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Dynamics of late spring and summer phytoplankton communities on Georges Bank, with emphasis on diatoms, *Alexandrium* spp., and other dinoflagellates

Rachel M. Gettings, David W. Townsend *, Maura A. Thomas, Lee Karp-Boss

School of Marine Sciences, University of Maine, Orono, ME, USA

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ABSTRACT

We analyzed the distribution, abundance, and succession patterns of major phytoplankton taxa on Georges Bank in relation to hydrography, nutrients, and size-fractionated chlorophyll concentrations (>20 μm; <20 μm) on three oceanographic cruises from late spring through summer 2008 (28 April–5 May, 27 May–4 June, and 27 June–3 July). The April–May phytoplankton community was dominated numerically by the diatoms *Skeletonema* spp., *Thalassiosira* spp., *Coscinodiscus* spp., and *Chaetoceros* spp., with highest total diatom cell densities exceeding 200,000 cells l^{-1} on the Northeast Peak. In May–June, low nitrate and silicate concentrations over the Bank, along with patches of slightly elevated ammonium, were apparently supporting a predominantly dinoflagellate population; the toxic dinoflagellate *Alexandrium* spp. reached 13,000 cells l^{-1}. Diatom cell densities on the second cruise in May–June were less than 60,000 cells l^{-1} and their spatial distributions did not overlap with the highest cell densities of *Alexandrium* spp. or other dinoflagellates. On the third and last cruise, in June–July, reduced nitrate and silicate concentrations were accompanied by a shift in the phytoplankton community: *Alexandrium* spp. cell densities were lower and heterotrophic and mixotrophic dinoflagellates, notably *Polykrikos* spp., *Gyrodinium* spp., *Gymnodinium* spp., and *Prorocentrum* spp., had become more abundant. Patches of regenerated silicate during the June–July period appeared to support a post-spring-bloom diatom community on the central crest of the Bank (total diatom cell densities $>180{,}000$ cellsl^{-1}) of *Leptocylindrus* spp., *Dactyliosolen* spp., and *Guinardia flaccida*. Multivariate statistical analyses of phytoplankton taxa and station locations revealed distinct assemblages of diatom and dinoflagellate taxa on the Bank throughout the late spring and summer. Results are interpreted in the ecological context of earlier-reported laboratory culture experiments on the competitive interactions between *Alexandrium fundyense* and diatoms.

1. Introduction

Georges Bank is a shallow submarine system located at the southern edge of the Gulf of Maine (Fig. 1). Renowned for its high rates of primary production and historically rich commercial fisheries, it covers an area of nearly 30,000 km^2 and stands out as one of the most prominent features of the Northwest Atlantic continental shelf region (Backus and Bourne, 1987). The main physical oceanographic features of Georges Bank are its intense tidal mixing and clockwise circulation pattern (reviewed in Townsend et al., 2006) which have been subjects of numerous studies over the past century, dating back to Henry Bryant Bigelow (1927). At the heart of the Bank's reputation as a productive fishing ground is its primary production by phytoplankton, which is among the highest of any continental shelf sea, exceeding 400 g C m^{-2} yr^{-1} on the crest of the Bank (O'Reilly et al., 1987).

Seasonally, phytoplankton growth conditions on Georges Bank become established well before spring – in late fall and early winter – when new nutrients are pumped onto the Bank and mixed laterally across it (Pastuszak et al., 1982; Rebuck, 2011), apparently allowing for relatively low, but nonetheless significant, wintertime phytoplankton growth, limited only by the seasonally-low light levels. Thus, phytoplankton growth on the Bank occurs year-round, albeit at relatively low levels (Thomas et al., 2003). The annual spring diatom bloom, however – more accurately described as a winter–spring bloom – may begin as early as January, a time when nutrient concentrations across the Bank are at or near their highest levels, when water temperatures are cold and frontal features are weakened (Mavor and Bisagni, 2001), and, most importantly, when the critical depth exceeds the water column depth over the shallow central portions (Townsend and Pettigrew, 1997; Townsend and Thomas, 2001, 2002; Hu et al.,

* Corresponding author.
E-mail address: davidt@maine.edu (D.W. Townsend).

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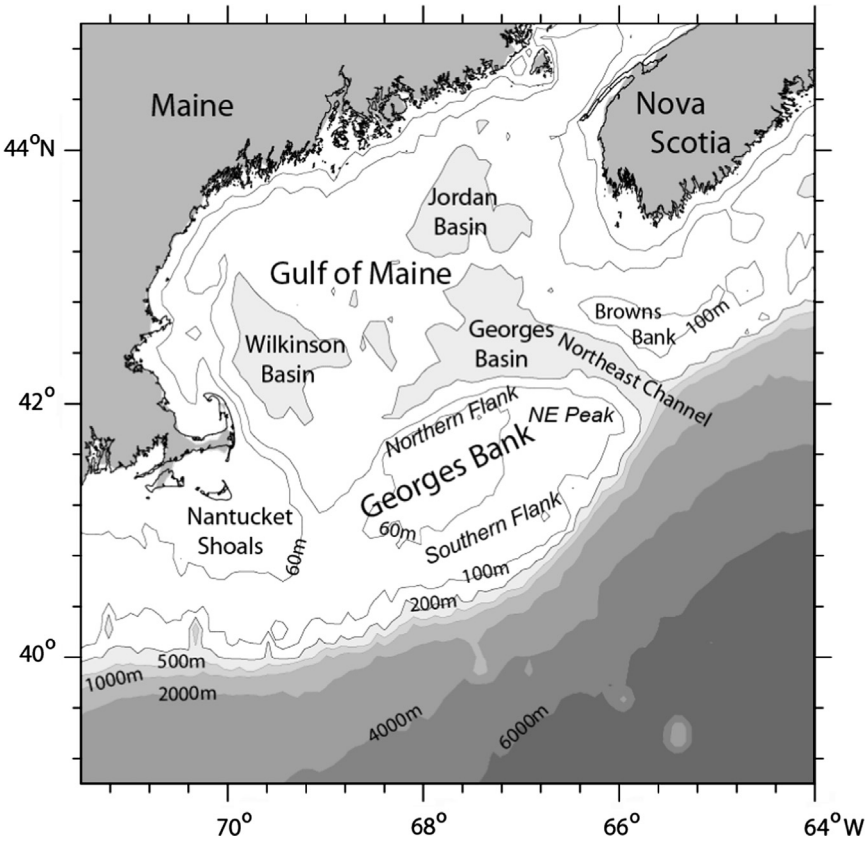

Fig. 1. Map of the Georges Bank–Gulf of Maine region, and features referred to in the text.

2008). In their studies of the Georges Bank spring bloom in the late 1990s, Kemper (2000) and Townsend and Thomas (2001) reported that silicate is depleted quickly, before nitrate, and limits diatom production on the Bank by as early as February over the central crest. Later in the spring and early summer, localized patches of regenerated silicate appear to stimulate a second pulse in diatom production, concurrent with a developing dinoflagellate and nanoflagellate population (Kemper, 2000; Townsend and Thomas, 2002). Dissolved inorganic nitrogen (nitrate plus nitrite), on the other hand, also eventually runs down, becoming depleted to levels that limit all phytoplankton growth by April; the rest of the year primary production appears to depend largely on recycled nitrogen (Draxler et al., 1985; Horne et al., 1989, 1996; Townsend and Thomas, 2002). Recent modeling work by Hu et al. (2008), however, has shown that fluxes of new nitrogen (principally nitrate) and silicate to Georges Bank continue throughout the year, driven by tidal pumping of deep, nutrient-rich waters principally from beyond the Bank's northern edge.

The continual input of new nutrients to the system via tidal pumping throughout the year not only allows for high rates of primary productivity across parts of the shallow Bank ecosystem, but also sets the upper limit to the production of higher trophic level organisms, including zooplankton and commercially exploited fishes (Townsend and Pettigrew, 1997). As the modeling efforts of Hu et al. (2008) have shown, nutrient injections are especially important along the northern edge of the Bank, which is often where the highest surface nutrient concentrations are observed (Pastuszak et al., 1982; Townsend and Thomas, 2002). This spatial pattern led Townsend et al. (2006) to propose the "donut" hypothesis of phytoplankton production, whereby greater nutrient fluxes to the northern flank generate high phytoplankton cell densities downstream on the Northeast Peak, which are in turn advected in a clockwise (anti-cyclonic) circulation around the edges of the Bank in a band-like pattern (the donut), resulting in overall greatest secondary production farther downstream, on the southern half of the Bank.

The principal source of new nutrients reaching Georges Bank and fueling its biological production is from beyond the shelf edge; deep slope waters enter the Gulf of Maine through the Northeast Channel, spill into the three interior basins and are eventually mixed onto the Bank's Northern Flank (Hu et al., 2008). Although detailed studies on phytoplankton community dynamics on Georges Bank are lacking, a general pattern of succession from spring-bloom diatoms to a phytoplankton community dominated by dinoflagellates has been observed (Cura, 1987; Kemper, 2000; Townsend and Thomas, 2002). Studies of diatom bloom formation and species succession in other shelf regions have demonstrated that diatoms dominate the phytoplankton community as long as silicate is present in concentrations greater than about 2 μM (Egge and Aksnes, 1992). Because the spring bloom on Georges Bank is composed primarily of diatoms, which take up nitrate and silicate in nearly equal proportions, and because source waters historically have had lower silicate concentrations relative to nitrate (Townsend et al., 2010), silicate ultimately becomes limiting first, curtailing the bloom as early as February when silicate concentrations are reduced to 2–4 μM (Townsend and Thomas, 2001, 2002). The remaining concentrations of nitrate, however, play a key role in determining subsequent phytoplankton community composition, and force a post-bloom species succession to flagellates. For the remainder of the year, recycled nitrogen would appear to fuel primary production on the Bank which results in a phytoplankton community dominated by dinoflagellates and nanoflagellates. Of particular importance on the Bank are species of the toxic dinoflagellate *Alexandrium* spp. (Cura, 1987; Kemper, 2000; McGillicuddy et al., 2014; Townsend et al., 2014).

In this communication we add further insights into the late-spring to summer phytoplankton community on Georges Bank, especially as related to distributions and abundances of the toxic dinoflagellate, *Alexandrium* spp. We present results of three post-spring-bloom oceanographic surveys of the Bank, between late April and early July of 2008, in which we analyzed the hydrography, nutrients and phytoplankton communities, and subjected those results to multivariate statistical analyses in order to discern spatial and temporal patterns among species assemblages as related to the physical oceanographic structure and nutrient fields across the Bank. We interpret those results in the context of earlier field studies (Townsend et al., 2005) and laboratory experiments (Gettings, 2010) that indicate the importance of interspecific competitive interactions in phytoplankton succession.

2. Materials and methods

Hydrographic surveys of temperature, salinity, nutrients, total and size-fractionated chlorophyll (>20 μm; <20 μm), and phytoplankton species abundance and distribution were conducted on Georges Bank during the spring and summer of 2008. Cruise dates were: 28 April–5 May (OC445) and 27 May–4 June (OC447) aboard the R/V *Oceanus*, and 27 June–3 July (EN448) aboard the R/V *Endeavor*. Standard CTD casts were made, and water samples were collected, at stations across Georges Bank (Fig. 2) using a SeaBird CTD and carousel water sampler equipped with 10-l Niskin bottles. Nutrient and chlorophyll measurements were taken at every station on each cruise. Water samples (20 ml) for nutrient analyses were taken at standard depths (1, 10, 20, 30, 40, 50, 100, 150 and 200 m or from within a few meters of the bottom), filtered through 0.45 μm Millipore cellulose acetate filters, immediately placed in a sea water ice bath for 5–10 min, and then frozen at −18 °C for subsequent analyses on shore for NO_3^-+NO_2^-, $Si(OH)_4$, PO_4^{-3}, and NH_4^+, using a Bran Luebbe AA3 Autoanalyzer and standard techniques. Chlorophyll analyses were performed only on the top 5 sample depths (e.g., to 40 m). For total chlorophyll measurements, 100 ml was filtered through a 25 mm GF/F glass fiber filter; the filter was placed in 90% acetone and kept in the dark at −18 °C for at least 12 h before analysis at sea using a Turner Model 10AU fluorometer. Size-fractionated chlorophyll (>20 μm and <20 μm) measurements were also obtained for this series of cruises. A second 100 ml sample from each station and depth was sieved through 20 μm Nitex mesh; sample water passing the sieve was then filtered through a 25 mm GF/F glass fiber filter and processed according to the same protocol just discussed, giving a measurement of chlorophyll in the <20 μm size fraction. This <20 μm value was subtracted from the total chlorophyll value to give a measure of chlorophyll in the >20 μm size fraction. Only chlorophyll and nutrient measurements from the surface (i.e., 1 m depth) are presented here.

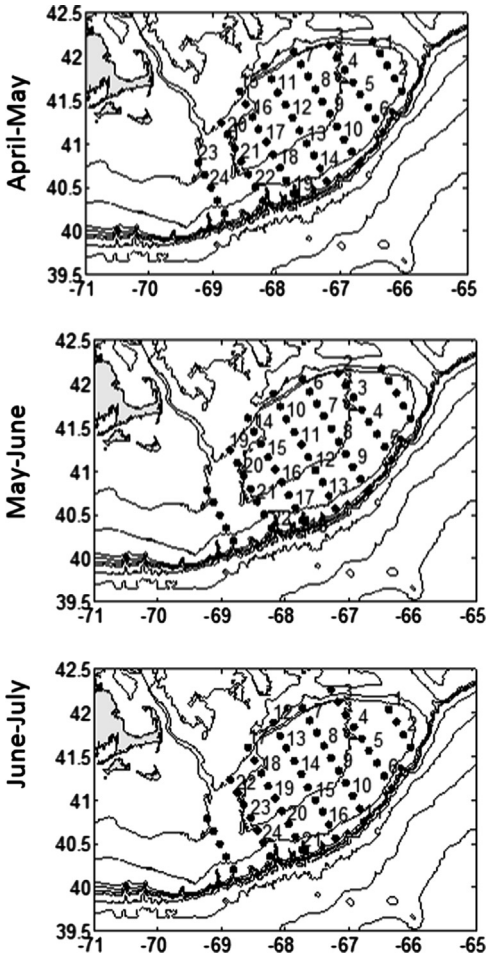

Fig. 2. Station locations for spring–summer 2008 cruises. *Top:* 28 April–5 May; *middle:* 27 May to 4 June; *bottom:* 27 June–3 July. The numbered stations are those where phytoplankton samples were collected and analyzed.

Samples for phytoplankton cell counts were taken at every other station (Fig. 2), and were based on 100 ml surface water (1 m) preserved in Lugol's iodine solution and transported back to the laboratory. A total of 70 stations were analyzed on the three cruises. Fifty microliter of each sample was transferred into a 100 ml graduated cylinder following mixing, and allowed to settle for a minimum of 48 h. The upper 40 ml of the settled sample was drawn off with a pipette, leaving 10 ml, which is a five-fold concentrate of the original sample. The concentrate was shaken and a 1 ml sub-sample was placed on a gridded Sedgwick-Rafter counting cell and examined under a compound microscope at 100× or 200× magnification. For enumeration of phytoplankton cells larger than 10 μm, the entire slide was counted, with each cell identified to the lowest taxon possible; in most instances, this was to genus. We did not identify dinoflagellate cysts to the species level, and they are grouped together in a "Cysts" category (we recognize that such a category may introduce covariance with dinoflagellate vegetative cells; nonetheless, we have elected to include them in our statistical analyses, explained below). For nanoplankton and small flagellate species (<10 μm), a single transect on the slide was counted. In both instances, a minimum of 100 cells were counted.

In order to evaluate error associated with our having performed only a single cell count at each station, we performed triplicate cell counts (e.g., three subsamples for cell counts were taken from a single water sample collected at sea) along one of our transects (5 stations; Fig. 2) for two of the three cruises (the April–May and May–June cruises). Diatoms, dinoflagellates, *Alexandrium* spp., and nanoplankton were enumerated.

2.1. Cluster analyses

All statistical analyses were performed using MYSTAT 12, version 12.02.00 of the SYSTAT 12 program software (http://www.systat.com/MystatProducts.aspx). Two different cluster analyses were performed.

First, a total of 22 taxa of diatoms and dinoflagellates was selected for analysis, based on their average abundances at the 70 stations sampled on the three cruises and taking into account their percent presence across all three cruises. All but 4 of the 22 most-abundant taxa were present at more than 30% of the stations; nonetheless those four taxa were abundant when they were present and therefore we included them in the analysis.

Abundances of each of the 22 taxa were standardized prior to the analyses by removing the mean. Hierarchical techniques were used to calculate distances of each individual taxon in relation to the remaining taxa. In this case, there are x taxa, each of which has a value for n variables (temperature, salinity, nutrients (nitrate), and chlorophyll), represented as the top 22 taxa and the 70 sampling stations across all three cruises, respectively. Distance (D) calculations between taxa were performed using the Euclidean distance formula generally written as

$$D_{1,2} = \sqrt{\sum_{i=1}^{n} (X_{1i} - X_{2i})^2}$$

where, for example, 1 and 2 represent two taxa and n is equal to the number of variables the taxon abundance was measured for, in this case 70 stations over the three cruises (Manly, 1994). This produces a dendrogram that illustrates how similar one particular taxon is to another, based on distances in ordinate space. By using relative abundances of the major phytoplankton taxa, rather than simply their absence or presence at a particular station, we can observe which particular diatoms and dinoflagellates tend to coexist with one another, and also those that exist at roughly similar cell densities.

The Ward (1963) method was used to link groups, and major groups revealed in the dendrogram were identified subjectively by eye. The Ward linkage, sometimes referred to as the minimum-variance linkage, is similar to an analysis of variance (ANOVA) approach, whereby the groups are formed in an attempt to minimize an increase in within-group variance, which is ultimately less than if either of the two variables of interest were joined with a different cluster (McGarigal, 2000).

In order to analyze phytoplankton distributions and abundance trends in space and time on Georges Bank, a second cluster analysis was performed to group stations based on the abundances of the twenty-two taxa. The same approach to clustering was applied as above, and station clusters were again identified subjectively. Forming station clusters that contain similar abundances of taxa reveals spatial trends both within and among the three cruises and aids in identification of successional patterns in the plankton. In addition, it allows for comparison of the water properties (i.e., salinity, temperature, nutrients, chlorophyll) associated with each station cluster for use in linking oceanographic and biological characteristics on the Bank.

In addition to cluster analyses to identify similarities in phytoplankton taxa, we employed Principal Component Analysis (PCA) using standardized abundances to identify similarities among phytoplankton taxa in 2-D space. This additional analysis was performed in order to observe orientation of phytoplankton in coordinate space on the Bank and to find groups of phytoplankton taxa that appear to coexist in a similar manner across a number of stations, again, in both space and time. Comparing the cluster analysis and PCA reveals similar results with respect to the groupings of certain taxa based on their abundances. The goal of a PCA analysis is to define groups such that the variance is minimized: in this particular case, to project the abundance of a number of taxaon to one or two principal components, which in general account for most of the variability in the samples (Manly, 1994). Observation of the factor loadings for each of these principal components provides insight into which taxa or groups (diatoms or dinoflagellates) account for most of the variability in our samples (stations).

3. Results

3.1. Hydrography and nutrients

Near-surface temperatures and salinities for the three 2008 cruises are given as areal contour plots in Fig. 3 along with satellite

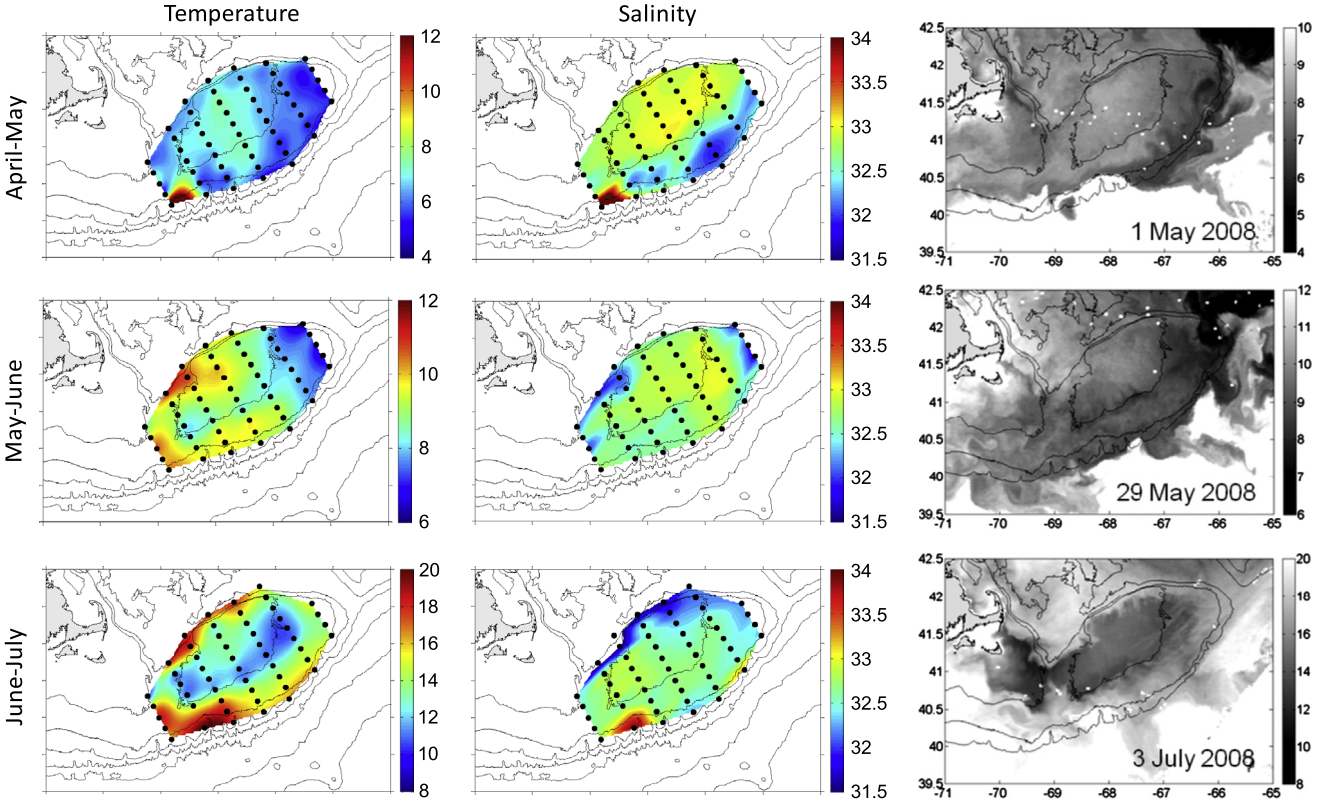

Fig. 3. Contour plots of near-surface temperature (°C) and salinity for each of the three cruises, along with a corresponding satellite SST image for the date indicated. *Top:* 28 April–5 May; *middle:* 27 May–3 June; *bottom:* 27 June–3 July.

images of sea surface temperatures (SST) for a relatively cloud-free day during each cruise. Surface temperatures on the April–May cruise ranged from about 4 to 7 °C over the central parts of the Bank, with the coldest waters associated with the Northeast Peak, most likely the result of an influx of colder Scotian Shelf Water that was restricted to the eastern-most part of the Bank (e.g., Ji et al., 2006). The SST image from 1 May 2008 shows that the tidal mixing front, identified by a narrow strip of cooler waters, indicating frontal upwelling, was already developing between the 60 and 100 m isobaths (Fig. 3). The tidal mixing front develops around the well-mixed waters throughout the Bank in winter, as thermal stratification develops in the deeper waters where tidal mixing does not extend to the surface; the front constitutes the boundary between the two regimes. The Bank warmed to about 8–11 °C over the central portions by the May–June cruise period, with the coldest water still confined to the eastern-most portion of the Bank. The tidal mixing front was well developed along the Southern Flank. Warmest surface temperatures were observed during the June–July cruise period when they reached a maximum of about 19 °C around the outer edges of the Bank, beyond the tidal mixing front separating cooler waters (10–12 °C) across the more central, tidally-mixed regions.

The influence of an influx of generally colder and fresher Scotian Shelf Water from the east was also evident in the salinity distributions (Fig. 3). Relatively fresher waters, with salinities of 32–32.6‰, were observed across much of the eastern portion of the Bank in April–May, while the western portions were saltier, with salinities of 32.8–33.0‰. In May–June, salinities still ranged from 32‰ to 33‰, with highest salinities observed along the southeastern portion of the Bank. By the third cruise in June–July, fresher surface waters from the western Gulf of Maine were intruding along the northern edge of the Bank, with salinities of 31.2–31.4‰ at some stations, while the remainder of the Bank, including the Southern Flank, varied only from about 32.5–32.8‰.

In general, surface nutrient concentrations on Georges Bank throughout the spring–summer months were low, having already been drawn down during and following the annual spring phytoplankton bloom (Figs. 4 and 5). Surface nitrate plus nitrite (NO_3^-+NO_2^-) concentrations on all three cruises were less than 3.5 μM, and were only in excess of 2.0 μM during the April–May cruise along the northwest edge of the Bank (Fig. 4), most likely the result of localized upwelling and nutrient injections there (Hu et al., 2008). Surface concentrations of NO_3^-+NO_2^- on the next cruise, in May–June, were depleted to less than 1 μM across most of the Bank's surface area (two stations were exceptions; Fig. 4), and remained low through the June–July cruise when only a single station had concentrations greater than 1 μM. Surface silicate ($Si(OH)_4$) concentrations were also depleted on the first cruise in April–May (Fig. 4), except at two stations: just off the Bank's Northern Flank, and one station on Nantucket Shoals, each of which had concentrations >5 μM. Silicate concentrations had increased to 2–5 μM at several stations on the next cruise in May–June. Because there were no apparent concomitant increases in NO_3^-+NO_2^- concentration, it is likely that increased pulses of Si $(OH)_4$ occurred as a result of increasing temperatures and subsequent dissolution of biogenic silica (diatom frustules from the previous winter–spring bloom), as observed in earlier studies (Townsend and Thomas, 2002), rather than a localized upwelling event. Surface silicate concentrations dropped again during the third cruise in June–July, to less than 2 μM across most of the Bank.

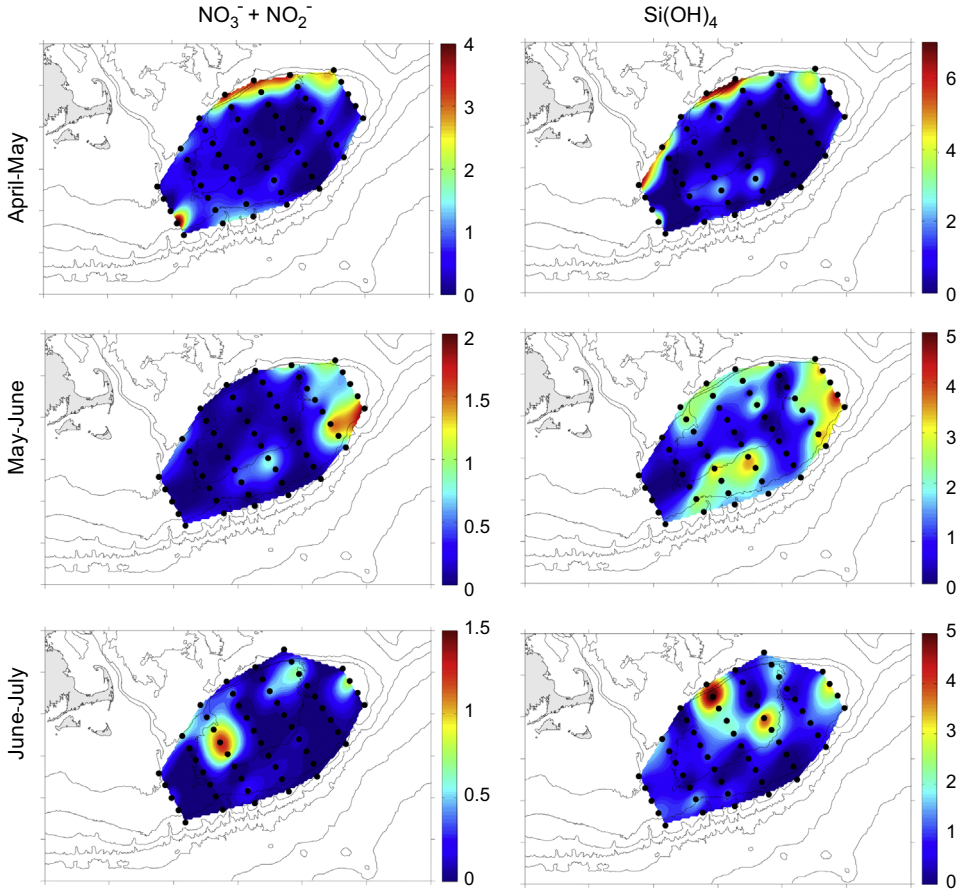

Fig. 4. Contour plots near-surface concentrations (μM) of nitrate plus nitrite (NO_3^-+NO_2^-, *left panels*) and silicate ($Si(OH)_4$, *right panels*) for each of the three cruises. *Top:* 28 April–5 May; *middle:* 27 May–3 June; *bottom:* 27 June–3 July.

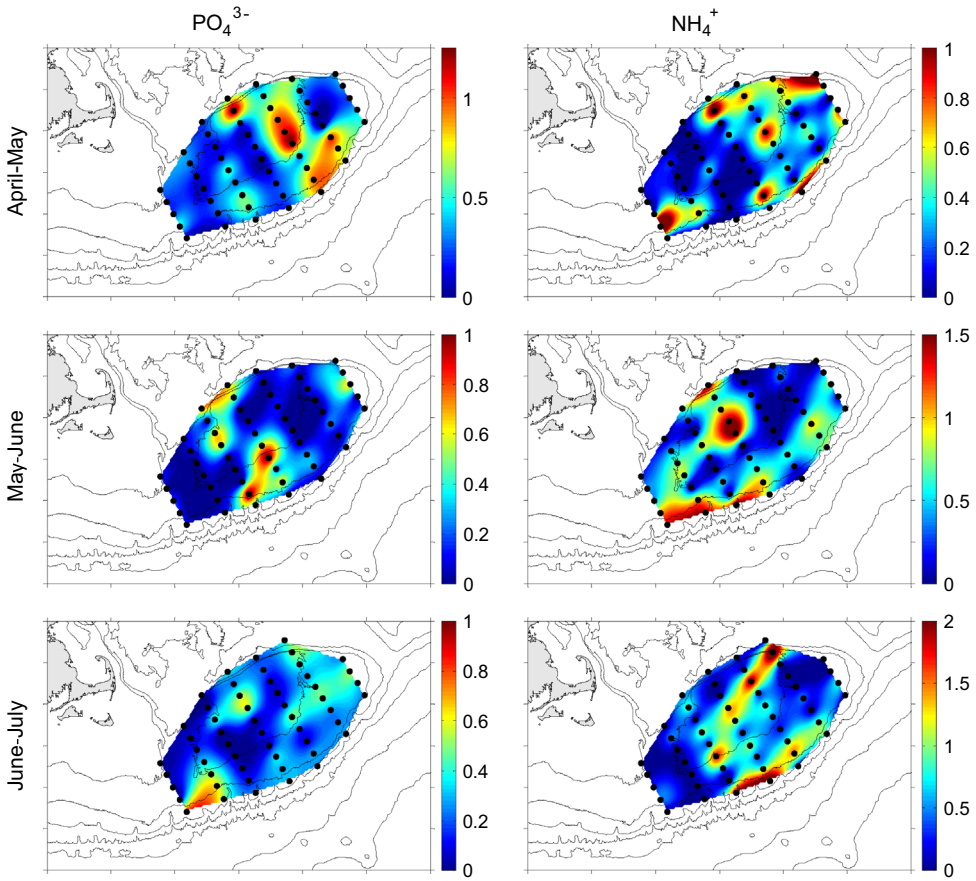

Fig. 5. Contour plots of near-surface concentrations (μM) of phosphate (PO_4^{3-}; *left panels*) and ammonium (NH_4^+; *right panels)* for each of the three cruises. *Top:* 28 April–5 May 2008; *middle:* 27 May–3 June; *bottom:* 27 June–3 July.

Surface phosphate (PO_4^{-3}) concentrations were depleted across most of the Bank's area during the April–May period, to concentrations less than 0.2 μM over much of the Bank. Exceptions were three patches of slightly elevated concentrations, which did not exceed 1.5 μM (Fig. 5). Patches of slightly elevated phosphate (>1 μM) were also observed during the May–June and June–July cruises. Despite those localized patches, phosphate levels remained low throughout most of the Bank after the first cruise in April–May, and were less than 0.1 μM over much of the Bank. A plot of all NO_3^-+NO_2^- surface concentrations versus PO_4^{-3} for each of the three cruises shows that, in general, it is nitrogen, not phosphorus that was limiting on the Bank during our summer sampling period (Fig. 6), but there were several stations where the N:P ratios were greater than the Redfield ratio of 16:1, and where there were positive values of NO_3^-+NO_2^- but near-zero values of phosphate. Surface ammonium (NH_4^+) concentrations were low throughout the three cruises, with concentrations at or below 0.5 μM at most stations, but there were a number of localized patches where it exceeded 2 μM (Fig. 5). These sites of ammonium regeneration where phosphate was absent or at very low concentrations may represent phosphate limitation, as discussed more completely in Townsend et al. (2014).

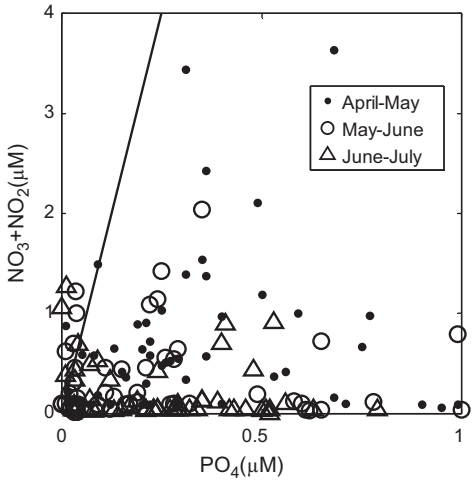

Fig. 6. NO_3^-+NO_2^- versus PO_4^{3-} concentrations (μM) for surface water samples collected at all stations on the three cruises, with 16:1 Redfield line inserted.

3.2. Phytoplankton analyses

3.2.1. Chlorophyll distributions

Total and size-fractionated (>20 μm and <20 μm) chlorophyll-*a* concentrations are given in Fig. 7. In general, the >20 μm size fraction was similar in spatial distributions to those of total chlorophyll on all three cruises, suggesting that the larger phytoplankton account for the majority of the phytoplankton biomass on Georges Bank. This is evident during the April–May cruise where total and >20 μm chlorophyll levels reached greater than 8 μg l^{-1} on some parts of the Bank, in particular along the central and southwestern portions. The <20 μm size fraction concentrations were much lower across the Bank during the April–May cruise, only exceeding 4 μg l^{-1} at a few stations on the southwestern portions. During the next cruise period, in May–June, total and >20 μm chlorophyll concentrations were relatively low (<2 μg l^{-1}) across much of the Bank except for a patch on the Northeast Peak where concentrations exceeded 8 μg l^{-1}.

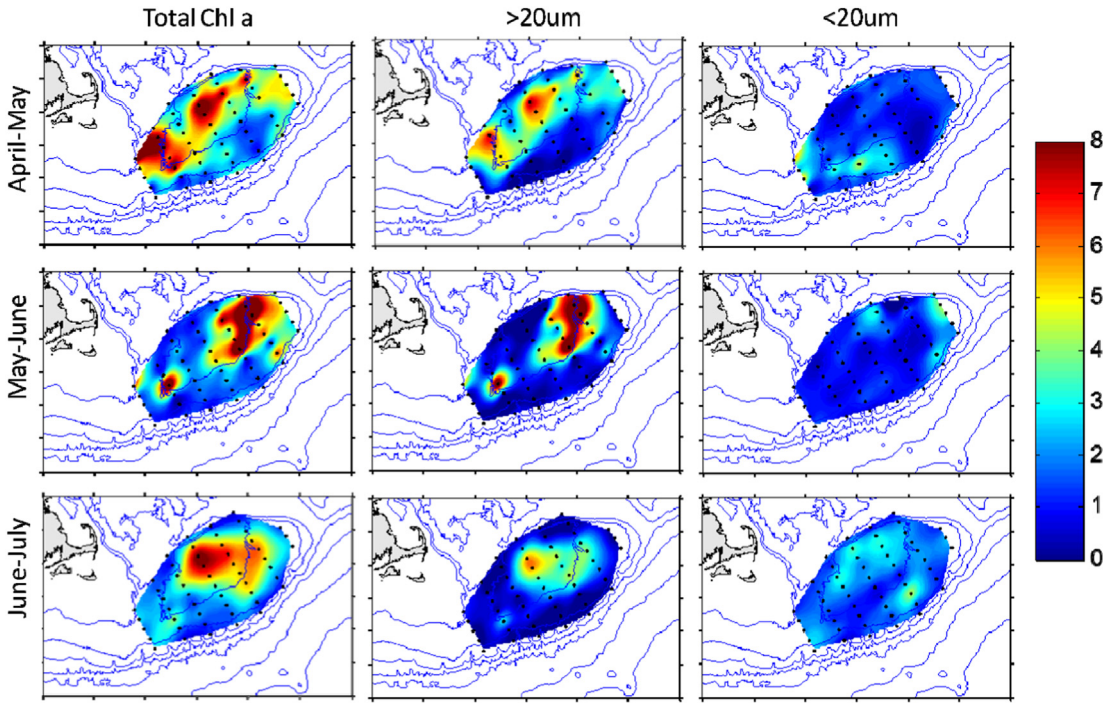

Fig. 7. Contour plots of near-surface chlorophyll-*a* distributions in μg l^{-1} given for total chlorophyll, the >20 μm fraction and the <20 μm fraction as indicated for the three cruises. *Top row:* 28 April–5 May; *middle row:* 27 May–3 June; *bottom row:* 27 June–3 July.

The <20 μm chlorophyll size fraction remained at less than 2 μg l^{-1} across the Bank in May–June, with the exception of slightly higher concentrations (ca. 3 μg l^{-1}) on the Northeast Peak. By the time of the June–July cruise, total and >20 μm chlorophyll concentrations had decreased somewhat, and the >20 μm fraction did not exceed 8 μg l^{-1} at any stations. Slightly higher concentrations were evident at some stations on the Bank crest, while the outer edges of the Bank were low, with concentrations less than 1 μg l^{-1}. The <20 μm phytoplankton population contributed slightly more to the total chlorophyll concentrations during the June–July period on the central crest of the Bank, with concentrations increasing to 3–4 μg l^{-1} at some stations.

3.2.2. Phytoplankton community structure

A total of 31 phytoplankton taxa were identified on Georges Bank during the spring–summer of 2008, which included 16 dinoflagellates, 13 diatoms, and 2 nanoplankton taxa. Of the 31 taxa, eight were identified to species. The most-abundant taxa were *Phaeocystis* spp., *Cryptomonas* spp., and other unidentified nanoplankton. Diatoms were present in high cell concentrations ($>100{,}000$ cells l^{-1}) at some stations but their distributions were generally patchy, leaving the spring–summer community sampled on these three cruises dominated largely by dinoflagellates and nanoplankton.

To assess the probable error associated with our having performed only a single cell count at each station, we performed triplicate counts at stations along a single transect on each of the first two cruises. The results for the four major phytoplankton groups (diatoms, dinoflagellates, *Alexandrium* spp. and nanoplankton) are given in Fig. 8, and reveal that, in general, cell counts of the four groups were within one standard deviation of the mean.

Cell densities across Georges Bank of the four major phytoplankton groups from among the 31 taxa are given in Fig. 9 for the April–May cruise. Like the nutrient distributions, it was evident from these results that the annual spring bloom had ended by the time of our first cruise, as diatom cell densities were relatively low throughout most of the Bank. Highest cell densities of diatoms were confined to the Northeast Peak where they were in excess of 200,000 cells l^{-1} (mainly comprised of *Coscinodiscus* spp., *Thalassiosira* spp., and *Skeletonema* spp.) reflecting the apparent injection of new nutrients there (e.g., Figs. 4 and 5). While elevated total chlorophyll levels (4–6 μg l^{-1}) were associated with the diatom-dominated Northeast Peak, the highest total and >20 μm chlorophyll levels (Fig. 7) were, in general, not associated with the highest densities of diatoms (Fig. 9).

While diatom cell densities were relatively low outside the Northeast Peak, they nonetheless dominated the phytoplankton community in April–May over much of the Bank, with diatoms making up the majority of the top 25 most-abundant taxa (Table 1). Overall dinoflagellate cell densities, including *Alexandrium* spp., were relatively low, and did not exceed 20,000 cells l^{-1} (Fig. 9) during the April–May period. Only six major dinoflagellate taxa and a group of unidentified flagellate cysts were in the top 25 taxa observed on the April–May cruise. However, a number of dinoflagellate taxa including *Alexandrium* spp., *Gyrodinium* spp., *Protoperidinium* spp., and unidentified dinoflagellate cysts were present at nearly every station, possibly signaling that the seasonal increase in the dinoflagellate population had commenced (Table 1). Nanoplankton cell densities were relatively low in April–May, as compared with the remaining two cruises, with cell densities less than 1,000,000 cells l^{-1} on the Bank (Fig. 9). Results from the second cruise in May–June reveal that an apparent shift in phytoplankton community structure had occurred. Diatom cell densities were lower, generally less that 60,000 cells l^{-1}) across the Bank, including the Northeast Peak (Fig. 10), where cell densities in excess of 200,000 cells l^{-1} were observed during the previous cruise. Dinoflagellate cell densities had increased along the Southern Flank as reflected in the apparently annual *Alexandrium* bloom (McGillicuddy et al., 2014; Townsend et al., 2014), with dinoflagellate cell densities reaching 70,000 cells l^{-1} at some stations (Fig. 10). It was during this May–June survey that we observed the highest cell densities of *Alexandrium* spp., exceeding 7000 cells l^{-1} on the Southern Flank (Fig. 10). In addition to

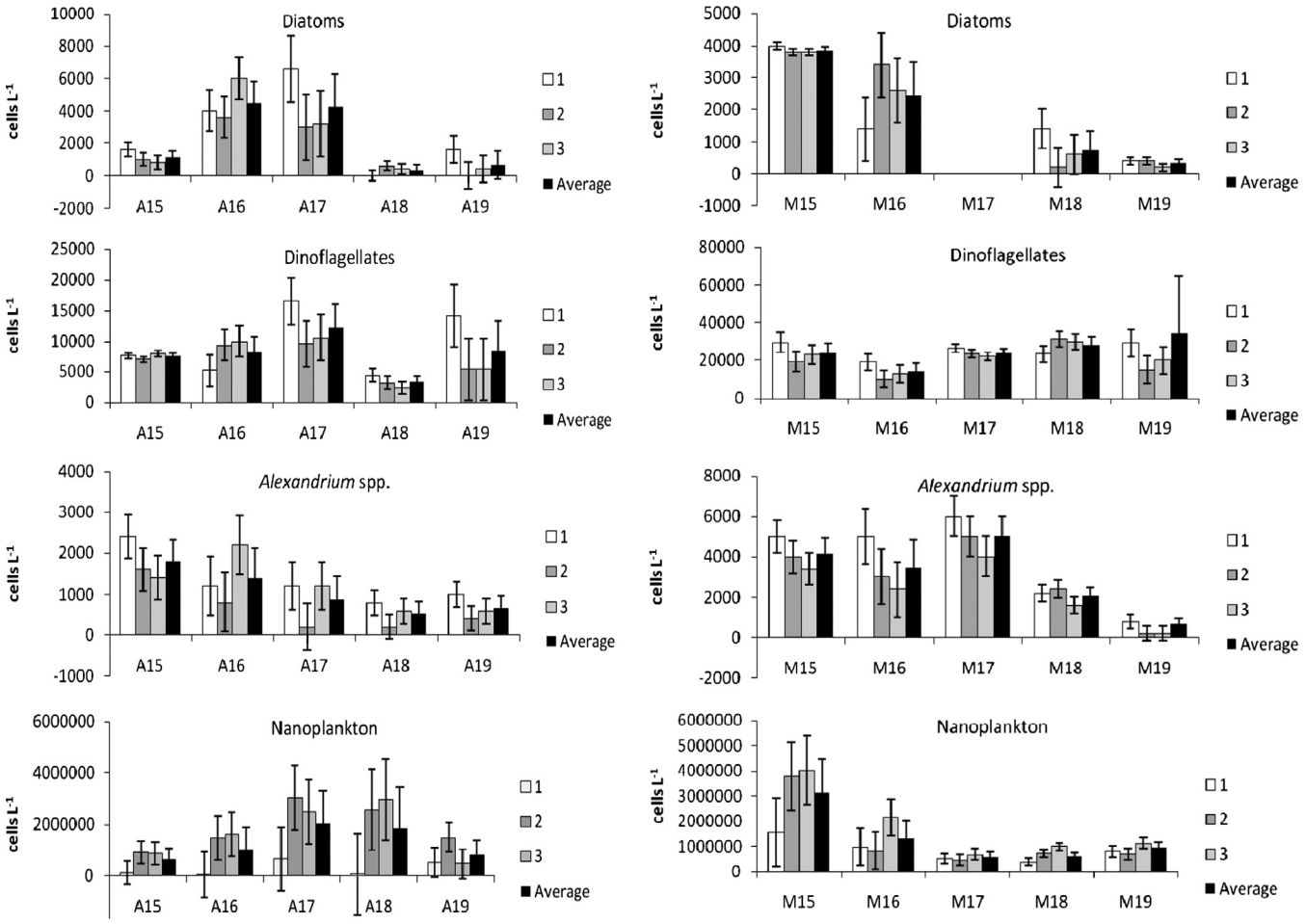

Fig. 8. Results of triplicate counts of the major phytoplankton groups: diatoms, dinoflagellates, *Alexandrium* spp., and nanoplankton, for the first two cruises: 28 April–5 May and 27 May–4 June, along a single transect on each cruise. The station number (Fig. 2) is given preceded by A for the first cruise and M for the second cruise. Error bars represent standard deviations, and to make reading easier, they are plotted on each of the three sample bars, as well as the average.

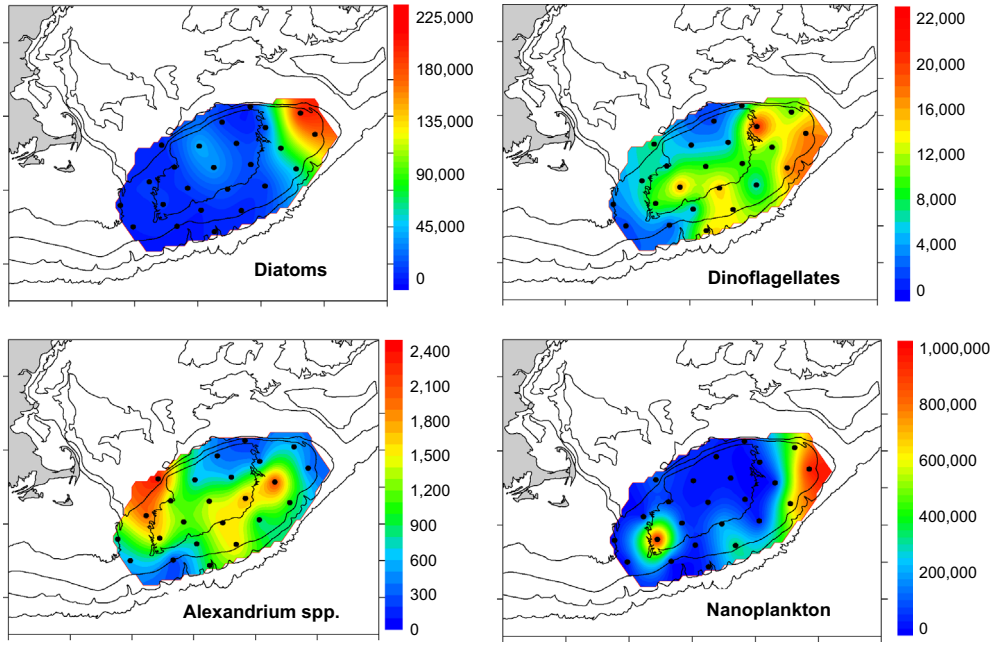

Fig. 9. Contour plots of cell densities of the four major phytoplankton taxa for the 28 April–5 May cruise given in cells l^{-1}; *top left:* diatoms; *top right:* dinoflagellates; *lower left: Alexandrium* spp.; *lower right:* nanoplankton.

Table 1
Results of April–May cruise (28 April–5 May 2008). Rank order of the 25 most-abundant phytoplankton taxa observed, and rank order of the number of samples in which that taxon was found (number of samples equals number of stations = 24).

Taxon	Class	Rank order of average abundance per sample	Rank order of number of samples observed
Phaeocystis spp.	Prymnesiophyceae	1	4
Other nanoplankton		2	4
Cryptomonas spp.	Cryptophyceae	3	3
Coscinodiscus spp.	Coscinodiscophyceae	4	5
Skeletonema spp.	Coscinodiscophyceae	5	10
Leptocylindrus spp.	Coscinodiscophyceae	6	7
Thalassiosira spp.	Coscinodiscophyceae	7	7
Amphidinium spp.	Dinophyceae	8	8
Scrippsiella spp.	Dinophyceae	9	6
Chaetoceros spp.	Coscinodiscophyceae	10	11
Pseudo-nitzschia spp.	Bacillariophyceae	11	13
Cysts		12	3
Gryodinium spp.	Dinophyceae	13	4
Alexandrium spp.	Dinophyceae	14	1
Dactyliosolen spp.	Coscinodiscophyceae	15	12
Stephanopyxis spp.	Coscinodiscophyceae	16	15
Protoperidinium spp.	Dinophyceae	17	2
Gymnodinium spp.	Dinophyceae	18	7
Guinardia striata	Coscinodiscophyceae	19	14
Ceratium spp.	Dinophyceae	20	9
Dinophysis spp.	Dinophyceae	21	7
Paralia sulcata	Coscinodiscophyceae	22	16
Prorocentrum spp.	Dinophyceae	23	11
Rhizosolenia spp.	Coscinodiscophyceae	24	17
Gonyaulax spp.	Dinophyceae	25	18

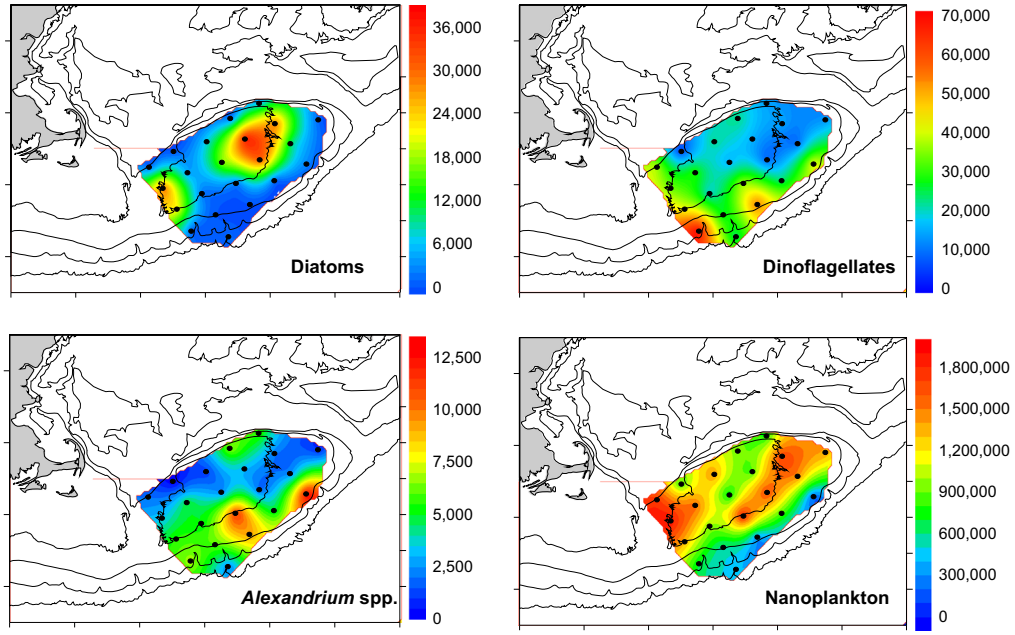

Fig. 10. Contour plots of cell densities of the four major phytoplankton taxa for the 27 May–4 June cruise given in cells l^{-1}; *top left:* diatoms; *top right:* dinoflagellates; *lower left: Alexandrium* spp.; *lower right:* nanoplankton.

Alexandrium spp., increased densities of *Scrippsiella* spp., *Heterosigma* spp., and *Amphidinium* spp. were also observed during the May–June cruise, with 13 dinoflagellate taxa among the top 25 taxa (Table 2). Slight increases in the nanoplankton community were apparent in May–June, but they did not overlap spatially with the dinoflagellate population (Fig. 10). Highest total and >20 μm chlorophyll concentrations did not appear to coincide with the increase in dinoflagellate cell densities, but instead corresponded with the peak in diatoms, although diatom cell densities were 5–10 fold lower in May–June than the previous cruise period.

By the time of our third survey cruise in June–July, the peak of the *Alexandrium* spp. bloom had apparently passed, leaving cell concentrations less than 2000 cells l^{-1}; the general dinoflagellate population had also decreased across much of the Bank, leaving only a single station on the southeast edge of the Bank with dinoflagellate cell concentrations in excess of 60,000 cells l^{-1} (Fig. 11). The dinoflagellate community was dominated by *Ceratium* spp., *Gyrodinium* spp., *Gymnodinium* spp., unidentified flagellate cysts, and *Polykrikos* spp., a heterotrophic dinoflagellate that was relatively abundant during the third survey (Table 3).

Table 2
Results of April–May cruise (27 May–4 June 2008). Rank order of the 25 most-abundant phytoplankton taxa observed, and rank order of the number of samples in which that taxon was found (number of samples equals number of stations = 24).

Taxon	Class	Rank order of average abundance per sample	Rank order of number of samples observed
Phaeocystis spp.	Prymnesiophyceae	1	1
Other nanoplankton		2	4
Cryptomonad spp.	Cryptophyceae	3	1
Alexandrium spp.	Dinophyceae	4	2
Amphidinium spp.	Dinophyceae	5	1
Guinardia flaccida	Coscinodiscophyceae	6	12
Scrippsiella spp.	Dinophyceae	7	3
Heterosigma spp.	Raphidophyceae	8	9
Cysts		9	1
Heterocapsa spp.	Dinophyceae	10	6
Pseudo-nitzschia spp.	Bacillariophyceae	11	12
Gymnodinium spp.	Dinophyceae	12	2
Protoperidinium spp.	Dinophyceae	13	3
Coscinodiscus spp.	Coscinodiscophyceae	14	5
Gryodinium spp.	Dinophyceae	15	1
Ceratium spp.	Dinophyceae	16	5
Dactyliosolen spp.	Coscinodiscophyceae	17	13
Dinophysis spp.	Dinophyceae	18	8
Gonyaulax spp.	Dinophyceae	19	7
Prorocentrum spp.	Dinophyceae	20	10
Leptocylindrus spp.	Coscinodiscophyceae	21	14
Thalassiosira spp.	Coscinodiscophyceae	22	11
Chaetoceros spp.	Coscinodiscophyceae	23	12
Paralia sulcata	Coscinodiscophyceae	24	13
Guinardia striata	Coscinodiscophyceae	25	13

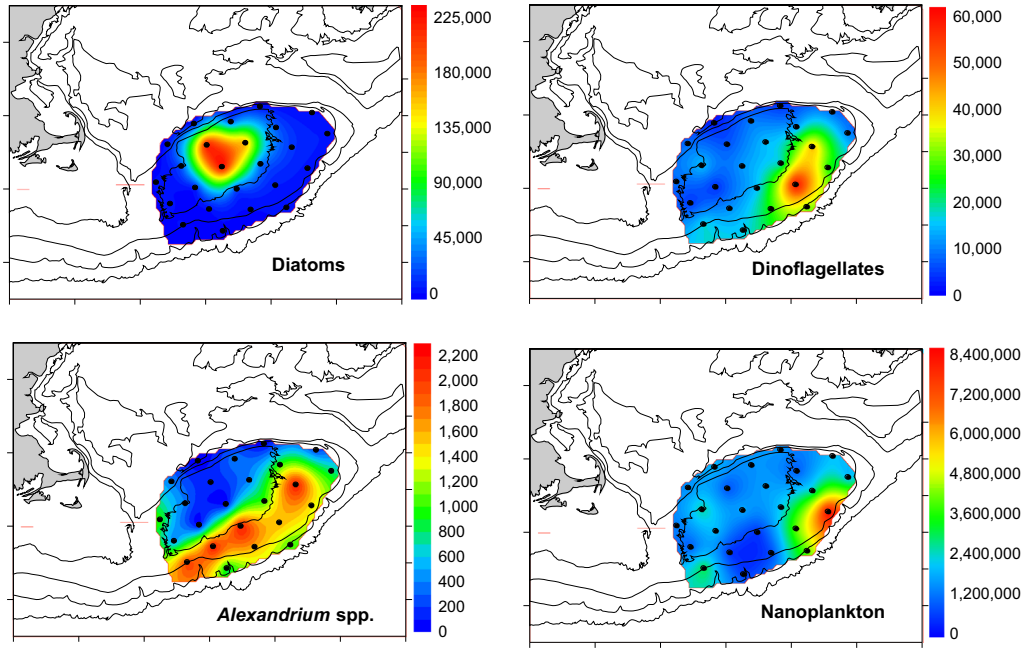

Fig. 11. Contour plots of cell densities of the four major phytoplankton taxa for the 27 June–3 July cruise given in cells l^{-1}; *top left:* diatoms; *top right:* dinoflagellates; *lower left: Alexandrium* spp.; *lower right:* nanoplankton.

An interesting increase in diatom cell densities was apparent in the central portion of Georges Bank during this last cruise, with more than 180,000 cells l^{-1} at some stations (Fig. 11), which we suspect was a response to the regeneration of silicate discussed earlier; the elevated diatom cell densities corresponded with the total and $>20\,\mu m$ chlorophyll concentrations. The diatom composition at the end of June included high densities of *Leptocylindrus* spp., *Pseudo-nitzschia* spp., and *Guinardia flaccida* (Table 3). Highest densities of nanoplankton were observed during this last cruise, with more than 8,000,000 cells l^{-1} on the southeast edge of the bank (Fig. 11). The higher densities of nanoplankton were reflected in the $<20\,\mu m$ chlorophyll concentrations with some stations exhibiting 4–5 $\mu g\ l^{-1}$ (Fig. 7).

3.3. Statistical analyses of phytoplankton community

3.3.1. Cluster analyses

Results of the cluster analysis, used here to analyze similarities among phytoplankton taxa based on their relative abundances on the three cruises, revealed four distinct taxonomic groups

Table 3
Results of June–July cruise (27 June–3 July, 2008). Rank order of the 25 most-abundant phytoplankton taxa observed, and rank order of the number of samples in which that taxon was found (number of samples equals number of stations = 24).

Taxon	Class	Rank order of average abundance per sample	Rank order of number of samples observed
Phaeocystis spp.	Prymnesiophyceae	1	1
Other nanoplankton		2	1
Cryptomonad spp.	Cryptophyceae	3	2
Leptocylindrus spp.	Coscinodiscophyceae	4	8
Heterosigma spp.	Raphidophyceae	5	2
Cysts		6	2
Gryodinium spp.	Dinophyceae	7	5
Gymnodinium spp.	Dinophyceae	8	6
Scrippsiella spp.	Dinophyceae	9	3
Guinardia flaccida	Coscinodiscophyceae	10	12
Ceratium spp.	Dinophyceae	11	4
Heterocapsa spp.	Dinophyceae	12	4
Amphidinium spp.	Dinophyceae	13	4
Pseudo-nitzschia spp.	Bacillariophyceae	14	11
Coscinodiscus spp.	Coscinodiscophyceae	15	7
Polykrikos spp.	Dinophyceae	16	9
Skeletonema spp.	Coscinodiscophyceae	17	10
Alexandrium spp.	Dinophyceae	18	4
Prorocentrum spp.	Dinophyceae	19	6
Chaetoceros spp.	Coscinodiscophyceae	20	11
Protoperidinium spp.	Dinophyceae	21	6
Paralia sulcata	Coscinodiscophyceae	22	14
Gonyaulax spp.	Dinophyceae	23	11
Guinardia striata	Coscinodiscophyceae	24	13
Dactyliosolen spp.	Coscinodiscophyceae	25	13

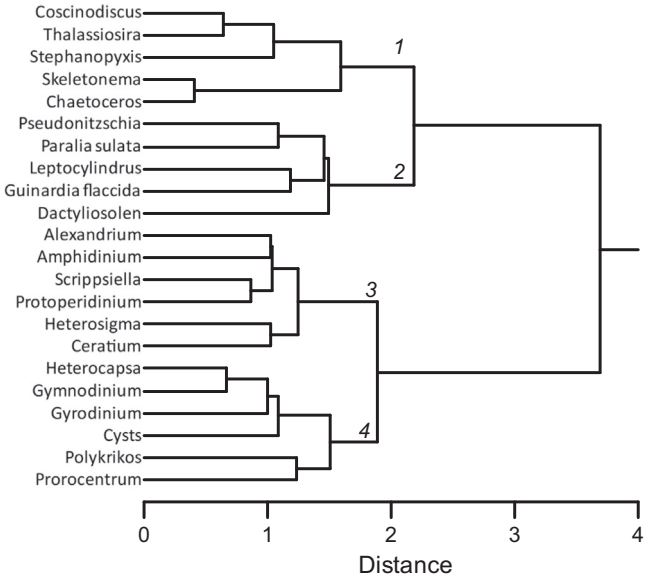

Fig. 12. Dendrogram resulting from cluster analysis of the 22 most-abundant taxa using Euclidean distances. Four groups were formed subjectively using Ward linkage.

(Fig. 12); the spatial distributions of each cluster group are given in Figs. 13 and 14.

Phytoplankton Cluster 1 was comprised solely of centric diatoms, including *Coscinodiscus* spp., *Thalassiosira* spp., *Stephanopyxis* spp., *Skeletonema* spp., and *Chaetoceros* spp. These taxa were present in highest cell densities ($>150{,}000$ cells l^{-1}) on the Northeast Peak during the April–May cruise (Fig. 13). The taxa in Cluster 1 became less abundant as the summer progressed, with fewer than 15,000 cells l^{-1} in May–June. The highest densities of this diatom group shifted from the Northeast Peak in April–May, to a more central location in May–June and June–July.

Phytoplankton Cluster 2 was also made up entirely of diatoms, including: *Pseudo-nitzschia* spp., *Leptocylindrus* spp., *G. flaccida*, and *Dactyliosolen* spp. Cluster 2 taxa exhibited similar spatial patterns to 1, with highest concentrations on the Northeast Peak on the first cruise, but with a second patch on the central crest of the Bank (Fig. 13). While both Clusters 1 and 2 taxa were observed at similar locations on the Bank in April–May, cell densities of Cluster 2 taxa were lower, with a maximum density of only about 20,000 cells l^{-1}. Densities of cells in Cluster 2 increased slightly in May–June, with localized patches ($>20{,}000$ cells l^{-1}) at some centrally-located stations, and reached highest densities of approximately 220,000 cells l^{-1} in June–July, which were again located on the central crest (Fig. 13).

Phytoplankton Clusters 3 and 4, all dinoflagellates, except for *Heterosigma* spp., a raphidophyte in Cluster 3, occupied a much broader spatial distribution across the three cruises. Taxa in Cluster 3 included *Alexandrium* spp., *Amphidinium* spp., *Scrippsiella* spp., *Protoperidinium* spp., *Heterosigma* spp., and *Ceratium* spp.; their cell densities were relatively low in April–May, and were located primarily on the southeastern edges of the Bank (Fig. 14). By May–June, Cluster 3 cell densities had increased to greater than 40,000 cells l^{-1} at some stations, and were located farther to the southwest along the southern edges of the Bank. Cell densities were lower in June–July, with maximum densities of only about 24,000 cells l^{-1}.

Dinoflagellates in Cluster 4, which included: *Heterocapsa* spp., *Gymnodinium* spp., *Gyrodinium* spp., unidentified flagellate cysts, *Polykrikos* spp., and *Prorocentrum* spp., were generally less abundant than Cluster 3 taxa (Fig. 14). Cluster 4 cell densities were less than 15,000 cells l^{-1} April–May, with highest cell densities on the Northeast Peak coinciding with high diatom densities of Cluster 1 (Fig. 13). In May–June, Cluster 4 cell densities remained relatively low compared to Cluster 3, with a maximum of about 13,000 cells l^{-1} along the southern edge of the Bank. In June–July, however, maximum cell densities for Cluster 4 increased to about 45,000 cells l^{-1}, with highest densities again associated with the southern edge of the Bank, where Cluster 3 was also abundant.

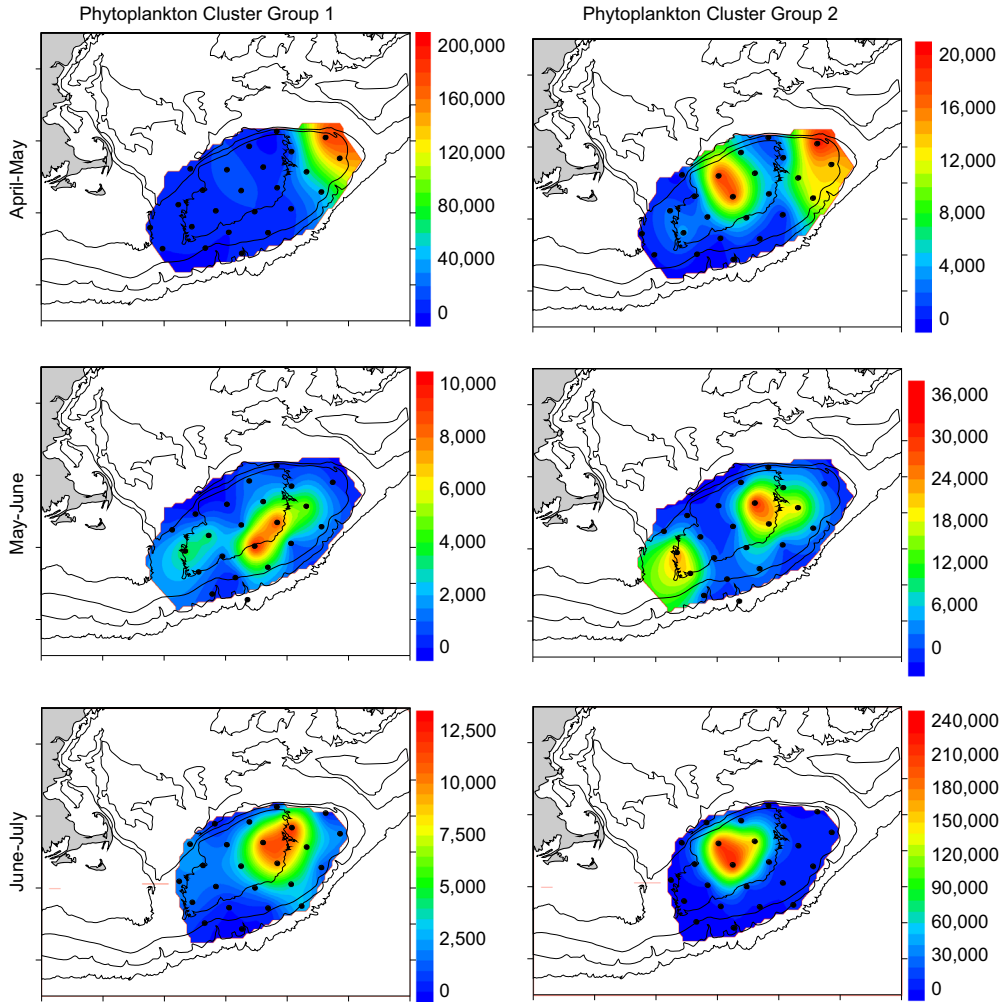

Fig. 13. *Left:* Contour plot of the distribuition in cells l^{-1} of phytoplankton taxa in Cluster Group 1 (*Coscinodiscus* spp., *Thalassiosira* spp., *Stephanopyxis* spp., *Skeletonema* spp., and *Chaetoceros* spp.); *right:* Cluster Group 2 taxa (*Pseudo-nitzschia* spp., *Paralia sulcata*, *Leptocylindrus* spp., *Guinardia flaccida*, *Dactyliosolen* spp.) for the cruise dates indicated. Contours are cells l^{-1}. *Top:* 28 April–5 May 2008; *middle:* 27 May–3 June; *bottom:* 27 June–3 July.

The dinoflagellates of Cluster 4 reached their highest cell densities of the summer during this last cruise period, and exhibited similar spatial trends as Cluster 3.

3.3.2. Principal Component Analysis

Principal Component Analysis (PCA) performed on standardized cell densities of the top 22 phytoplankton taxa displayed similar results to that just discussed. Plotted using principal components 1 and 2, which accounted for 39% of the variance in the samples (22.7% and 16.4%, respectively), the taxa making up the diatoms in Cluster 1 tended to group close together in coordinate space, as did all taxa in Cluster 2, with the exception of *Pseudo-nitzschia* spp., the only pennate diatom included in the analysis (Fig. 15). Clusters 3 and 4 did not form distinct groups in the PCA, but they were separate from the diatom taxa of Clusters 1 and 2. Further breakdown of the component loadings revealed that the dinoflagellates used in the analysis were responsible for most of the variance for principal component 1, suggesting that differences in dinoflagellate abundances accounted for most of the variability in the data. Diatom taxa accounted for most of the variability in principal component 2, which is not surprising as diatoms tended to be relatively low in abundance, only exhibiting a few localized patches of increased abundance throughout the summer. Shifts within the dinoflagellate community appeared to be less dramatic versus changes to the diatom community (often on the order of hundreds of thousands of cells), and could be the reason dinoflagellates tended to associate together in the PCA with no discernable groups among them. This was also evident in the cluster analysis where all dinoflagellate taxa grouped together, whereas Clusters 1 and 2 diatoms were less closely related and revealed a more obvious separation (Fig. 15).

3.3.2.1. Station clusters. A second cluster analysis was performed to examine how stations from the three cruises group together based on the cell densities of the top 22 phytoplankton taxa in order to assess linkages between oceanographic features and phytoplankton distributions. The analysis formed six station clusters ranging from as few as three stations in a cluster, to as many as approximately 30 in another cluster (Fig. 16). Station Cluster 1 joined four stations from the April–May survey exclusively (Figs. 16 and 17), all of which were on the Northeast Peak (Fig. 18). Further breakdown of the percentages of each of the four phytoplankton abundance cluster groups revealed the dominance of diatom Phytoplankton Cluster Group 1 at this set of stations (Fig. 19). The small station cluster that formed appeared to be the result of the high cell density patch of diatoms on the crest of the Bank in April.

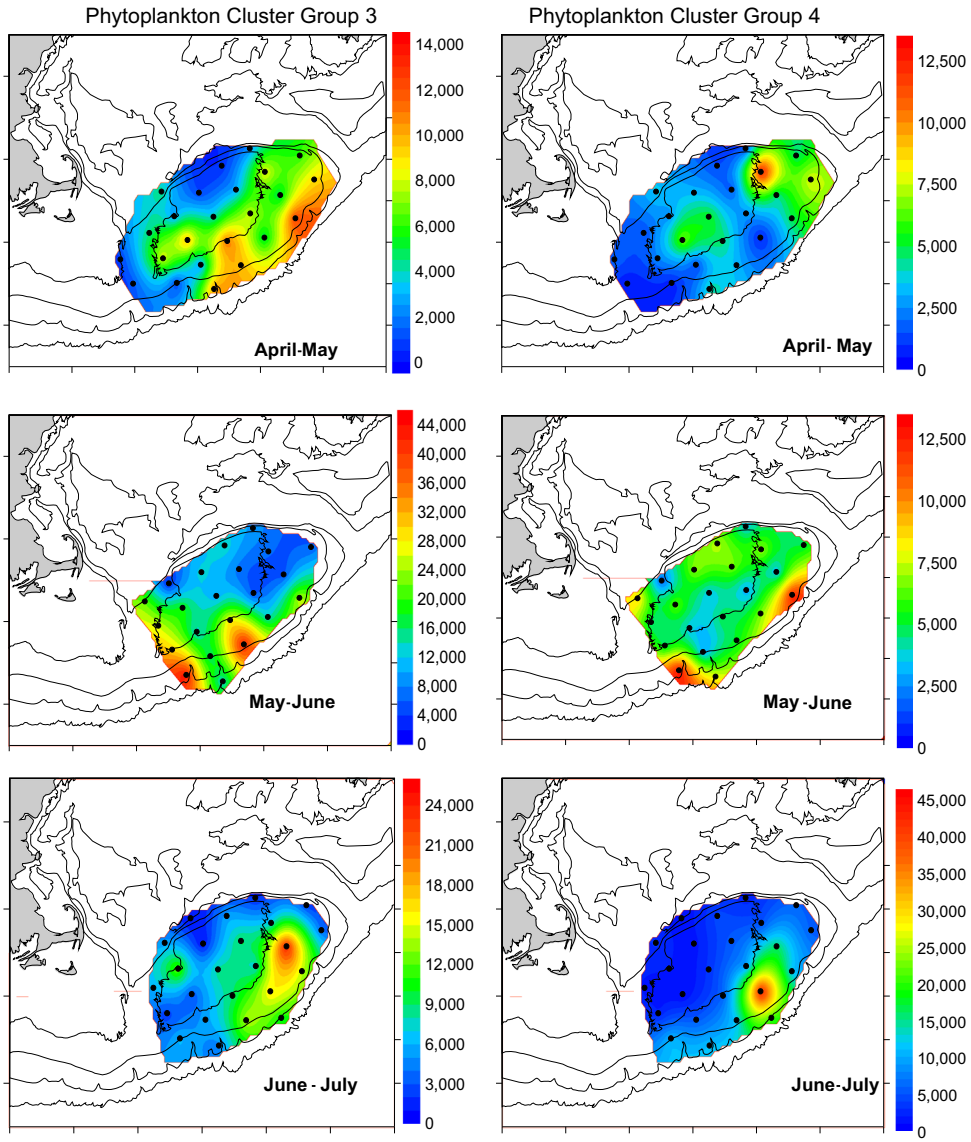

Fig. 14. *Left:* Contour plot of the distribuition in cells l^{-1} of phytoplankton taxa in Cluster Group 3 (*Alexandrium* spp., *Amphidinium* spp., *Scrippsiella* spp., *Protoperidinium* spp., *Heterosigma* spp., *Ceratium* spp.); *right:* Cluster Group 4 taxa (*Heterocapsa* spp., *Gymnodinium* spp., *Gyrodinium* spp., unidentified cysts, *Polykrikos* spp., *Prorocentrum* spp.), for the cruise dates indicated. Contours are cells l^{-1}.

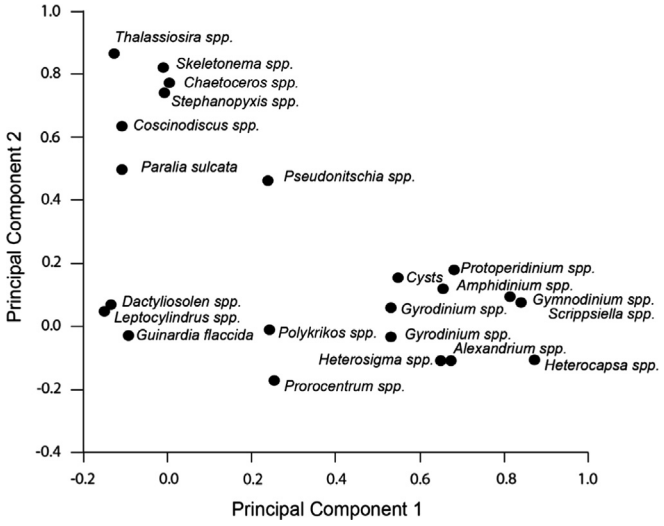

Fig. 15. Twenty-two phytoplankton taxa plotted using principal components 1 and 2 from the Principal Component Analysis.

Station Clusters 2 and 3 contained a mix of stations from the three cruises (Figs. 16 and 17). Station Cluster 2 did not include stations from the April–May cruise, but was $>75\%$ comprised of stations from the second cruise, in May–Ju ne (Fig. 17), and was dominated by dinoflagellates in Phytoplankton Cluster Group 3, which accounted for greater than fifty percent of the phytoplankton abundance (Fig. 19). Dinoflagellates in Phytoplankton Cluster Group 4 also contributed substantially to Station Cluster 2, making up approximately 30% (Fig. 19). The locations of stations in Station Cluster 2 were along the western and southern regions of the Bank in May–June and along the southeastern edge in June–July (Fig. 18).

Station Cluster 3 was equally represented by diatom clusters and dinoflagellate clusters (Fig. 19). Station Cluster 3 contained 16 stations and the majority of these stations were from the April–May cruise; those remaining were mostly from the June–July cruise, with only one station from the May–June cruise included (Fig. 16). The lack of dominance of a single phytoplankton group (i.e., the diatoms or dinoflagellates of Phytoplankton Clusters 1–4) is possibly the result of the shift in the phytoplankton community after the April–May cruise. The transition from a diatom- to dinoflagellate-dominated community could explain why diatoms

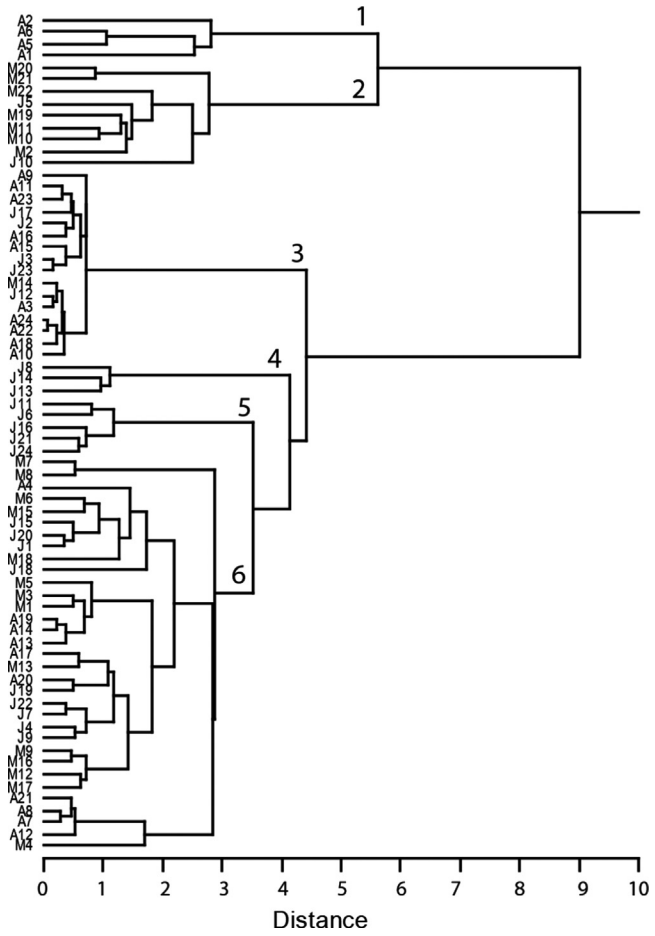

Fig. 16. Dendrogram of the 70 stations sampled during the three cruises using Euclidean distances: 28 April–5 May station number preceded by A; 27 May–4 June station number preceded by M, 27 June–3 July station number preceded by J. Six groups were subjectively formed using Ward linkage.

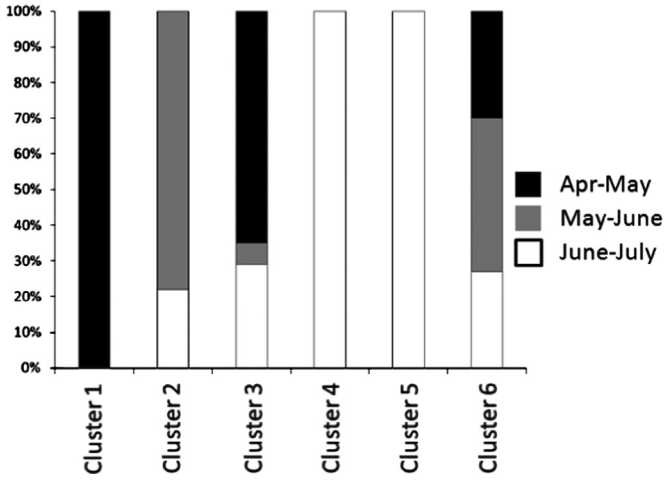

Fig. 17. Percentage of stations from the three cruises in each of the six station clusters in Fig. 16.

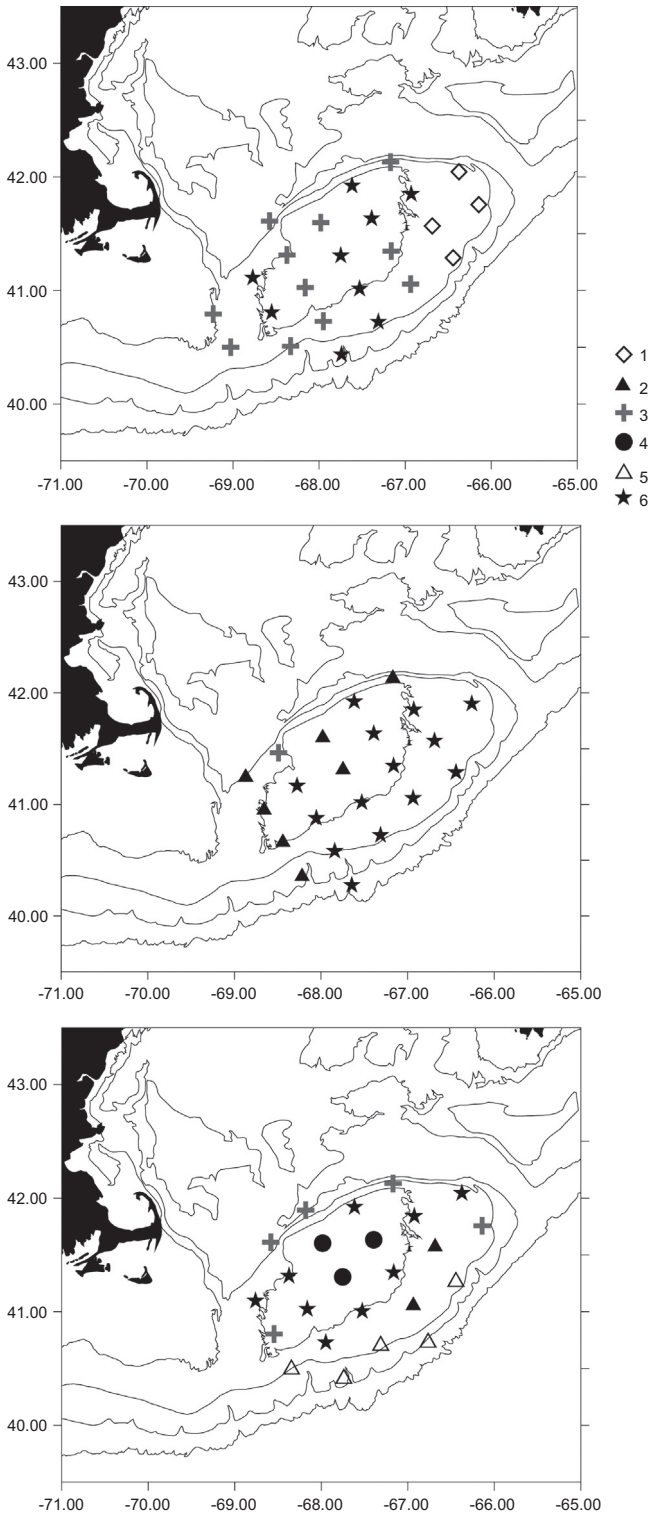

Fig. 18. Locations of the six station clusters in Fig. 16 for the three cruises. *Top:* 28 April–5 May; *middle:* 27 May–4 June; and *bottom:* 27 June–3 July.

and dinoflagellates were seen in relatively equal proportions at those stations.

Station Cluster 4, like the first cluster, was small, grouping only three stations, all part of the June–July cruise and all located in a small patch on the central crest of the Bank (Figs. 16–18). Like Station Cluster 1, Cluster 4 appeared to be grouped together based on the high densities ($>100{,}000$ cells l^{-1}) of diatoms; however, diatom Phytoplankton Cluster Group 2 overwhelmingly dominated these three stations (Fig. 19).

The switch in dominance from diatom Phytoplankton Cluster Group 1 in April–May to diatom Phytoplankton Cluster Group 2 in June–July (Fig. 17) suggests that a significant successional pattern from one type of diatom group to another occurred from late spring to late summer. Station Cluster 5 was also exclusively

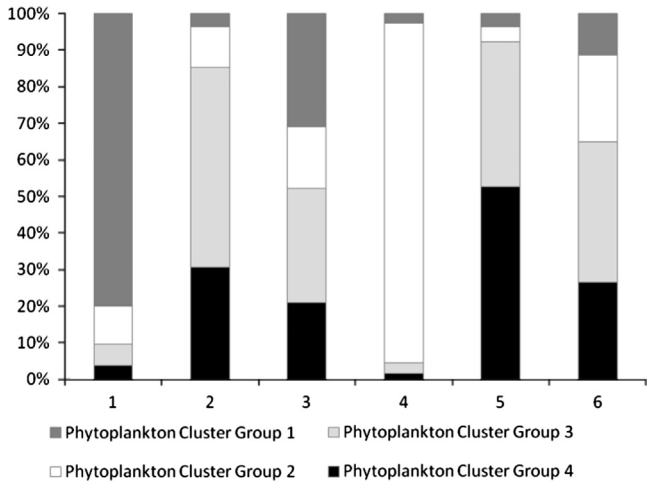

Fig. 19. Average percentage of phytoplankton taxa Clusters Groups 1–4 for each of the six station clusters in Fig. 16.

composed of June–July stations and occupied the Southern Flank of the Bank (Figs. 16–18). It was Station Cluster 5 that contained the highest percentage of Phytoplankton Cluster Group 4, which exhibited the highest overall cell densities during the end of the summer.

Station Cluster 6 was the largest cluster with 33 stations, spanning all three cruise dates (Figs. 16–18). The distribution of stations from this cluster on the Bank did not appear to have any significant pattern or oceanographic significance (Fig. 18).

4. Discussion

The annual recharge of dissolved inorganic nutrients across Georges Bank in the fall and early winter (Pastuszak et al., 1982; Hu et al., 2008; Rebuck, 2011) sets up the winter–spring diatom bloom. By late winter, when light conditions become favorable for the faster-growing diatoms, the bloom commences. This much is fairly well known. For example, Sears (1941) recorded densities of *Chaetoceros debilis* and *Chaetoceros decipiens* on Georges Bank in March and April of more than 500,000 cells l^{-1}. Other workers have also recorded species of *Thalassiosira* (*Thalassiosira nordenskioldii* and *Thalassiosira gravida*), *Coscinodiscus* sp., and *Navicula* sp. making up the majority of the phytoplankton community from as early as January through late April (Lillick, 1940; Bigelow, 1926; Sears, 1941; Falkowski and Von Bock, 1979). Diatom growth continues over the course of the spring until as late as early April when nutrients, in particular silicate, become depleted over most of the Bank's area (Kemper, 2000; Townsend and Thomas, 2001). This general picture of phytoplankton succession on Georges Bank is supported by the results we report here, but in addition, our results reveal a number of successional patterns among, and within, functional phytoplankton groups which in most cases can be related to key physical oceanographic processes operating on the Bank.

Following the winter–spring bloom on Georges Bank, seasonal warming leads to vertical stratification of the water column beyond the 60 m isobath, while the shallower central regions remain vertically well-mixed by tides (e.g., Loder, 1980). While much of the primary production in that central region is recycled production (Horne et al., 1989), it is the tidal pumping of nutrients from deeper waters beyond the Bank's edges that sets the upper limit of new primary production through the spring and summer months (Flagg, 1987; Townsend and Pettigrew, 1997; Hu et al., 2008). Hu et al. (2008) showed that the Northern Flank receives the greatest nutrient flux from tidal pumping, evidence of which is given here in Fig. 4 for the April–May and May–June cruises, which shows higher nitrate and silicate concentrations along the Northern Flank and on the Northeast Peak. Hu et al. also showed that lateral mixing of those tidally-pumped nutrients across the broad Bank is quite inefficient; computer simulations showed that after two and half months (80 lunar tides), the flux is sufficient to increase nitrate concentrations across the central portions of the Bank by only 1–2 μM. Thus, with the exception of the Northern Flank and the Northeast Peak, once the tidal mixing fronts become established in late spring and early summer, lateral fluxes of nutrients across the Bank are further impeded. By June–July we see little evidence of nitrate at the surface on the Northern Flank or Northeast Peak, suggesting that the flux is nearly matched by phytoplankton uptake there; subsurface nitrate distributions clearly show highest nutrient concentrations in those same areas of the Bank (not shown). Like nitrate, silicate concentrations were also depleted across the entire Bank by April–May, except along the outer edge of the Northern Flank, but there was evidence of regeneration of biogenic silica on the next two cruises (Fig. 4). In general, the taxonomic composition of the phytoplankton community shows some coherence with general location on the Bank, and thus, presumably, with oceanographic processes.

During the April–May period, the most-abundant diatom taxa, which were confined to the Northeast Peak (Fig. 13), were likely remnants of the winter–spring bloom; taxa in that Phytoplankton Cluster Group 1 included the diatoms *Coscinodiscus* spp., *Skeletonema* spp., *Chaetoceros* spp., and *Thalassiosira* spp., which together exceeded 180,000 cells l^{-1} at those stations. High cell densities of these taxa are typical during late spring conditions in other regions of the world, when most of the silicate has been taken up (e.g., Trigueros and Orive, 2001). The genera *Chaetoceros*, *Skeletonema*, and *Thalassiosira* have rapid growth rates and can apparently still outgrow and outcompete dinoflagellates even when silicate is drawn down to near-limiting concentrations in late spring and early summer (Grenny et al., 1973; Parsons et al., 1978).

The presence of highest cell densities of dinoflagellates in Phytoplankton Cluster Group 4 (*Heterocapsa* spp., *Gymnodinium* spp., *Gyrodinium* spp., *Polykrikos* spp., and *Prorocentrum* spp.) on the Northeast Peak (but at densities considered low for dinoflagellates; Fig. 14) suggests that a shift in community structure might be underway during the April–May period. Unidentified dinoflagellate cysts (intact) also made up a significant portion of Phytoplankton Cluster Group 4 and may signal the start of a developing dinoflagellate population following the diatom bloom. Unlike the diatoms in Phytoplankton Cluster Group 1, relatively high cell densities of dinoflagellates in Phytoplankton Cluster Group 3, which included *Alexandrium* spp., were located in the central and southeast portions of the Bank, not along the Northern Flank (Fig. 14). Dinoflagellates generally exhibit slower growth rates than diatoms, which can quickly exploit available resources and dominate the phytoplankton community (Banse, 1982; Yang et al., 1996), so when sufficient nutrient resources are available, as is often the case along the Northern Flank, diatoms remain abundant. It would appear that the Phytoplankton Cluster Group 3 dinoflagellates are unable to compete with the faster-growing Cluster Group 1 diatoms. *Alexandrium fundyense*, for example, exhibited significantly slower growth rates than the diatom *Ditylum brightwellii* in culture experiments reported by Gettings (2010), which had surplus nutrients levels. Thus, it is likely that elevated silicate concentrations along the edge of the Northern Flank and Northeast Peak in April–May allowed Cluster Group 1 diatoms to dominate, or otherwise prevented, via a competitive interaction, the successional replacement by dinoflagellate populations.

The relatively high cell densities of Phytoplankton Cluster Group 3 dinoflagellates along the southeastern edge (Southern Flank) of the Bank in April–May was coincident with a slug of cold and relatively fresh Scotian Shelf Water that had been advected onto the Bank, along with this phytoplankton community. Interestingly, dinoflagellates of Phytoplankton Cluster Group 4 co-occurred on the Northeast Peak with diatoms of Cluster Group 1 (Figs. 13 and 14). This capability of Group 4 dinoflagellates to coexist at relatively higher cell densities there compared to the rest of the Bank may be a result of alternative nutritional strategies often employed by Cluster Group 4 dinoflagellates. Species of *Prorocentrum* and *Polykrikos*, for example, exhibit both mixotrophy and heterotrophy, allowing them to not only coexist with diatoms but perhaps to ingest them (Jacobson and Anderson, 1996; Matsuyama et al., 1999). Some studies have shown heterotrophic dinoflagellates co-occurring with high cell densities of diatoms and in some cases they are suggested to be important in the termination of diatom blooms, often when nutrients are not limiting (Hansen, 1991; Bralewska and Witek, 1995; Tiselius and Kuylenstierna, 1996).

Continuous supplies of both new and recycled nutrients to Georges Bank, combined with a generally well-mixed water column, create conditions for phytoplankton production that are often patchy in nature (Franks and Chen, 1996). By late April, warming of the well-mixed waters on the shallow crest of the Bank is evident (Fig. 3), and nutrient concentrations, in particular nitrate and silicate are depleted across most of the Bank's area (Fig. 4). With little input of new nutrients, diatom growth during the April–May period had ceased across most of the Bank. Phytoplankton taxa in Cluster Groups 3 and 4, in particular *Alexandrium* spp., were becoming established across the central and southern portions of the Bank, in waters of increasing temperature and vertical stratification, with low nutrient levels, outside the tidal mixing fronts—conditions well-suited for dinoflagellates but not diatoms (Spector, 1984; Taylor, 1987).

By May–June, phytoplankton on Georges Bank were transitioning to a summer community, as much of the Bank was becoming more strongly stratified and therefore more isolated from nutrient sources beyond the Bank's edges. Developing tidal mixing fronts limit horizontal exchanges across the Bank, and increasing light levels would be expected to promote greater uptake rates of new fluxes of nutrients. Results from the May–June cruise showed patchy distributions of silicate, most likely from regeneration of biogenic silica from the spring diatom bloom as there were no concomitant increases in nitrate. Townsend and Thomas (2002) suggested that silicate regeneration on Georges Bank was dependent on seasonal warming; not only is dissolution of diatom frustules affected by temperature, but so too is microbial activity in the breakdown of the organic film coating the frustules, which must precede dissolution. While nitrate and phosphate remained low in May–June, slightly elevated concentrations of ammonium were observed at some stations (Fig. 5), which may be important to dinoflagellate production, in particular the *Alexandrium* spp. population, which reached highest cell densities across the southern half of the Bank in May–June (Fig. 10). Alternatively, it is possible as alluded to above, that we are seeing highest cell densities of dinoflagellates in Phytoplankton Cluster Group 3 (Fig. 14), which includes *Alexandrium* spp., in waters advected from the Northeast Peak, along with higher subsurface nitrate concentrations. The diatoms of Cluster Group 1 were no longer present at high cell densities in May–June, and did not exceed 10,000 cells l^{-1} anywhere on the Bank (Fig. 13). This absence of high cell densities of Group 1 diatoms is no doubt in response to nutrient limitation, as well as resulting competitive interactions with other taxa. Diatoms were not completely absent, however. While Group 1 diatoms were quite low in abundance, diatoms in Cluster Group 2 had increased from the previous cruise period (Fig. 13), but were not nearly as abundant as Group 1 taxa in April–May. The dinoflagellates in Cluster Group 4 were at low, background cell densities and were distributed across the Bank's area (Fig. 14) in May–June. The inability of these Cluster Group 4 dinoflagellates to become equally well-established as those in Cluster Group 3, despite relatively high cell densities at some stations (e.g., $>12{,}000$ cells l^{-1}), suggests that these taxa have a slower growth rate, and may be competitively inferior to the dinoflagellates and raphidophyte of Group 3, and thus unable to become dominant once a Group 3 population is established. Nonetheless, their patchy distribution and presence at nearly every station on Georges Bank during the May–June period suggests that the Group 4 taxa may be feeding on dinoflagellates and other phytoplankton cells, and therefore would be able to maintain limited population numbers with the dinoflagellates of Group 3. Distributions of dinoflagellates of both Cluster Groups 3 and 4, including *Alexandrium* spp., did not overlap with areas of higher cell densities of diatoms.

The relatively high cell densities of diatoms of Cluster Group 2 in May–June was likely in response to fluxes of regenerated biogenic silica, and recycled nitrogen, as their distribution on the central crest would make it unlikely that they were receiving new nutrient fluxes from the Bank's edges. Thus there has been a succession on the top of the Bank from a diatom community dominated by taxa in Cluster Group 1, which likely dominated the spring bloom, to taxa of Cluster Group 2, a group that may be competitively superior at lower nutrient levels. Group 2 taxa, notably species of *Leptocylindrus* and *Guinardia*, are often a major component of summer communities in other regions of the world (Casas et al., 1999; Trigueros and Orive, 2001; Gayoso, 1999; Schapira et al., 2008). The localized patch of Group 2 diatoms on the crest, at stations where dinoflagellates (i.e., Group 3 taxa), were lower in abundance suggests a competitive interaction among taxa in the two groups. Alternatively, if the dinoflagellate bloom remained confined in a frontal feature, a secondary diatom population could become dominant outside of this region where the dinoflagellate population is not established but where limited silicate is available for uptake.

Limited temporal sampling of stations on Georges Bank (i.e., one cruise per month) makes it difficult to comment on the nature of these distributional patterns, whereby high abundances of *Alexandrium* spp. and the dinoflagellates and raphidophyte of Group 3 remain separated from increased densities of the successor Group 2 diatoms. However, regeneration of silica, as suggested by observations during the late May cruise, could be a mechanism that supported the observed numerical dominance of Group 2 diatoms and allowed them to establish late-summer populations until nutrients again become limiting. What remains curious is the apparent inability of Group 2 diatoms to maintain higher cell concentrations (relative to dinoflagellates) at more than a few localized patches on the Bank despite relatively widespread increases in silicate, presumably due to biogenic silica regeneration. Smayda and Reynolds (2003) suggested that it is not the ability of some dinoflagellates to be competitively superior and exploit light and nutrients, but rather their tolerance of stress that allows them to outcompete diatoms in summer months. Warming temperatures along with increased light levels and low concentrations of inorganic nutrients on Georges Bank in the summer may explain in part why the dinoflagellate population is able to persist at higher abundances than diatoms, which are still present in relatively low numbers.

Among the most interesting results of this study were those from the June–July survey, which was characterized by the decline of the *Alexandrium* bloom and a shift toward a Cluster Group 4 dinoflagellate-dominated community. Cell densities of *Alexandrium*

spp. dropped to less than 3000 cells l^{-1}, but the highest densities were still between the 60 and 100 m isobaths on the southern half of the Bank (Fig. 11). The remaining dinoflagellates and raphidophyte of Group 3 were centered just south of the Northeast peak (Fig. 14) and had dropped to less than 25,000 cells l^{-1}. Still farther to the south and east, but also between the 60 and 100 m isobaths, were the Cluster Group 4 dinoflagellates which reached cell densities of $>40{,}000$ cells l^{-1} (Fig. 14). The reduction in numbers of Group 3 taxa from those seen in May–June is unlikely the result of continued nitrate depletion, which at subsurface depths was similar to the May–June nutrient field (not shown). During both the May–June and June–July cruises, it is likely that both Groups 3 and 4 dinoflagellates were utilizing recycled ammonium or, in the case of Group 4 dinoflagellates, employing alternative feeding strategies, e.g., heterotrophy or mixotrophy. The similar spatial patterns of Groups 4 and 3 dinoflagellates in June–July support this hypothesis, in that species of *Prorocentrum*, *Polykrikos*, and *Gyrodinium* are known to ingest larger dinoflagellate cells similar to those of Group 3 taxa (Hansen, 1992; Nakamura et al., 1995; Jeong et al., 2001, 2004; Kim and Jeong, 2004; Sherr and Sherr, 2007). *Polykrikos* spp. was not observed at any station during the first two cruises to Georges Bank in summer 2008. The general presence and increased abundance of these Group 4 dinoflagellates suggests that the late summer community on Georges Bank represents a succession to a community that is significantly mixotrophic and/or heterotrophic. We often observed what appeared to be ingested cells within *Polykrikos* spp. and *Gyrodinium* spp. cells. Previous studies of *Polykrikos* spp. in other waters reported similar abundance and spatial distributions of this heterotrophic dinoflagellate with bloom forming dinoflagellates, including *Gymnodinium* spp., also a Group 4 dinoflagellate in our study (Matsuyama et al., 1999). Supporting laboratory experiments also reveal that *Polykrikos* spp. is capable of feeding on *Gymnodinium* and other red tide species, including species we observed on Georges Bank: *Scrippsiella* spp., *Amphidinium* spp., *Ceratium furca*, *Gyrodinium* spp., and *Gymnodinium* spp., and thus may be important in controlling their population numbers (Sampayo, 1998; Matsuyama et al., 1999; Jeong et al., 2001).

Unidentified dinoflagellate cysts, which were included in phytoplankton Cluster Group 4 also increased in abundance in the June–July period. The higher numbers of cysts can be attributed to the decline of Group 3 dinoflagellates as a result of unfavorable environmental conditions (Anderson et al., 1985; Kremp and Heiskanen, 1999; Nagai et al., 2004).

The decline in *Alexandrium* spp. cell densities in Jun–July is likely a combination of adverse growing conditions and, perhaps, ingestion by zooplankton and/or other heterotrophic dinoflagellates (Petitpas et al., 2014). Cluster Group 3 dinoflagellates include *Protoperidinium* spp. and *Amphidinium* spp., which may be capable of grazing down bloom-like densities of harmful algal bloom species (e.g., Jeong and Latz, 1994; Buskey, 1997). Additional laboratory studies have observed preferential feeding of *Protoperidinium* on species of *Ceratium* (Olseng et al., 2002) which were also a part of the Group 3 population on Georges Bank. The clustering of *Protoperidinium, Ceratium* spp., and *Alexandrium* spp. based on similar abundance patterns at each station, suggests that heterotrophic feeding may need to be considered, at least not ruled out, as a factor in controlling *Alexandrium* populations on Georges Bank.

Competitive interactions between diatoms and dinoflagellates in natural assemblages are not well understood nor heavily studied, perhaps because dinoflagellate populations generally follow diatom blooms, and lack of sufficient sampling often prevents further investigation into community changes on the time scales of days, rather than months. It is generally assumed that dinoflagellates do well once nutrient levels limit growth of diatoms, which would otherwise outcompete them. But, beyond these physical and chemical limitations, the apparent inability of populations of *Alexandrium* and other dinoflagellates to become established in certain regions of Georges Bank relative to other areas, as shown in this study, is a difficult problem to sort out. We are thus led to suspect that coupled with physical and chemical drivers, interspecific competitive interactions are probably at work. Competitive interference by methods other than fast nutrient uptake and growth rates, might be a strategy employed by some taxa to compensate for slower growth, or rid the water column of other competitors (i.e. resource exploiters), in this case, the diatom population (Roy and Chattopadhyay, 2006; Roy, 2009). Somehow terminating bloom-like concentrations of diatoms would allow increases in dinoflagellate populations that were previously held in check and unable to compete with spring taxa. Conversely, persistence of diatoms, or a return to favorable growing conditions for diatoms, could prevent increases in the dinoflagellate population, which may be the case in June and July on Georges Bank, where we observed summer diatom taxa dominating regions on the Bank, perhaps keeping dinoflagellate abundance low. Recent studies have suggested that some species of diatoms are capable of resisting allelopathic interference by dinoflagellates which can also alter the phytoplankton community (Prince et al., 2008). This could be a means by which Group 2 diatoms on Georges Bank, in particular *G. flaccida*, co-occur with *Alexandrium* spp.

Competitive interactions between dinoflagellates and other groups of phytoplankton are often suggested to be the result of releases of allelopathic chemical compounds or substances that essentially limit diatom growth. This has been demonstrated in laboratory culture work for the same species of *Alexandrium* we observed on Georges Bank and in the Gulf of Maine (Arzul et al., 1999; Fistarol et al., 2004). Gettings (2010) observed in laboratory experiments what might be allelopathic interference between *A. fundyense* and the diatom *D. brightwellii.* Those results revealed a dependence on initial cell densities of each species, suggesting that a threshold concentration of *A. fundyense* is required to impact diatom growth, but that otherwise, the faster-growing diatom impeded growth of *A. fundyense.* When grown in a mixed culture of both *A. fundyense* and *D. brightwellii* and when cell densities were low, *A. fundyense* was apparently incapable of establishing itself and was outcompeted by the diatom, which grew well both in culture by itself, as well as in the presence of *A. fundyense*. But at higher cell densities, Gettings (2010) observed a reciprocal interaction. That is, once *A. fundyense* became established and reached relatively high cell densities, its growth was no longer impeded by *D. brightwellii*; rather, the reverse was evident: *A. fundyense* inhibited the growth of the diatom. This inhibition of the growth of *Alexandrium* spp. by diatoms had been suggested earlier based on field observation (Townsend et al., 2005).

5. Conclusions

The study of species succession and competitive interactions among phytoplankton taxa is a challenging task and much more work is clearly needed, not only on Georges Bank, but throughout the entire Gulf of Maine and in coastal and open ocean ecosystems in general. Observations of competition between bloom forming species, in particular diatoms and dinoflagellates, which often comprise the spring and summer phytoplankton community in many coastal and continental shelf regions, will remain difficult, but should be pursued along with laboratory experiments. Only by combining field and laboratory research on competitive interactions, in particular allelopathy between diatoms and dinoflagellates, as well as alternative nutritional strategies, such as heterotrophy and mixotrophy, can we hope to develop models of phytoplankton

species succession in marine environments as complex and as important as Georges Bank.

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