorometric measurements, been principally limited to information inferred from discrete sampling. This is juxtaposed with the importance of coastal environments with respect to the disproportionately high productivity of these ecosystems, and the mounting number and intensity of anthropogenic impacts. There is a need therefore to develop sampling tools and approaches that can discern biological change rapidly and at the same scales as the physical dynamics.

Turbulent boundary conditions combine with strong episodic atmospheric forcing resulting in the numerous physical processes that define the complexity in the coastal ocean. Along the New Jersey coast, upwelling begins as a uniform band of cold water along the coast in response to southwesterly winds [Hicks and Miller, 1980; Neuman, 1996]. Interactions with the bottom initially cause a two-dimensional front to evolve into three recurrent upwelling centers located on the downstream sides of three seafloor topographic highs. The locations of these upwelling centers appear to be relatively fixed and have been observed during each summer over the last eight years [Glenn et al., 1996, 2003]. The lifetime of these transient upwelling centers can last from a few days to a full month depending on the local wind conditions and/or the presence of storms, which can be common during the late summer in the Mid-Atlantic Bight. The recurrent upwelling centers are separated from the warm offshore waters by a sharp upwelling front. While the upwelling centers themselves are typically about 25 km in diameter, they contain many relevant features that occur at smaller scales, such as fronts, convergence/divergence zones and coastal jets.

The translation and impacts of these physical dynamics on biological systems have been understudied, given the relative scales of the processes that drive dynamics in coastal regions [Karl and Dore, 2001]. The focus to date has been from a mesoscale perspective, examining the forcing effects, such as coastal upwelling on biomass abundance and distribution [Iriarte et al., 2000; Nave et al., 2001]. Rees et al. [1999] examined storm-induced nutrient pulses and resulting bloom formation and found regional deep mixing was responsible for a doubling of nitrate uptake and a 40% increase in the f ratio. The depth of the mixed layer relative to light attenuation has also been used in coastal systems as a predictor for mesoscale phytoplankton accumulation [Augustí and Duarte, 1999; Brown et al., 1995]. Results from observational studies have been supported by modeling efforts which have shown biomass accumulation to be sensitive to transient wind events leading to upwelling [Carbonel and Valentin, 1999], and to the competing forces of sinking rates relative to the intensity of turbulent diffusion [Ebert
et al., 2001]. These studies show that despite sampling limitations, there is a good working understanding of the general mechanisms influencing the accumulation and bulk distributions of phytoplankton, however, much less is known about the processes selecting for phytoplankton taxonomic assemblages.

Past studies investigating the dynamics of the phytoplankton community as a function of size have shown large particles, represented by diatoms and dinoflagellates are regularly inversely correlated with cyanobacteria and prochlorophytes in coastal systems [Stemmana et al., 2002; Toon et al., 2000]. Large cells tend to dominate in upwelling regions; however, picoplankton can remain a significant contributor to the overall biomass [Chen, 2000]. Cell size has also been shown to be closely correlated with new production, with higher f ratios associated with larger cells [Rees et al., 1999]. In a temporal context, large diatoms transition to nanoflagellates and picoplankton as stable water masses age [Ruardij et al., 1997], with terrestrial nutrient inputs and changes in nutrient ratios often complicating the predicted patterns of succession [Moncheva et al., 2001]. Mediation of light and nutrients through water column turbulence has been shown as a selection mechanism for various phytoplankton groups [Margalef, 1978]. However, examples have been shown where these classical models are not directly applicable [Li, 2002; Ryther and Hulburt, 1960].

Satellite-based optical approaches have given us a meaningful mesoscale perspective for observing and elucidating biological dynamics [DeVilliers, 1998; Sathyendranath et al., 2001] in open ocean environments. The recent challenge has been to expand the utility of optical data in coastal waters to provide distributions of optical constituents and further delineate chlorophyll distributions into respective phytoplankton taxa, with much of this effort focused on the detection of harmful algal bloom species [Schofield et al., 1999]. Despite the inherent difficulties in discriminating between distinct phytoplankton species from natural mixed populations [Garver et al., 1994], there has been progress in noninvasive optical detection of phycobilin-containing algae, such as cyanobacteria, and particular chlorophyll a-chlorophyll c-containing algae, such as Karenia brevis (=Gymnodium brevis (Davis) Steidinger) from in situ hyperspectral absorption measurements [Kirkpatrick et al., 2000; Millie et al., 2002]. Disproportionate loadings of optical constituents in coastal waters from terrestrial runoff [Kirkpatrick et al., 2003], nutrient input, rapid biogeochemical cycling, phytoplankton community changes, and particle resuspension events [Johnson et al., 2001] have led to difficulties in developing retrieval algorithms of optical properties and delineation of phytoplankton groups from
remote platforms. In order to improve interpretation of coastal ocean color and the biogeochemical significance [Glenn et al., 2004] we need a better understanding of changes in community composition driven by physical forcing. Developing this methodology requires a multidisciplinary approach, whereby change in one parameter can be evaluated in the context of others (see Oceanography, 13(1), 2000). It is also important that these studies occur within highly instrumented locations in order to take advantage of the significant refinements in optical instrumentation and the deployment platforms [Dickey and Chang, 2001; Maffione, 2001] and to better identify the scales of significant change [Glenn et al., 2000; Kratzer et al., 2000; Schofield et al., 2002].

In this study, we address two issues relating to the structuring of phytoplankton communities in the coastal ocean. First, we take advantage of several platforms to understand the physical forcing leading to the distribution of chlorophyll biomass and structuring of phytoplankton communities in the coastal ocean. Second, we evaluate our ability to optically detect these changes in phytoplankton biomass and community structure. We will examine cycles of upwelling and downwelling in the coastal ocean, their influence on the strength and depth of the pycnocline, and how these changes relate to the overall distribution of phytoplankton biomass and community structure. Observed changes in the autotrophic community will then be related to the spectral quality of the water column inherent optical properties and above water hyperspectral reflectance in which we identify specific wavelengths to predict phytoplankton community structure.

**Methods**

This effort was conducted at the Long-term Ecosystem Observatory (LEO-15), where an array of sampling platforms including satellites, research vessels and robotic vertical profilers, make up an integrated observation network in a 30 X 30 km coastal area of the Mid-Atlantic Bight [Schofield et al., 2002]. Measurements of in-water physical, optical and biological data, as well as discrete samples were taken from cross-shore transect lines A and N from 12 July through 6 August 2001 (Figure 1). The transect lines were approximately 20-km long, ranging in bathymetry from 10 m inshore to 28 m offshore. In addition, a time series of temperature and fluorescence profiles were taken from a robotic profiling node located on the A line. The profiling node and the instrumentation package are described by Oliver et al. [2004].
Shipboard Sampling

Shipboard sampling was conducted by two vessels; the R/V Caleta and the R/V Walford. Data from the R/V Caleta were collected continuously from a towed Guildline miniBAT undulating platform. Mounted on the platform were a Falmouth Scientific, Inc. Micro CTD and a WET Labs WETStar fluorometer. CTD data were parsed into 0.25-km distance and 0.25-m depth bins (undulating > 2 m), and were used to quantify the depth of maximum stratification defined by the Brunt-Väisala buoyancy frequency ($N^2$),

$$N^2 = \frac{\frac{\partial \rho}{\partial z}}{\rho g},$$

where $g$ is gravity, $\rho$ is density and $z$ is depth. CTD data were also used to calculate the value of the maximum density gradient. Data from 13 cross-shore transects were used in this study.

The R/V Walford sampled the study area using a profiling instrument cage equipped with a WET Labs nine-wavelength absorption/attenuation meter (ac-9) (412, 440, 488, 510, 555, 630, 650, 676, and 715 nm), a six-wavelength backscatter/fluorometer HOBI Labs HydroScat-6 (442, 488, 532, 589, 620, and 676 nm), and a Sea-Bird SBE-19 CTD. Absorption data were temperature [Pegau et al., 1997] and scattering corrected by subtraction of absorption at 715 nm from all a channels [Zaneveld and Kitchen, 1994]. All data were binned to 0.25-m depth intervals. Only the fluorescence data from the HydroScat-6, with excitation at 488 nm and detection at 676 nm, were used in this study. In addition to profiling, downwelling irradiance ($E_s$) and upwelling radiance ($L_{sfc}$) from 328 to 1014 nm (0.34-nm resolution) were collected using a HOBI Labs HydroRad-3 (the third sensor, $E_u$, was not used in this study). The fiber-optic sensors were suspended 4 m perpendicular to the ship, 3 m above the ocean surface. The $L_{sfc}$ sensor was oriented at a zenith angle of 20° to avoid angles higher than 50° during significant ship motion of the relatively small research vessel [Mueller et al., 2003]. The azimuth angle of the sensor was between 90° and 270° (relative to the sun's azimuth of 0°) when taking measurements to reduce the effects of ship shadow. Thirty spectra of $E_s$ and $L_{sfc}$ were collected sequentially per station. Spectra with an $L_{sfc}$ spectral mean difference of >15% were removed (along with the corresponding $E_s$ spectra) to avoid sun glint effects prior to calculating mean spectra for $E_s$ and $L_{sfc}$. Mean spectra for each station were only used in this study if the mean represented more than 20 of the original 30 spectra. The ratio of the two spectra ($L_{sfc}/E_s$), referred to as reflectance (R) throughout the manuscript, was used as an approximation of remote sensing reflectance defined by NASA protocols [Mueller et al., 2003]; sky reflectance was not measured during this experiment. For this study, the hyperspectral data set was reduced to 46 distinct wavelengths at 8.2-nm intervals between 400 and 750 nm because of statistical limitations and relevance to visible phytoplankton absorption.
Discrete samples for phytoplankton pigmentation were collected from the surface (<1 m) using a 10-L Niskin bottle. Samples for pigmentation analyses were filtered onto a 47-mm GF/F filter and stored at -80°C until analyses.

**Remote Sensing**

Sea surface temperature was collected from the NOAA 12 and NOAA 14 advanced very high resolution radiometers (AVHRR), processed according to [Bernstein, 1982]. Up to nine passes per day were collected at the Rutgers University Institute of Marine and Coastal Sciences (IMCS), New Brunswick, NJ. A total of 42 cloudless scenes taken between 0600 and 1000 were used in this study. Ocean color data (47 scenes) were obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) by the IMCS HRPT station and processed for chlorophyll a retrieval according to Stumpf et al. [2000].

**Analytical Procedures**

Samples for pigment determination were extracted for 12 hours in 5 mL of 90% acetone and sonicated for 30 s. Samples were vortexed for 30 s and centrifuged at 2700 RPM for 2 min, and run through a 0.2-μ m inline filter (Osmonics). Samples were analyzed on a Hewlett Packard 1100 series HPLC equipped with a diode array spectrophotometer according to Wright and Mantoura [1997]. Pigment peaks, were identified on the basis of retention time and absorption spectra. Peak concentrations were calibrated using a dilution curve from standard pigments (DHI, Water and Environmental, Denmark). A Shimadzu 2501 UV-VIS spectrophotometer was used to determine the pigment concentration of the standards.

Abundances of each phytoplankton group within a water sample were obtained from output of CHEMTAX, on the basis of the pigment concentrations obtained from HPLC analysis [Mackey et al., 1996]. CHEMTAX uses factor analysis and a steepest descent algorithm to find the best fit to the data based on an initial set of pigment ratios for specific taxa determined by the user. The phytoplankton taxa included in this analysis were: diatoms, dinoflagellates, cyanobacteria, cryptophytes, haptophytes (containing fucoxanthin, 19°-hexfucoxanthin, and chlorophyll-c3), prasinophytes, and chlorophytes. While the pigment ratios can vary with light history and among particular species within specific taxonomic groupings, and influence model output, this method has been evaluated successfully with numerous lab and field data sets [Ansoteguietal., 2001; Higgins and Mackey, 2000; Mackey et al., 1998, 1996; Millie et al., 2002; Wright and van den Enden, 2000].

Internal consistency in the in situ fluorescence data measured from multiple instruments as well as the discrete chlorophyll a determined by HPLC are required for any discussion of biomass distributions and extrapolation to changes in the community structure. These relationships have been shown to vary significantly, especially at the surface, because of solar stimulated fluorescence [cf. Falkowski and
Raven, 1997] and by the contribution to fluorescence by chlorophyll b [Trees et al., 2002]. Effects of solar quenching in this study, however, were not evident, likely because of the high attenuation of the water [Schofield et al., 2004]. Differences in the detection wavelengths of the instruments used here (685 nm for the WET Labs WETStar and 676 nm for the HOBI Labs HydroScat-6) may also introduce phytoplankton specific differences in the fluorescence signals. In this study, the proxy measures for phytoplankton biomass (in situ chlorophyll fluorescence and discrete measures of chlorophyll a) were all significantly correlated. Surface data from the in situ fluorescence measured using the WETStar (the upper 2 m of the undulating profiles) and the HydroScat-6 (profiling) fluorometers were significantly correlated ($r^2 = 0.50$, $p < 0.01$, $n = 47$). The correlations between discretely measured chlorophyll a and both the WETStar and the HydroScat-6 fluorometers were also significant ($r^2 = 0.57$, $p < 0.01$, $n = 27$ and $r^2 = 0.67$, $p < 0.01$, $n = 110$, respectively). Contour figures generated in this manuscript were linearly interpolated at the minimum timescale and space scale actually sampled.

**Statistical Methods**

Canonical Correlation Analysis (CCA) was the primary means of discerning significant relationships between physical, biological, and optical data. CCA is a multivariate technique, which optimizes the coefficients of a linear combination of predictors and a linear combination of responses, such that their correlation is maximized [Dillon and Goldstein, 1984; Mardia et al., 1979]. The second-order canonical correlations find linear combinations that maximize the correlation subject to being uncorrelated with previous canonical variables. The number of canonical correlations is limited to the minimum of the number of variables in the two sets. Statistical significance of each successive correlate ($p < 0.05$) is determined using Wilk's Lambda and confirmed with Pillai and Lawley-Hotelling. Wilk's Lambda calculates the F statistic and is used to determine the significance of the canonical correlation. It is analogous to testing the significance of a univariate regression using a z test. CCA is a good approach for understanding dynamic relationships because it takes into account the interplay that may exist between variables, while at the same time enabling identification of those parameters that were the most significant contributors to the relationship. This is true only when parameters are standardized, achieved here by using a derived correlation matrix of the parameters for each CCA. These attributes of CCA increase our ability to accurately interpret relationships between physical, biological and optical parameters, and thereby facilitate a clearer understanding of the dynamics present in a complex system. CCA has been applied in previous studies to identify relationships, similar to those being examined in the current study, between planktonic community structure and the physical and chemical dynamics associated with an upwelling event in the Iberian Upwelling system [Joint et al., 2001].
As in a regression, the CCA yields coefficients that are associated with each parameter in their respective linear combinations. These coefficients can be used to help evaluate the contribution of a particular parameter to the overall relationship between predictors and responses. This approach, while often applied as by Joint et al. [2001], can be difficult to interpret when the number of parameters involved increases. In order to address this issue we have developed a new approach that applies a general linear model in which the individual components of the predictor linear combination are used to predict the response variable or rather, the linear combination resulting from the CCA. This enabled objective interpretation of CCA results, as we were able to identify the statistical significance of each individual parameter's contribution to the correlation as a whole. This approach effectively decreases the number of parameters used to aid interpretation of relationships.

In addition to CCA and the general linear model, a Generalized Least Squares Regression Analysis (GLS) was applied in order to evaluate and interpret the univariate relationships between indicators of overall phytoplankton biomass and physical variables. Physical variables included depth of the pycnocline and the maximum gradient. A generalized least squares approach was taken in order to account for spatial autocorrelation in the data, which can sometimes lead to overestimates of r values. This model used an AR(1) autocorrelation structure for each transect, observations were equally distributed every 0.25 km [Carrol and Ruppert, 1988; Davidian and Giltinan, 1995; Littel et al., 1996; Venables and Ripley, 1997].

In this study, we combine the use of CCA and GLS in four tests to understand the physical forcing of biomass and community structure, and the influence of community structure on the inherent and apparent optical properties. The first CCA was used to determine the strength and significance of the relationship between two physical variables ($N^2$ and max density gradient) and the bulk chlorophyll biomass signal represented by surface fluorescence and total fluorescence. The second CCA was used to calculate relationships between these two physical parameters and the phytoplankton community composition. The last two CCA tests were used to determine which wavelengths of the inherent and apparent optical properties best describe the measured community composition. Last, we evaluate the results of our CCA analysis on the apparent optical properties as a predictive tool for detection of phytoplankton community structure.

**Results**

**Upwelling and Downwelling Regimes in the Mid-Atlantic Bight**

The nearshore waters of the Mid-Atlantic Bight in the summer season are characterized by a two-layered system separated by a strong offshore pycnocline. The vertical and horizontal position of the
pycnocline relative to the coastline varies considerably during alternating upwelling/downwelling states and is dependent on the intensity and duration of forcing events. There are two dominant conditions that coalesce to produce a given cross-shelf density gradient [Münchow and Chant, 2000]. Strong winds from the southwest produce upwelling conditions where the nearshore pycnocline angles upward in the water column producing an alongshore horizontal front (Figure 2a). In the opposite downwelling condition, the nearshore pycnocline angles downward from the horizontal offshore pycnocline and is often in contact with the bottom boundary layer (Figure 2c). The strength of the downwelling or upwelling determines the relative offshore position of the benthic or surface “front”, respectively. In either of these conditions, inshore stratification throughout the water column is comparatively weak and allows for thorough mixing to the bottom. For intermediate conditions, there is spreading of the isopycnals with a strong alongshore current [Yankovsky et al., 2000]. In addition to the upwelling and downwelling, there are uniform vertical displacements of the pycnocline across the shelf from larger mesoscale forcing that contribute to the overall physical variability in the study area (Figure 2).

Generally, phytoplankton are concentrated along the pycnocline when it is shallow in upwelling conditions (Figure 2b) and are distributed more evenly throughout the water column when the pycnocline is deeper, particularly during strong downwelling events (Figure 2d). Phytoplankton are concentrated inshore with the biomass being transported offshore via eddy formation mediated by bottom topography [Glenn et al., 1996]. High concentrations of biomass in the water column can be further enhanced during moderate upwelling and downwelling events when stratification is weak and benthic phytoplankton are resuspended.

From the beginning of May until the end of August 2001, the nearshore coastal region along the N transect line (Figure 1) showed the seasonal pattern of sea surface warming (Figure 3a). Regional warming peaked at the end of June with cooler waters (-18°C) evident inshore in July suggesting a strong upwelling event at the end of June [Glenn et al., 2004]. With the exception of weak inshore upwelling (cooling) events toward the end of June and July, and the beginning and end of August, the region was characterized by high temperatures, indicating predominantly downwelling conditions. The regional distribution of chlorophyll also showed a seasonal increase in biomass through the spring and into the summer (Figure 3b). Phytoplankton biomass from May through August 2001 was concentrated along the coast and showed periodic increases and decreases. The frequency of these events was approximately every two weeks and increased in intensity further offshore with time. These seasonal phytoplankton biomass dynamics were consistent with the previously described atmospherically forced upwelling/downwelling nature of this shelf region [Glenn et al., 1996, 2004].
the context of these regional temperature and chlorophyll patterns, this study follows two nearshore upwelling events in a predominantly downwelling condition from 12 July through 6 August 2001.

**Physical and Biological Dynamics in Relation to Community Composition**

The experiment was dominated by alternating upwelling and downwelling conditions driven by changes in the prevailing winds (Figure 4a). Temperature measured by a nearshore robotic profiler demonstrates this episodic forcing and is consistent with the dynamics inferred by the remotely sensed data (Figures 4a and 4b). The vertical distribution of phytoplankton biomass over this period showed low concentrations in the cold upwelled shelf water and high concentrations generally seen above the pyconocline during periods of strong stratification (Figure 4). Biomass showed an increased concentration during down-welling conditions suggesting growth throughout the weakly stratified water column. The water mass replacing the upwelled waters on 27 July had significantly higher concentrations throughout the water column, with the entire water column showing enhanced phytoplankton loads inshore through the end of the study (Figures 2 and 4c).

With the cross-shore pycnocline depth varying on timescales of days, it is not possible to characterize the regional dynamics from single transects or stationary profilers. Figure 5 provides an integrated view of the physical dynamics of this coastal site for the duration of the study as a function of distance offshore. The maximum density gradient and the depth of the maximum buoyancy frequency ($N^2$) indicate a strong shallow density gradient when the study began (Figures 5a and 5b), consistent with the inshore time series data (Figure 4b). The gradient remained strong but was pushed deeper during 16 July and pushed up temporarily on 17 July. This brief forcing event is consistent with the upwelling favorable winds on 17 and 18 July (Figure 4a). For the greater part of the study, downwelling conditions prevailed to the degree that the maximum $N^2$ depth was the bottom depth (Figure 5b). Under these conditions, for example, on 23 and 24 July and from 31 July to 3 August, there were minimal vertical density gradients particularly inshore and these minimal gradients occasionally extended up to 10 km offshore. Data show a weak relaxation in downwelling on 28 July (Figure 5a), however, this was most likely residual from the upwelling from the prior two days (Figure 4b).

The cross-shore integrated fluorescence above the maximum $N^2$ depth generally showed increasing phytoplankton biomass over the course of the study (Figure 5c). With the exception of two periods of high fluorescence offshore at the beginning and end of the study, there was a cross-shore gradient with higher concentrations inshore. The cross-shore integrated fluorescence was largely dependent on the depth of the maximum $N^2$, with the highest concentrations of phytoplankton biomass occurring in conjunction with the strong downwelling conditions, when the bottom was “exposed” to surface
mixing. Integrated fluorescence above the maximum $N^2$ depth and surface fluorescence were significantly correlated for 10 of the 13 transects ($p < 0.01$, $n = 80$ for each transect). The three cases where the correspondence was weak occurred during the two periods of intense downwelling described above (Figure 5b). Because of these large fluctuations in the depth of the maximum $N^2$ inshore relative to the bottom depth, the relationship between surface fluorescence to the total depth-integrated fluorescence showed higher variance inshore with greater consistency >10 km offshore (Figure 6). Offshore the surface fluorescence was uniformly ~11% of the total integrated values rising to over 20% inshore. The twofold increase in the inshore fluorescence ratio between surface and the integrated total was driven primarily by the increases in surface fluorescence (data not shown) and to a lesser extent the shallow water depths (Figure 5b). For the entire cross-shore data, 70% of the variance in the ratio was driven by changes in surface fluorescence. Consequently, surface measurements provide the best indicator for overall distribution of phytoplankton biomass during this study. There was a significant correlation between the SeaWiFS chlorophyll a (Figure 3b) and the surface fluorescence for all paired cross-shore time series data ($r^2 = 0.49$, $p <0.01$, $n = 39$), despite the satellite sensing only the first attenuation length, which was typically <2 m depth. This provides further confidence for interpretation of both the seasonal biomass trends and the in situ physical dynamics. Discrete surface measurements of chlorophyll a also showed a general increase in the concentration with time, with higher concentrations inshore (Figure 5d). There was also a clear temporal propagation of high chlorophyll a offshore. A decrease in the cross-shore concentration was measured on 1 and 2 August 2001, coinciding with the period of intense downwelling when clear shelf waters on the surface are pushed onshore (Figures 4b and 5a).

**Phytoplankton Community Structure**

In addition to quantifying phytoplankton biomass distributions, this study provided the opportunity to examine the dynamics of community structure with changes in the physical regime. The dominant phytoplankton taxa during the study were diatoms, averaging 35% and occasionally representing more than half of the biomass (Figure 7a). There were higher concentrations of diatoms early in the sampling season and inshore, but generally there were no conspicuous shifts or trended changes in the group. Dinoflagellates averaged 20% of the phytoplankton biomass, but showed more changes than diatoms (Figure 7b). Early in the sampling period, dinoflagellates decreased when diatoms peaked, and by late in the experiment, beginning 27 July, dinoflagellates were almost nonexistent while diatom biomass remained at 30% of the total. The decrease in percent of total biomass in dinoflagellates was marked with a proportional increase in cyanobacteria biomass (Figure 7c). This prominent shift in community structure was coincident with the intense downwelling that occurred during the first two
days of August (Figure 5a). Cryptophytes averaged 10% of the total biomass and, unlike the trend in chlorophyll a, “moved” onshore with time with a slight increase during the same downwelling event that corresponded to the increase in cyanobacteria (Figure 7d). Prasinophytes contributed <10% for most of the season and showed the opposite pattern of the haptophytes (Figure 7f) and a similar pattern to the overall phytoplankton biomass trends (Figure 5d). Over the study period, chlorophytes represented a background contribution of <10% (data not shown).

Coherence of Physical Variables with Phytoplankton Biomass Distributions and Community Structure

A canonical correlation analysis (CCA) yielded a significant correlation between the two physical variables, defined by the depth of maximum $N^2$ and the maximum density gradient, and the phytoplankton abundance/distribution, as defined by surface fluorescence and total integrated fluorescence. Moreover, the relationship is explained in two dimensions, as both of the correlates are statistically significant (Table 1). For the first correlate, surface fluorescence was most related to the maximum gradient. In the second correlate the total integrated fluorescence was most related to the depth of maximum stratification (Table 1). There is a negative relationship in the first correlate between surface fluorescence and the maximum gradient, indicating increases in the phytoplankton biomass at the surface during periods of weaker stratification. Furthermore, in the second correlate the coefficients of the physical parameters have opposite signs suggesting that increases in total integrated fluorescence are related to increases in the depth of maximum stratification and decreases in the maximum gradient (Table 1). This result is consistent with Figure 5, which illustrates that the total phytoplankton biomass increases during downwelling conditions where the maximum gradient is low and the depth of maximum stratification is either deep or at the bottom.

When the relationship between surface fluorescence and the two physical variables is evaluated using the univariate Generalized Least Squares regression, only the depth of maximum stratification is a significant predictor of surface fluorescence ($p<0.001, n = 1010$). This result, in conjunction with the coefficients of the first correlate suggests that surface fluorescence tends to increase during less stratified conditions with shallower depths of maximum stratification. Interestingly, neither of the physical variables are significant predictors of the total integrated fluorescence in the univariate test ($p > 0.05, n = 1010$). This contrast in the univariate and multivariate results illustrate the variability between surface fluorescence and total integrated fluorescence particularly nearshore (Figure 6).
A CCA was used to examine the relationship between the physical variability of this coastal site and the temporal and spatial changes in phytoplankton taxa. When comparing the relative abundance of the seven phytoplankton groupings identified by CHEMTAX to the maximum density gradient and depth of maximum $N^2$, significant relationships were found. A maximum of two correlates was possible because only two physical variables were included, and both correlates were determined to be statistically significant (Table 2). In the first correlate, cyanobacteria, dinoflagellates and diatoms contributed the most to the significance with the highest coefficients. They were negatively related to the maximum gradient indicating that as the maximum density gradient decreased, these three groups of phytoplankton increased (Table 2). Cryptophytes had the largest contribution to the second correlate and were negatively related to the depth of maximum $N^2$. Diatoms and dinoflagellates also contributed significantly to the second correlate. These results indicate that these groups were favored during conditions characterized by a shallow weakly stratified pycnocline. Although diatoms may not be a typically dominant group in offshore waters advected onshore during downwelling events, the significance of diatoms in this analysis appears to be caused from resuspension of benthic diatoms nearshore, when there was little or no density gradient (Figure 7a). This interpretation is supported by observations of benthic diatom mats frequently covering the bottom during the summer months (J. Dobarro, unpublished data, 2000) and microscopic observations of near-shore samples taken at the profiling mooring (Figure 1), which showed a presence of raphid pennate diatoms. Consistent with CCA results, which suggest dinoflagellates were favored during weak stratification and shallow maximum $N^2$ depths, dinoflagellates showed a marked increase corresponding to the relaxation of the downwelling conditions from 23 to 27 July. On 29 July, dinoflagellates show a dramatic decrease to less than 10% of the phytoplankton biomass corresponding to the start of the second period of intense downwelling (Figure 7b). The period of intense downwelling, when cyanobacteria dominated and dinoflagellates were nearly nonexistent, was the primary driver of the negative relationship between dinoflagellates and depth of maximum $N^2$ and would be consistent with other periods during the experiment when weaker downwelling conditions were associated with increased dinoflagellate biomass (Figure 7b).

**Phytoplankton Community Structure and Optical Variability**

The surface biomass patterns corresponded well with the changes in the spectral absorption and attenuation (Figures 5d and 8), with absorption decreasing during the strong downwelling event from 31 July to 3 August (Figure 8a). Using a general linear model we established relationships between biomass and specific wavelengths of the inherent optical properties (IOPs). The strong correlations
between chlorophyll and absorption ($r^2 = 0.81, n = 110$) and attenuation ($r^2 = 0.83, n = 110$), particularly in the blue (440 and 488 nm) and red (650 and 676 nm) wavelengths indicate that phytoplankton were a dominant optical constituent of the study site even in nearshore Case II waters where other optical constituents were also contributing [Schofield et al., 2004].

The relationships between community dynamics and optical signatures were evaluated by comparing absorption and attenuation to the community biomass structure, obtained by multiplying percent community abundance with the measured chlorophyll a concentrations. The CCA between absorption and community structure identified the first four correlates as significant (Table 3 and Figure 9a). In the first correlate, the four predominant phytoplankton groups during the season (diatoms, dinoflagellates, cyanobacteria, and cryptophytes) were the most significant contributors to the correlation. Of the eight absorption wavelengths only absorption at 676 nm was identified as a significant contributor to the correlation, suggesting that the first correlation primarily describes the relationship between absorption and phytoplankton biomass. This is further supported by the coefficients of the four phytoplankton taxa, which were positively related to the coefficient of absorption at 676 nm (Table 3). In the second correlate, the most abundant phytoplankton group, diatoms, are not significant. Cyanobacteria, along with dinoflagellates, haptophytes, and chlorophytes were identified as the significant contributors. Consistent with this contribution of less abundant taxa is the presence of highly significant absorption wavelengths at 412, 440, and 510 nm as well as 676 nm (Table 3). These additional taxa and wavelengths suggest that not only will changes in overall biomass be evident in the optical signature, but also that shifts in the community structure are significantly related to changes in the optical signature. Cyanobacteria were the most significant to the second correlate and their increased contribution to the community absorption likely added significance in the blue. Although peak absorption for phycobiliproteins is greater than 550 nm [Rowan, 1984], the significance at 510 nm may result from the combination and contribution of the carotenoid pigments from the other taxa. In the third correlate, 676 nm was the only significant wavelength identified, suggesting again a relationship between absorption and overall biomass. Only half of the variance of the relationship between absorption and phytoplankton community structure was described by the fourth correlate (Table 3).

The first four correlates were again significant when comparing attenuation with community abundance (Table 4 and Figure 9b). As with the first and third correlates comparing absorption (Table 3), attenuation at 676 nm was significant in all four of the correlates, reflecting the importance of changes in overall phytoplankton biomass (Table 5). This is further supported by the results, which identified only red and blue wavelengths as significant contributors to each of the four correlations.
Additionally, in the first correlate, two of three phytoplankton taxa identified as significant contributors were diatoms and cyanobacteria, which were the two most dominant phytoplankton taxa during more than half of the study. The significant relationships between phytoplankton community abundance and IOPs further suggest the abundance of phytoplankton taxa would be related to the above water reflectance ratio of incident surface irradiance ($E_s$) to upwelling radiance ($L_{src}$).

Reflectance ($R; L_{src}/E_s$) data were compared to phytoplankton community abundance using CCA and the two were highly correlated (Figure 10). These analyses showed significance in the first four correlates (Figure 11). All phytoplankton classes contributed significantly to the relationship described in the first correlate, while only 5 of the 46 wavelengths included in the CCA were significant (Figure 11a). Of the 5 wavelengths, 3 were located in the blue portion of the reflectance spectrum (409.9, 458.8, and 474.5 nm) and one in the red, near maximum chlorophyll a absorption, at 660.2 nm. The fifth wavelength corresponded to the wavelength of maximal reflectance at 568.9 nm (Figure 11a). There was a negative relationship between the two most dominant taxa, diatoms and dinoflagellates, and $R$ at 660.2 nm and a negative relationship between cyanobacteria and the peak reflectance wavelength of 568.9 nm. In the second correlate, haptophytes and cryptophytes were no longer significant contributors, and thirteen wavelengths were identified as significant, only one of these wavelengths overlapped with the significant wavelengths in the first correlate. Diatoms, dinoflagellates, and cyanobacteria were negatively related to $R$ in the blue and red (Figure 11b). All phytoplankton groups except for dinoflagellates and haptophytes were significant contributors to the third correlate and eight wavelengths ranging from blue to red were identified as significant contributors to the correlation, of eight wavelengths identified in the third correlate as significant contributors, none of them overlapped with those wavelengths identified in the first correlate.

Common wavelengths between the second and third correlates occurred at 450.5, 514.2, and 682.5 nm. As in the first correlate, all of the phytoplankton groups in the fourth correlate were significant (Figures 11c and 11d). Of the eleven significant wavelengths in the fourth correlate, two overlapped with the first correlate (474.5 and 660.2 nm) and two with the third (514.2 and 667.6 nm). The additional significant wavelengths in the second, third, and fourth correlates and the falling out of dominant taxa as significant contributors in the second and third correlates (Figure 11), indicate that these correlates not only reflect the relationship between bulk phytoplankton biomass and $R$ but also the relationship between less dominant taxa and more subtle spectral shifts in the $R$ measurement.

**Predicting Phytoplankton Community Structure with Apparent Optical Properties**

Given that all phytoplankton taxa were determined to be significant contributors to the correlation between reflectance ($R$) and phytoplankton community, a multilinear model was developed to predict
phytoplankton community abundance from R. Coefficients for the model were generated using a random 75% of the data and cross validated with the remaining 25%. The model was developed with the successive addition of the significant wavelengths from each of the four correlates. The inclusion of all 25 wavelengths identified in the CCA resulted in the best prediction of phytoplankton community abundance (Table 5). With the exception of diatoms, the model was able to significantly predict each of the other six phytoplankton taxa (Table 5, p < 0.01).

Discussion

The coastal ocean in the Mid-Atlantic Bight is characterized by mean southwesterly flow with frequent upwelling and downwelling events that are mediated by atmospheric forcing [Beardsley and Boicourt, 1981; Glenn et al., 1996, 2000]. The scale of these periodic events is on the order of days, which manifest themselves on kilometer scales from the coastline [Münchow and Chant, 2000]. Sampling on these scales is therefore required to evaluate physical processes and evaluate their impact on biological communities. There has been a concerted effort in the past two decades to advance beyond phytoplankton biomass measurements and to understand what regulates algal assemblages. Phytoplankton community structure within a water mass has been shown to change rapidly in response to water column stabilization [Moline, 1998], differential nutrient availability [Pinckney et al., 1999, 1998], light quality/quantity [Prézelin et al., 1989; Schofield et al., 1993, 1991] and selective grazing [Kopczynska, 1992]. Variations in phytoplankton communities can differentially influence primary productivity, nutrient utilization [Moline et al., 2002], and trophic ecology of a region (i.e., harmful algal blooms). Mapping phytoplankton community structure has been problematic as it is difficult to sample a specific water mass over a sufficient area long enough to detect change. Recent work has shown that nearshore upwelling along the Mid-Atlantic Bight does not necessarily follow the traditional model of a two dimensional system, adding complexity to identifying the sources of water masses. Chant et al. [2004] show that the replacement of surface water does not simply originate from cross-shore flow and that topographically mediated alongshore jets often supply the upwelling centers from the north. Examination of the temperature-salinity (T-S) data from the cross-shore transects showed that two separate water masses dominated under stratified conditions, cold saline bottom water, and warm surface water (~1 ppt less saline; data not shown). Over the course of the 2–3 upwelling/downwelling cycles during the experiment, the T-S signature of the surface waters did not change. The T-S signatures from the bottom water, however, indicated there was a different water mass after 23 July (slightly warmer and ~0.5 more saline) that was maintained until the end of the experiment. As the analysis was focused on the surface water communities and the period after 23 July
was dominated by down-welling conditions, the impact on these results was most likely minimal. An indirect effect of this could have been an altered nutrient regime at the pycnocline, which has been shown to impact physiology and be responsible for an additional 25% increase productivity [Ruardij et al., 1997].

During the course of this experiment, physiological changes in the autotrophic community were detected, as indicated by the fluorescence yield (the ratio of fluorescence to absorption at 676 nm). This ratio is a rough proxy of the photosynthetic efficiency of the autotrophic biomass when normalized to the ambient light field; with the most efficient cells showing lower fluorescence yields relative to their ability to absorb light [Falkowski and Raven, 1997]. The fluorescence yields tracked the cross-shore physical dynamics and were found to be significantly different on the basis of samples taken during upwelling versus downwelling conditions (p < 0.01; t test). Higher values were associated with downwelling conditions (mean relative fluorescence yield = 0.045 ± 0.0007) and correspondingly, during the three upwelling events on 17 and 28 July, the ratio was lower (mean relative fluorescence yield = 0.040 ± 0.0001; Figures 4 and 5). There was also a trended increase in the ratio after 28 July accompanying the shift in taxonomic composition, suggesting the phytoplankton community during this time was senescing and/or that particular taxa were at differing physiological states. This is further evidence that the bottom water change on 23 July did not significantly influence surface communities. Cyanobacteria, which were advected into the study area during this period by down-welling, have been shown to have higher fluorescence yields [Campbell et al., 1998; Sundberg et al., 1997].

The trend in chlorophyll accumulation tracked the maximum density gradient, with increasing chlorophyll associated with the decrease in stratification offshore over time. The CCA results also confirmed the significance of the decreasing density gradient favoring biomass accumulation and increased abundances of the dominant taxa (Tables 1 and 2). The nearshore phytoplankton community showed high proportions of diatoms during upwelling events with lower fluorescent yields, likely to be benthic communities that were resuspended in weakly stratified water. Resuspension of benthic assemblages adds a potentially challenging task of differentiating between the effects of episodic physical forcing and the impact of resuspension on water column communities. The high frequency of weak stratification inshore during both upwelling and down-welling conditions, makes this differentiation even more difficult. In addition, benthic communities have been shown to have a high diversity (J. W. Louda and P. Monghkransri, Comparisons of spectrophotometric estimates of chlorophylls a, b, c and
‘pheopigments’ in Florida Bay seston with that obtained by high performance liquid chromatography-photodiode array analyses, submitted to Bulletin of Marine Science, 2002). Resuspension may explain the temporal trends in less abundant taxa over time, with decreasing haptophyte concentrations and increasing prasinophytes concentrations. Haptophytes are predominately water column cells [Lee, 1999], while prasinophytes have a significant number of benthic nonmotile marine species [Graham and Wilcox, 2000]. Although results here imply that more work in this area is needed, from an ecological perspective, the simple application of traditional deterministic models of phytoplankton succession and dominance [Margalef, 1978] might not directly apply in these shallow environments. In fact, the CCA analysis indicated that dominant taxa were responding to the physical environment similarly, with the coefficients for the taxa having the same signs (Table 2). The maintenance and consistency of diatoms at 30–50% of the total biomass during the rapid changes in physical dynamics over the study is also suggestive of more than a single selection mechanism. Although different in location and scope, results parallel those found by Li [2002], who documented stability in one group of phytoplankton, while two others were apparently responding in the classical sense to resource limitation and the intensity of water column stratification.

The changes in phytoplankton biomass and community structure were significantly correlated to in water spectral absorption and attenuation over the course of this study. The significance was primarily evident in the blue and red wavelengths representing the fluctuating contributions of chlorophylls and carotenoids of each taxonomic group (Tables 3 and 4). Biomass fluctuations appeared to drive the variability in absorption for both the dominant (Table 3, first correlate) and less dominant taxa (Table 3, third correlate). The second correlate showed more significance in the blue, with cyanobacteria being the most significant taxa. This is consistent with cyanobacteria having a higher blue to red absorption ratio. In a separate CCA (data not shown), cyanobacteria were identified as the most significant phytoplankton group when compared with spectral absorption ratios (relative to 555 nm), illustrating the relationship of the green wavelengths to the dominant phycobilin-containing taxa. This is important as it demonstrates the use of spectral ratios as a means of optically detecting phycobilin-containing taxa from non-phycobilin-containing taxa. The apparent negative correlation between cyanobacteria and absorption in the red, blue, and
green wavelengths of the second correlate is likely a reflection of the dynamics from 12 to 29 July where the contribution of cyanobacteria was almost always less than 12% and diatoms and dinoflagellates were predominately greater than 25 and 20%, respectively.

Cyanobacteria were also found to be significant in the first correlate when compared with attenuation. The significance at 440 nm supports the notion of the enhanced blue to red absorption ratio. The differences in the CCA results between absorption and attenuation are consistent with observations that the scattering cross section for chlorophyll is relatively flat and that scattering is fourfold greater than absorption, thus minimizing the strength of the correlates. However, for cyanobacteria, which scatter light efficiently at blue wavelengths and reduced scattering at red wavelengths, the results in the first correlate are consistent with phytoplankton size. It is apparent that variations in taxa are related to attenuation, specifically in the red and blue regions of the spectra. However, because of the multivariate nature of the relationships described by CCA direct interpretation of causality can be difficult, particularly as the number of significant parameters increases. In addition to the significant relationship in water, phytoplankton taxa were also significantly correlated to the hyperspectral above water measurements. Because these relationships refer to reflectance, the nature of the direct correlation between R and phytoplankton is that of an inverse relationship. Though because of the large number of phytoplankton taxa and wavelengths identified as significant contributors especially in the second, third, and fourth correlates it is difficult to make direct interpretations about specific taxa and wavelengths. In light of this, Figures 11a–11d suggest that R dynamics are indicative of changes in overall biomass, this is evident in the negative correlation between diatoms (the most predominant and least dynamic taxa during the study) and wavelengths in the blue and red portion of the spectrum in each of the four correlates. Cyanobacteria were also identified as significant contributors in all four correlates and consistently showed a negative relationship with wavelengths in the region of maximal reflectance, suggesting the influence of phycobilins on the R signal. Using the R from above water measurements, 25 wavelengths were found to be significant. These wavelengths correspond to areas where there are significant differences in the absorption (particularly in the blue and red wavelengths) of chlorophylls, carotenoids and phycobilins [Antonov, 1997a, 1997b; Bricaud et al., 1995; Johnsen et al., 1994; Kirkpatrick et al., 2000; Millie et al., 1995; Schofield et al., 1999]. Of the 25 significant wavelengths, 21 corresponded to significant inflection points in R (determined by a fourth derivative analysis [Antonov, 1997b; Ruffin and King, 1999]), suggesting that individual taxa are differentially influencing the reflectance signal and that this change is detectable. A similar hyperspectral reflectance-based discrimination of microalgae has been recently demonstrated for benthic communities in optically shallow marine environments [Stephens et al., 2003]. Further
extension of these results in a multiple linear model show that these wavelengths may be used as predictors for phytoplankton community structure. The lack of predictability for diatoms was to be expected given their relatively uniform distribution in time and space and that the intrinsic predictive ability of the model was based on the variability of the community structure during the experiment.

Reflected in their association with the highest estimate of $r^2 = 0.70$, cyanobacteria were predicted with the most confidence by R. This is likely due to their high variability during the study relative to the other taxonomic groups and that phycobilin-containing protein complexes have unique spectral characteristics. Interestingly R at 514.2 nm was the most common significant wavelength, being identified as a significant contributor in three of the four correlates and is most likely where the spectral variance of phycobiliproteins would be detected given the dynamics documented in this study. The period of the highest contribution of cyanobacteria and the largest community shift occurred during the intense downwelling period beginning on 27 July (Figure 7). This period was also characterized by a marked decrease in the spectral absorption (Figure 8a), which influenced the R and contributed to the strength of the model. Additionally, it is interesting and perhaps encouraging that despite potential influences varying sky reflectance of surface roughness, reflectance anomalies, and irradiances on the above-water measurements of R during the study, reflectance had significant power in predicting the different phytoplankton groups. Although these are preliminary results derived from limited variability in space and time, collectively they may represent a significant step forward with regard to the application of optics and hyperspectral remote sensing reflectance as means to discriminate phytoplankton community structure and dynamics in coastal environments.

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References


Figure 1. Location of the study within the Long-term Ecosystem Observatory off the coast of New Jersey. Two transect lines (A and N) were occupied over the course of the experiment from 12 July to 8 August 2001. The locations of the time series profiler and the Rutgers University Marine Field Station (RUMFS) are shown.
Figure 2. Depth distributions of temperature and fluorescence along the N line. Data were collected by a towed undulating platform on (a) and (b) 12 July 2001 and (c) and (d) 29 July 2001. The depth of the maximum density gradient is overlaid on the temperature contours (black line).
Figure 3. Time series of the cross-shore (a) AVHRR sea surface temperature and (b) SeaWiFS chlorophyll along the N line at the study site. Data were obtained from the beginning of May through August 2001. The passes for each platform used to construct the contours are shown by solid circles at the top of each panel. The study period is highlighted by the dashed box.
Figure 4. Time series of (a) wind velocity and direction and the depth distribution of (b) temperature and (c) fluorescence. The data were collected every 30 min between 15 July and 6 August 2001 by a vertical profiler located within the study site. Wind data were collected at the Rutgers University Marine Field Station (see Figure 1). Fluorescence data are only shown until 31 July 2001 because of fouling. Note that solar quenching of fluorescence was not evident in the time series.
Figure 5. Time series of the cross-shore distribution of (a) the maximum vertical density gradient (kg m$^{-3}$), (b) the depth of the maximum buoyancy frequency (N$^2$), (c) the fluorescence integrated to the depth of the maximum N$^2$, and (d) the corresponding distribution of surface chlorophyll a, measured from discrete samples taken along the A line (solid white circles). Data in Figures 5a – 5c were derived from transects collected by a towed undulating platform along the N line. Bathymetric depths for a given distance offshore are color coded for reference in Figure 5b. For example, 10 km offshore on 23 July 2001, N$^2$ was equivalent to the depth of the water column, indicating full mixing to the bottom. Horizontal bars are given along the top Figures 5a and 5c to indicate times of upwelling (blue) and downwelling (red).
Figure 6. The mean fluorescence ratio (surface: total depth-integrated) is shown as a function of distance offshore for all measurements taken during this study from 12 July through 6 August 2001. The standard deviation is shown in grey around the mean. Data from repeated transects shown in Figure 5c.
Figure 7. Time series of the cross-shore distribution of the percent composition of phytoplankton biomass for (a) diatoms, (b) dinoflagellates, (c) cyanobacteria, (d) cryptophytes, (e) haptophytes, and (f) prasinophytes. The time/location of discrete measurements taken along the A line are shown in Figure 5d (solid white circles). Horizontal bars are given along the tops of Figures 7a and 7d indicate times of upwelling (blue) and downwelling (red).
Figure 8. Time series of the cross-shore distribution of (a) absorption at 440 nm and (b) attenuation at 440 nm. The time/location of discrete measurements taken along the A line are shown as solid white circles in Figure 8a. Horizontal bars are given along the top of Figure 8a to indicate times of upwelling (blue) and downwelling (red).
Figure 9. The first canonical correlates of the phytoplankton community abundance (x variable) and (a) spectral absorption and (b) spectral attenuation (y variables). Both correlations were significant (p<<0.001, n = 110) at 0.91 and 0.90, respectively.
Figure 10. Results of the (a) first and (b) second canonical correlates when comparing the phytoplankton community abundance (x variable) and hyperspectral reflectance (y variable) as measured 3 m above the surface. The correlations were significant ($p << 0.001, n = 91$) at 0.97 and 0.93, respectively.
Figure 11. Results of the canonical correlation between the phytoplankton community abundance and the measured hyperspectral reflectance (R). The coefficients for the R wavelengths are shown for the (a) first, (b) second, (c) third, and (d) fourth canonical correlates. The four correlates were significant (p<<0.004, n = 91) at 0.97, 0.93, 0.92, and 0.91, respectively. Significant R wavelengths were determined by a general linear model (see section 2) and are shown as p < 0.01 (white bars), p = 0.01 to 0.05 (gray bars), and p > 0.05 (black bars). Significant phytoplankton groups are also shown for each significant correlate as p < 0.01 (bold) and p < 0.05 (italics). For illustration, R measurements taken within 1 km of the shoreline on 13 July and 1 August 2001 are overlaid in Figures 11a and 11b, respectively.
### Tables

**Table 1. Results of Canonical Correlation Between Physical Variables and Measures of Phytoplankton Biomass and Distribution**

<table>
<thead>
<tr>
<th></th>
<th>Canonical Correlate</th>
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<td></td>
<td>First</td>
<td>Second</td>
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<tr>
<td>Correlation</td>
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<td>0.000</td>
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<td>$Y_2 = \text{Total Fluorescence}$</td>
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<td>$-0.031$</td>
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*The step test, evaluated by Wilk's Lambda, identified both correlates as statistically significant ($p < 0.001, n = 1010$).

**Table 2. Results of Canonical Correlation Between Physical Variables and Phytoplankton Community Structure**

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<td>First</td>
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<td>$Y_1 = \text{Diatoms}$</td>
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<td>$-0.12$</td>
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<td>$-0.11$</td>
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<tr>
<td>$Y_3 = \text{Cyanobacteria}$</td>
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<td>$Y_4 = \text{Cryptophytes}$</td>
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<td>$Y_5 = \text{Haptophytes}$</td>
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<td>$Y_6 = \text{Prasinophytes}$</td>
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<tr>
<td>$Y_7 = \text{Chlorophytes}$</td>
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*The step test evaluated by Wilk's Lambda, identified both correlates as statistically significant ($p < 0.001, n = 67$).
Table 3. Results of Canonical Correlation Between Spectral Absorption and Phytoplankton Community Structure

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<td>-0.024&lt;sup&gt;b&lt;/sup&gt;</td>
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<sup>a</sup>The step test evaluated by Wilk’s Lambda identified the first four correlates as statistically significant (p < 0.01, n = 110).
<sup>b</sup>Significance of coefficients is p < 0.05.

Table 4. Results of Canonical Correlation Between Attenuation and Phytoplankton Community Structure

<table>
<thead>
<tr>
<th></th>
<th>Canonical Correlate</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>First</td>
<td>Second</td>
<td>Third</td>
<td>Fourth</td>
</tr>
<tr>
<td>Correlation</td>
<td>0.90</td>
<td>0.86</td>
<td>0.63</td>
<td>0.42</td>
</tr>
<tr>
<td>X₁ – Diatoms</td>
<td>0.034&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.032&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.056&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.034</td>
</tr>
<tr>
<td>X₂ – Dinoflagellates</td>
<td>-0.008</td>
<td>-0.041&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.042</td>
<td>-0.131&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>X₃ – Cyanobacteria</td>
<td>0.054&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.042&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.085&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.034</td>
</tr>
<tr>
<td>X₄ – Cryptophyta</td>
<td>0.096</td>
<td>-0.092</td>
<td>-0.204</td>
<td>0.095&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>X₅ – Haptophytes</td>
<td>-0.050&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.009</td>
<td>-0.080&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.019</td>
</tr>
<tr>
<td>X₆ – Prasinophytes</td>
<td>0.015&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.011</td>
<td>0.312&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.098</td>
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<tr>
<td>X₇ – Chlorophytes</td>
<td>-0.003</td>
<td>-0.038&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.054&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.111&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Y₁ – c412</td>
<td>-0.028&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.935</td>
<td>0.416</td>
<td>1.049</td>
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<tr>
<td>Y₂ – c440</td>
<td>2.373&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.412</td>
<td>1.645</td>
<td>-1.011</td>
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<tr>
<td>Y₃ – c488</td>
<td>-1.341&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.050</td>
<td>-1.480</td>
<td>2.326</td>
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<tr>
<td>Y₄ – c510</td>
<td>0.164</td>
<td>-0.677</td>
<td>0.099</td>
<td>-1.572</td>
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<tr>
<td>Y₅ – c555</td>
<td>0.358</td>
<td>0.403</td>
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<td>-2.319</td>
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<tr>
<td>Y₆ – c659</td>
<td>0.341</td>
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<td>-0.493</td>
<td>-2.798</td>
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<td>Y₇ – c690</td>
<td>-0.647</td>
<td>1.240&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.068&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.336</td>
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<tr>
<td>Y₈ – c776</td>
<td>-1.747&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-1.411&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-3.080&lt;sup&gt;b&lt;/sup&gt;</td>
<td>5.540&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Y₉ – c712</td>
<td>1.509&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.412</td>
<td>1.815</td>
<td>-2.542</td>
</tr>
</tbody>
</table>

<sup>a</sup>The step test evaluated by Wilk’s Lambda identified the first four correlates as statistically significant (p < 0.05, n = 110).
<sup>b</sup>Significance of coefficients is p < 0.05.