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Winter–spring transition of phytoplankton chlorophyll and inorganic nutrients on Georges Bank☆

David W. Townsend*, Andrew C. Thomas

School of Marine Sciences, University of Maine, 5741 Libby Hall, Orono, ME 04469, USA

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Abstract

Phytoplankton chlorophyll and inorganic nutrients were measured monthly during the winter–spring transition in 1997 on Georges Bank as part of the US Globec Program. We measured only chlorophyll and hydrography in January and June; nutrients were included in the February, March, April and May cruises. The winter–spring phytoplankton bloom on the Bank began early in 1997. Phytoplankton chlorophyll *a* concentrations were lowest in January ($< 1.0\,\mu g\,l^{-1}$), but by February concentrations ranged between 2 and $3\,\mu g\,l^{-1}$ on the western half of the top of the Bank (e.g., inside the 60 m isobath). Near-surface nitrate + nitrite concentrations in February were less than 6 μM over most of the Bank and below 4 μM on the western half. Near-surface silicate concentrations were generally less than 6 μM over most of the Bank in February, and were reduced to 2–3 μM inside the 60 m isobath; concentrations were depleted most on the western half of the top of the Bank, where they were less than 1 μM. Scotian Shelf Water intruded onto the Bank in February and remained distinct through April; near-surface nutrient concentrations in this Scotian Shelf Water in March were also low, and chlorophyll concentrations were high ($4–5\,\mu g\,l^{-1}$). The spring bloom was still underway in March, with increased chlorophyll concentrations spreading over most of the Bank. Silicate appeared to be the limiting nutrient beginning as early as February, with concentrations becoming depleted in March before nitrate + nitrite did. During April and May both silicate and nitrate concentrations were reduced to less than 1 μM in the near-surface waters over much of the top of the Bank; however, there were indications that silicate was being recycled on some parts of the Bank in May, which, in addition to recycled nitrogen, may have contributed to locally high chlorophyll concentrations observed in May and June. Higher near-surface nutrient concentrations also ringed the deeper edges of the Bank in late spring, where chlorophyll concentrations were generally high (greater than $5\,\mu g\,l^{-1}$) but also very patchily distributed.

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* Corresponding author. Tel.: 207-581-4367; fax: 207-581-4388.
E-mail address: davidt@maine.edu (D.W. Townsend).

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1. Introduction

Georges Bank is commonly considered to be among the most biologically productive marine ecosystems in the world ocean (Backus, 1987). Despite this presumed importance, the nature of primary production and nutrient dynamics has received remarkably little attention. From the few studies published to date, we know that primary production exceeds $400\,gC\,m^{-2}\,yr^{-1}$ in the central portion of the Bank (O'Reilly et al., 1987). Production appears to be highly seasonal in nature, and typically exhibits a pronounced late winter–early spring phytoplankton bloom (Riley, 1941), which is known to deplete available dissolved inorganic nitrogen from winter values of about $7\,\mu M\ NO_3$ to nearly undetectable levels by early May (Walsh et al., 1987). Following the spring bloom and continuing through early fall, the nutrient requirement for primary production is likely supplied by a combination of upwelling fluxes of "new" nutrients (cf. Dugdale and Goering, 1967; Eppley and Peterson, 1979) across the edges of the Bank, as well as recycling in the well-mixed regions over most of the top of the Bank (Loder and Platt, 1985; O'Reilly et al., 1987; Walsh et al., 1987; Townsend and Pettigrew, 1997). Cross-isobath mixing and nutrient injections onto Georges Bank appear to be most important along the Northern Flank of the Bank, where the topography is steepest and the hydrographic fronts are most pronounced (Loder et al., 1982; Loder and Platt, 1985; Loder and Greenberg, 1986; Horne et al., 1989; Townsend and Pettigrew, 1997). This provides a greater flux of nutrients to the northern edge, which is at the upstream end of the residual clockwise circulation pattern around the Bank. These higher nutrient concentrations on the northern flank of Georges Bank were first observed by Pastuszak et al. (1982), based on data from a limited number of stations. Townsend and Pettigrew (1997) supported and extended the observations of Pastuszak et al. (1982) with nitrate + nitrite samples collected in spring of 1993 and 1994.

Here we present a more complete survey of the time and space patterns of inorganic nutrients and phytoplankton chlorophyll on Georges Bank from winter to summer in 1997. Our results reinforce earlier observations of the spring bloom and suggestions of nitrogen limitation. In addition, we observed that silicate may become limiting to phytoplankton production as early as February and become recycled back into the water column beginning in May.

2. Materials and methods

Water collections were made at various depths at stations sampled during US GLOBEC broad scale survey cruises in 1997. The cruises were: 13–20 January (R/V *Albatross*); 11–22 February (R/V *Oceanus*); 16–29 March (R/V *Oceanus*); 20 April–3 May (R/V *Oceanus*; this cruise is referred to as the April cruise); 19–30 May (R/V *Oceanus*); 18–28 June (R/V *Albatross*). CTD casts for vertical profiles of temperature and salinity were made at Stations 1–40 (Fig. 1). Water samples for analyses of dissolved inorganic nutrients (DIN) and phytoplankton chlorophyll were collected from several depths on the same casts using Niskin bottles mounted on a rosette sampler. On all cruises except January and June, we collected additional near-surface water samples (ca. 2 m) at positions halfway between the regular stations.

Water samples for DIN were filtered through 0.45-μm Millipore cellulose acetate membrane filters, after first flushing the filters with sample water, and then frozen in 20 ml polyethylene

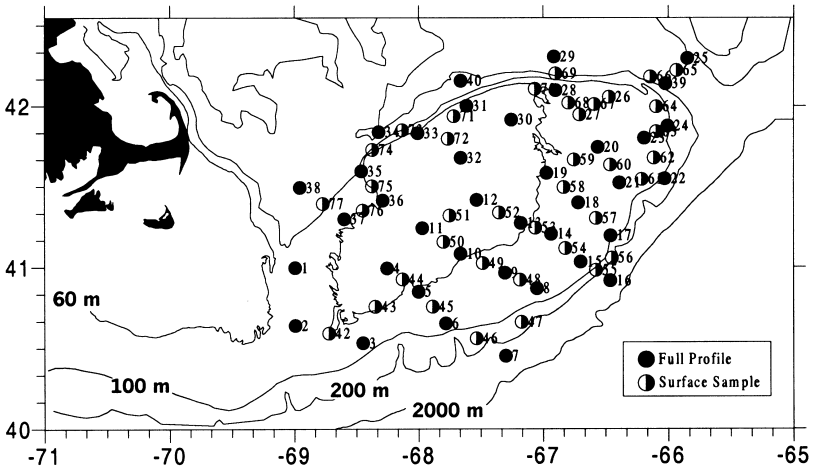

Fig. 1. Map of the Georges Bank area showing positions of stations sampled in 1997. The 60, 100, 200 and 2000 m isobaths are given.

scintillation vials by first placing the vials in a seawater–ice bath for about 10 minutes. Samples were analyzed for $NO_3 + NO_2$, NH_4, $Si(OH)_4$, and PO_4 on shore following the cruise using a Technicon II AutoAnalyzer and standard techniques (Whitledge et al., 1986).

Phytoplankton chlorophyll *a* was measured fluorometrically on discrete-water samples at all stations (Parsons et al., 1984) by collecting 100 ml from underway surface samples, and from the rosette bottle samples taken at depths selected to correspond to features revealed in the in situ fluorometer CTD cast. Samples were filtered onto GF/F filters, extracted in 90% acetone in a freezer for at least 6 h, and then analyzed at sea using a Turner Model 10 fluorometer.

The nutrient and chlorophyll measurements are interpreted in relation to the hydrographic data collected at all stations.

NOAA AVHRR images of sea-surface temperatures were recorded and processed at the University of Maine Satellite Oceanography Data Laboratory. Images were calibrated and processed to sea-surface temperature values using NOAA coefficients and standard split-window multi-channel algorithms (McClain et al., 1985), registered to a common grid at full resolution (1.1 km) and then land- and cloud-masked.

3. Results

Seasonal distributions of near-surface temperature, salinity, chlorophyll *a*, nitrate + nitrite, silicate and phosphate are presented as surface contour plots in Figs. 2–7. The corresponding AVHRR satellite images of sea-surface temperatures are given in Fig. 8.

Coldest water temperatures were not reached until February and March of 1997, when water temperatures were generally 4–5°C over much of the top of the Bank (Fig. 2). Waters colder than 4°C, which were associated with an influx of Scotian Shelf Water from the east, were confined to the eastern-most edge of the Bank. The fresher salinity characteristic of the Scotian Shelf Water is also

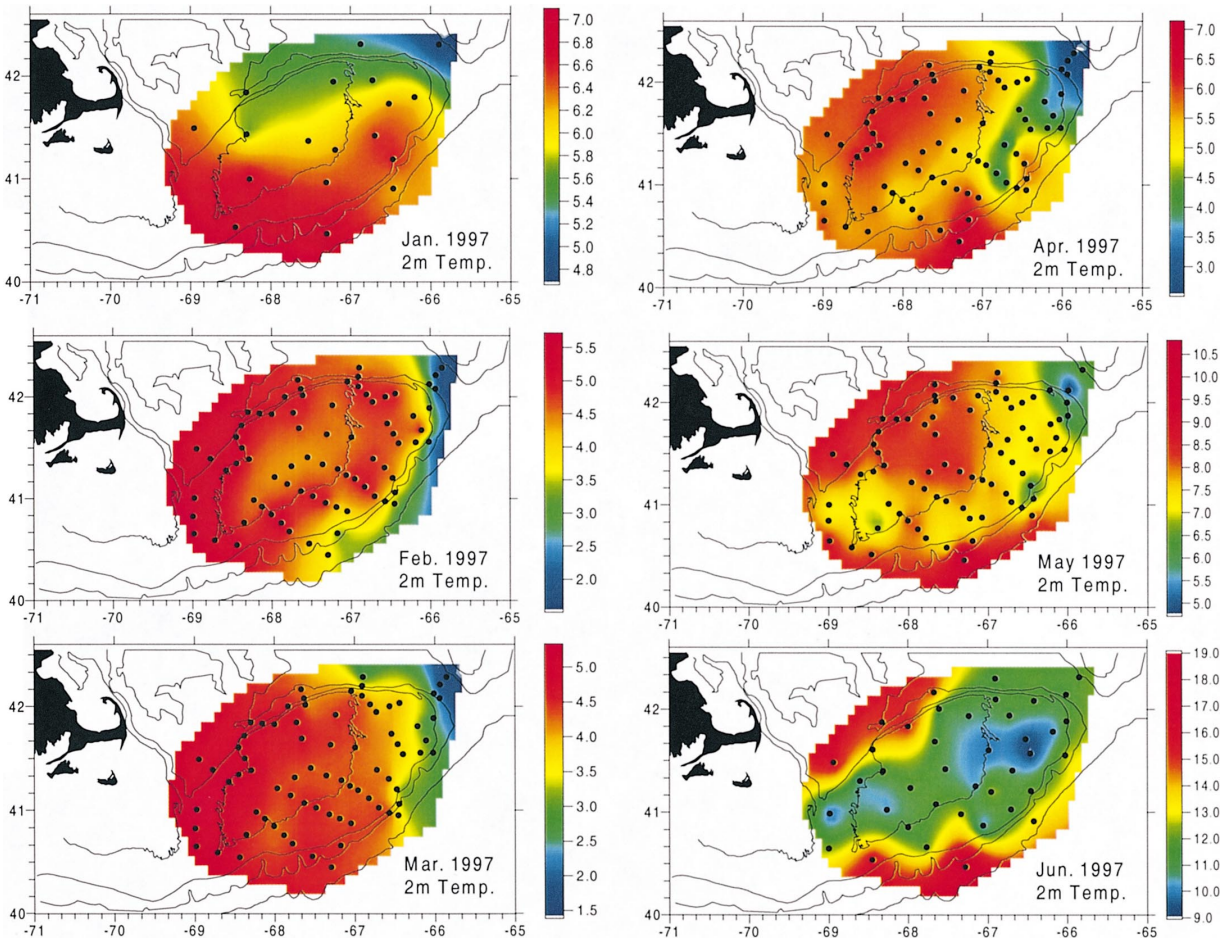

Fig. 2. Areal contour plots of surface temperatures during 1997 for the January to June cruises.

evident in Fig. 3. Warming of the top of the Bank became evident by April, when temperatures ranged from 5 to 6°C over much of the Bank, but the rate of warming was greatest in May and June. By May the surface waters of the top of the Bank were 10–12°C. The proximity of high-salinity Slope Water on the southern flank is apparent beginning in April and continuing into June (Fig. 3), and there is evidence of entrainment of Bank water in a warm-core Gulf Stream eddy beyond the southern edge of the Bank in May (Fig. 7).

Concentrations of chlorophyll *a* were lowest in January and were generally less than $1\,\mu g\,l^{-1}$ at most stations; the highest concentrations were only 1.7–1.9 $\mu g\,l^{-1}$ at Stations 9 and 12 (Fig. 4). The winter–spring phytoplankton bloom appears to have begun between the January and February cruises. In February, chlorophyll concentrations were greater than $1\,\mu g\,l^{-1}$ at most stations on top of the Bank, inside the 60 m isobath, and reached $3\,\mu g\,l^{-1}$ at Station 4. By March the bloom was well underway, with chlorophyll concentrations exceeding $5\,\mu g\,l^{-1}$ on parts of the Bank. By April

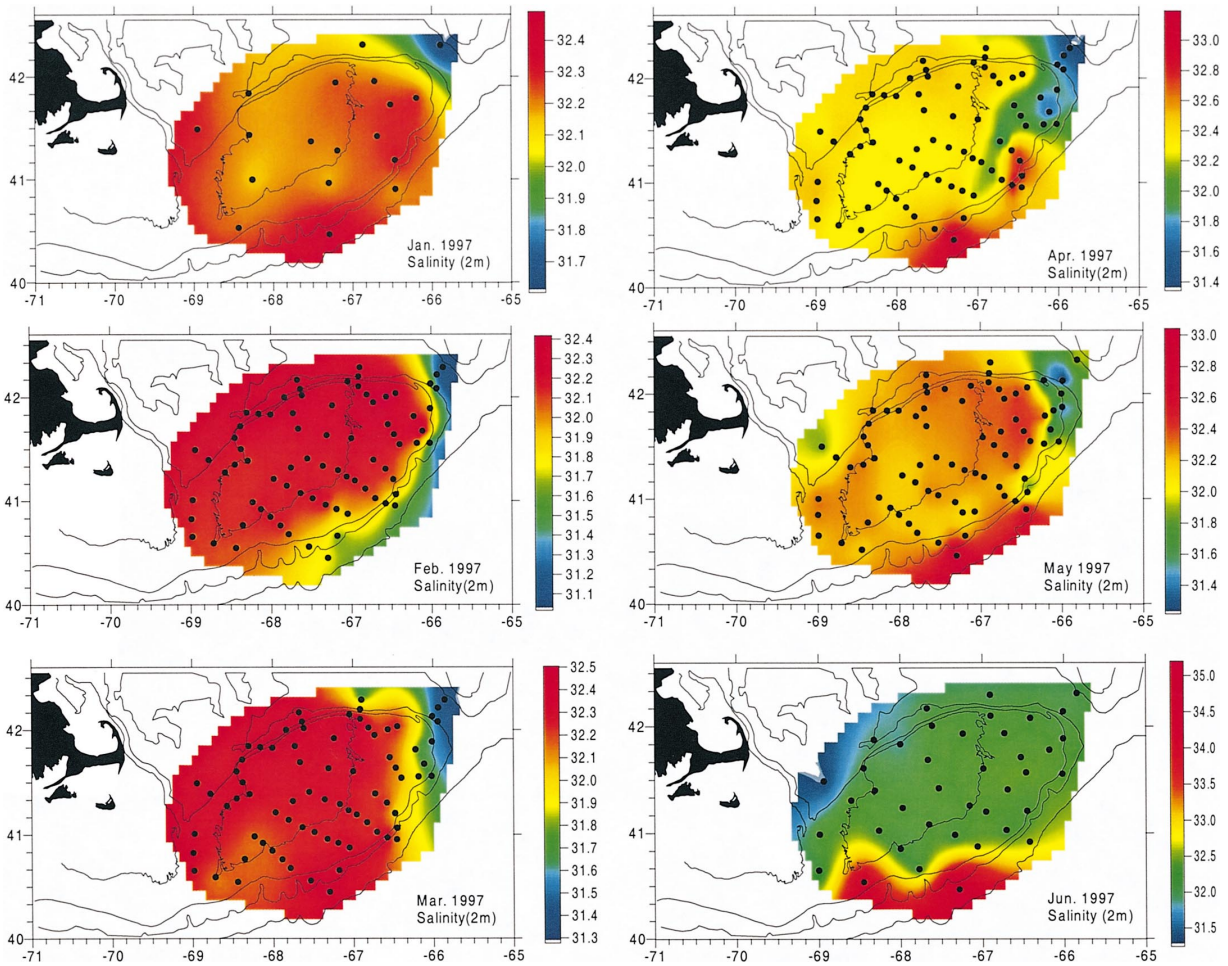

Fig. 3. Areal contour plots for surface salinities during 1997 for the January to June cruises.

the spring phytoplankton bloom was over, and chlorophyll concentrations exceeded $2\,\mu g\,l^{-1}$ at only a few stations. In May we observed patches of very high chlorophyll concentrations, exceeding $15\,\mu g\,l^{-1}$ at Stations 1, 4 and 14; but by June, the concentrations were low again, except on the Northeast Peak, where concentrations were $> 10\,\mu g\,l^{-1}$.

The concentrations of nitrate + nitrite became steadily depleted between February and May, in keeping with the general pattern of phytoplankton chlorophyll (Fig. 5). Levels of nitrate + nitrite on Georges Bank were generally 4–6 μM at most stations in February, except where chlorophyll was highest. Concentrations were still relatively high in Gulf of Maine waters just off the Northern Flank in February, where they exceeded 7 μM at the surface. The nitrate + nitrite concentrations were further depleted by the time of the March survey, especially in the southwest corner and southern part of the top of the Bank (inside the 60 m isobath). Concentrations remained greater than 4 μM over most of the Bank, however. By April, nitrate + nitrite concentrations were becoming depleted; most of the top of the Bank had less than 2 μM, and many stations had

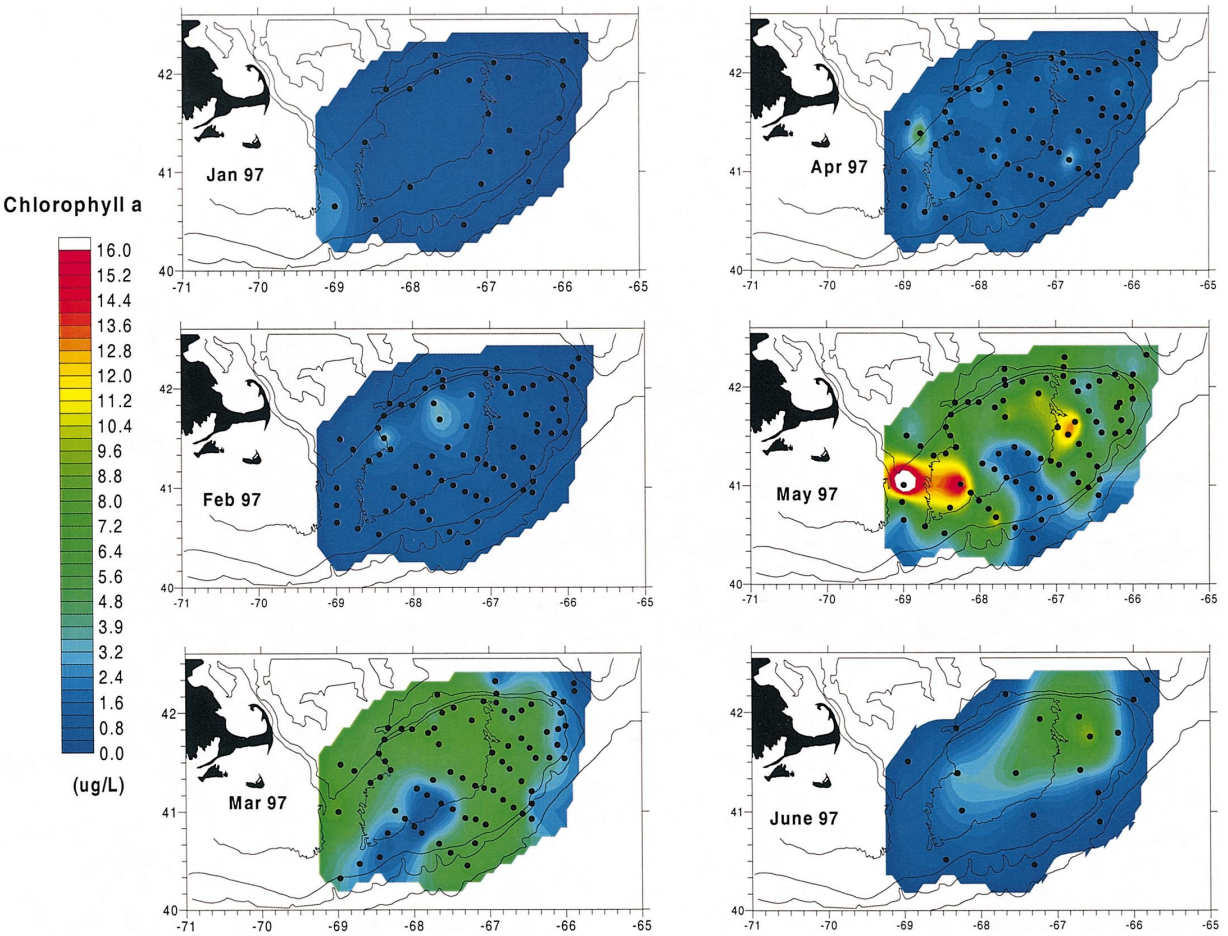

Fig. 4. Areal contour plots of surface chlorophyll (extracted chlorophyll *a*) during 1997 for the January to June cruises.

undetectable concentrations (e.g., Stations 4, 11 and 12). In May nitrate + nitrite was depleted in surface waters throughout the region except the Northeast Peak, where some stations had surface concentrations greater than 2 μM (e.g., Stations 20, 26, 31), in keeping with the notion of upwelling in that region of the Bank (Townsend and Pettigrew, 1997).

Silicate appeared to become limiting to the winter–spring diatom bloom before nitrogen (Fig. 6). Concentrations of silicate on the top of the Bank in February were less than 2 μM, while concentrations of nitrate + nitrite were 4–6 μM at the same stations. By April, surface silicate concentrations were less than 2 μM over most of the Bank, as well as in waters beyond the edges of the Bank. Localized patches of increased silicate concentrations were observed in May, which did not correspond to concomitant increases in nitrogen (nitrate + nitrite).

Concentrations of phosphate at surface stations in February were mostly in the range of ca. 0.5–1.0 μM (Fig. 7), and showed a steady decrease from March to May. The decrease was most apparent for the top of the Bank, similar to that of nitrate and silicate. In May there was evidence of

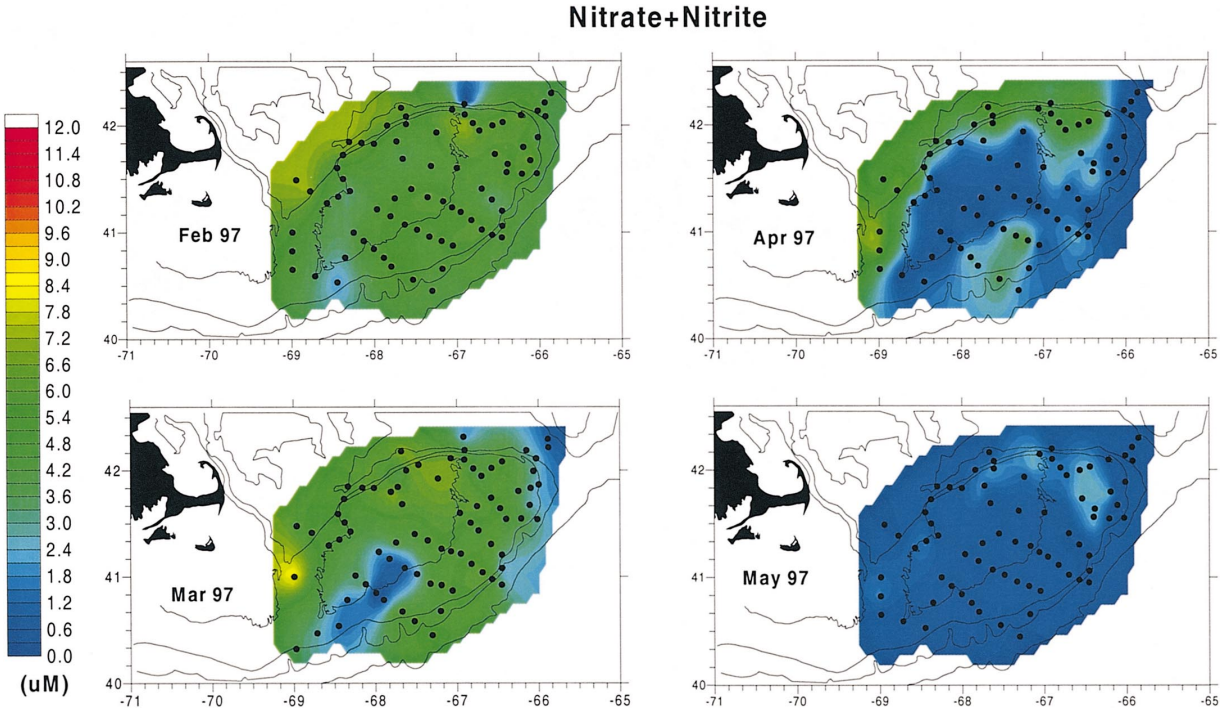

Fig. 5. Areal contour plots of surface nitrate + nitrite (μM) during 1997 for the February to May cruises.

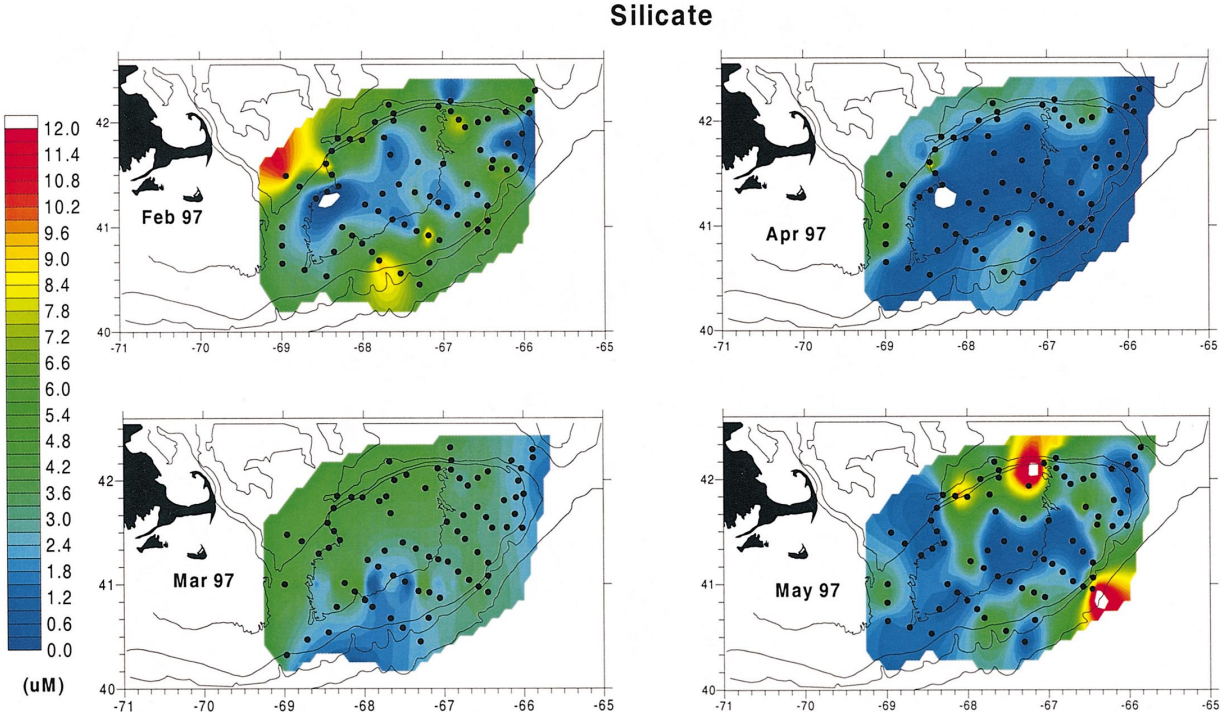

Fig. 6. Areal contour plots of surface silicate (μM) during 1997 for the February to May cruises.

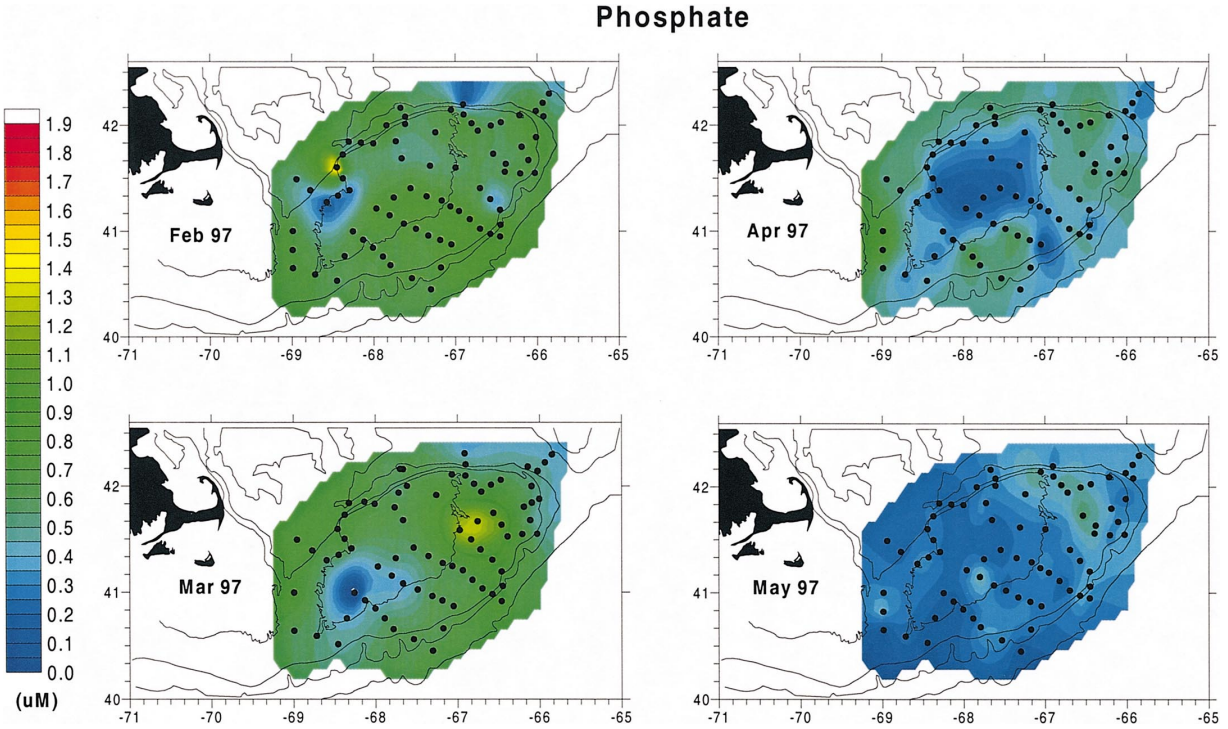

Fig. 7. Areal contour plots of surface phosphate (μM) during 1997 for the February to May cruises.

slightly higher concentrations in the vicinity of the Northeast Peak in keeping with upwelling and spreading of Gulf of Maine water into that area.

Surface concentrations of ammonia rarely exceeded 2.0 μM. Of the more than 800 total samples analyzed over the 4-month period February–May, only one exceeded 3.0 μM. Highest overall concentrations occurred in February, with much of the southern half of the Bank exhibiting surface concentrations between 1.0 and 1.7 μM. The distributions of ammonia, however, were very patchily distributed in March, April and May, and no spatial patterns, beyond that mentioned for February, could be discerned.

Analyses of SST patterns in concurrent satellite imagery (Fig. 8) during this period correspond well with the distributions discussed above. No images were available during the January cruise due to cloud cover. From February through May (Fig. 8a–e), coldest water was present along the eastern and southern sides of the Bank, continuous with a cold tongue of water (SST less than 4°C) originating over the Scotia Shelf. Temperature patterns over the top of the Bank were relatively homogenous during this period and were not well differentiated from surface water in the Gulf of Maine. Coldest temperatures (~ 4°C) were in March. By April 27 (Fig. 8d) surface temperatures over the Bank had warmed to 5–6°C. After April, the satellite data show strong warming over the Bank with temperatures of 8–9°C in May (Fig. 8e) and 9–12°C in June (Fig. 8f). In May there is evidence of warmer water over the center of the Bank than around both the southern and northern

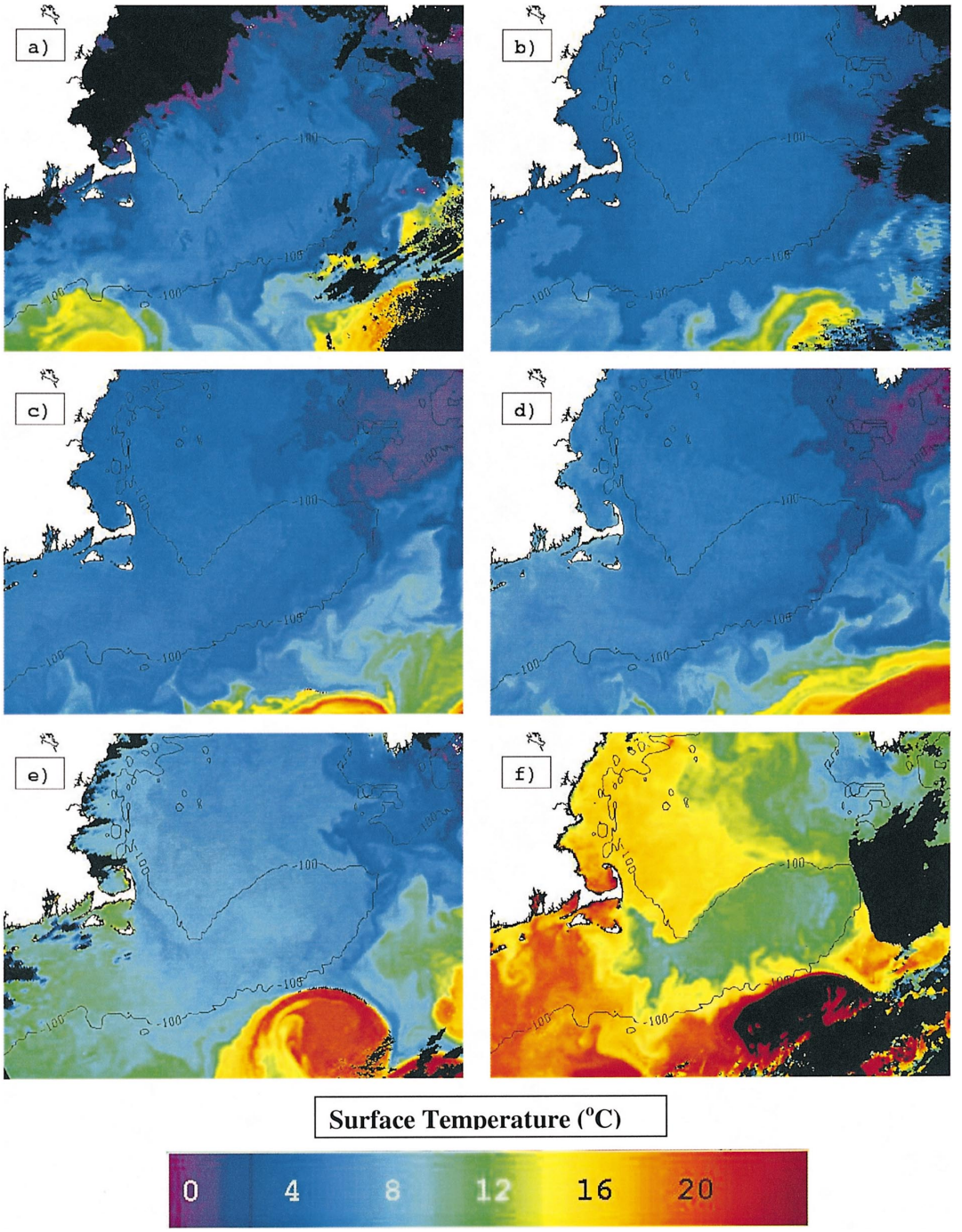

Fig. 8. Examples of NOAA AVHRR imagery coincident with each of the cruise periods (except January, 1997) showing large-scale patterns of sea-surface temperature. Images are from: (a) 18 February, (b) 24 March, (c) 16 April, (d) 27 April, (e) 14 May and (f) 27 June. A common color palette has been applied to each (bottom) and clouds and land masked to black. The 100 m bathymetric contour has been superimposed to show the position of Georges Bank.

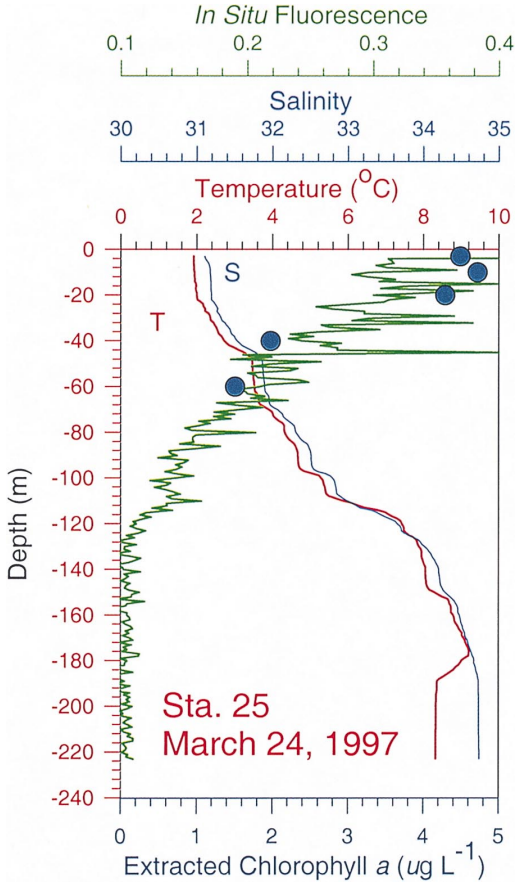

Fig. 9. Vertical profile of temperature, salinity, in situ chlorophyll fluorescence and extracted chlorophyll *a* at Station 25, which was within the Scotian Shelf Water mass in April.

edges. By June warm water associated with stratification over the deeper water in the Gulf of Maine contrasts sharply with colder water over George Bank. Temperature patterns over the Bank in June show that the coldest regions (9°C) were evident in the vicinity of the northeastern edge and the Great South Channel.

4. Discussion

Two interesting observations emerge from this data set: the first is the nature of the influx of a mass of Scotian Shelf Water onto Georges Bank, and its possible implications for the biological oceanography of the region; the second is the seasonal nature of phytoplankton biomass and apparent nutrient utilization and regeneration on the Bank. The Scotian Shelf Water mass observed on the Bank beginning in February and remaining distinct through April was carrying with it relatively high standing stocks of phytoplankton, as revealed by both in situ fluorescence

and extracted chlorophyll *a* concentrations. A profile of temperature, salinity and chlorophyll in this Scotian Shelf Water mass in April is given in Fig. 9, showing the deep penetration of cold and relatively fresh water to a depth of about 50 m, as well as the high levels of phytoplankton biomass accompanying these waters onto the Bank. Bisagni and Smith (1998) showed that the influence of Scotian Shelf Water on Georges Bank can be traced through its low-salinity signature and appears to be a recurring event with a 3–5 yr time scale, most prevalent in the February–March period. Chlorophyll *a* concentrations at the surface of the Scotian Shelf Water were on the order of 4–5 $\mu g\,l^{-1}$ in March, and declined only gradually with increasing depth, suggesting, along with the temperature and salinity profiles, that this surface water mass was as thick as 100 m. Interestingly, there was an abundance of fish eggs of the family Gadidae observed in March in this same water mass (J. Sibunka, unpublished), which suggested that not only were phytoplankton and nutrients (particulate and dissolved) being advected to Georges Bank from Canadian waters to the east, but early developmental stages of fishes were being advected as well. The overall impact of the import of Scotian Shelf Water to the Georges Bank area is a subject in need of further attention.

Data presented here for the winter–spring transition period (January to June) demonstrate that the phytoplankton bloom begins as early as February over the central shallow (< 60 m) regions of Georges Bank. This is reflected in both the chlorophyll and nutrient fields. Such late winter, early spring phytoplankton blooms are well described, particularly for shallow areas like Georges Bank, where bathymetry determines the base of the upper mixed layer (Townsend et al., 1994). In such environments, the spring bloom typically begins once the critical depth becomes shallower than the water depth, which apparently can occur even during winter under conditions of reduced cloud cover (Riley, 1941). Although we did not examine water samples microscopically, the early depletion of dissolved silicate suggests that the winter–spring bloom on Georges Bank is primarily made up of diatoms. In fact, silicate likely limited bloom production as early as February when surface concentrations approached typical values reported in the literature for diatom half-saturation constants (2–4 μM; Paasch, 1973). This is illustrated in Fig. 10, where we can plainly see a greater depletion of silicate at most stations on the top of the Bank. Only after silicate became depleted did we observe dissolved inorganic nitrogen reduced to levels that would limit phytoplankton production. We might expect, therefore, a shift in species composition of the phytoplankton stock on the Bank from diatoms to flagellates beginning in the February to March time period. By April, the Bank was depleted in both silicate and nitrogen, and phytoplankton concentrations were low.

While silicate may have been the limiting nutrient for the earliest portion of the winter–spring phytoplankton bloom, and hence became depleted early in the year, localized patches of increased silicate concentrations in the surface waters were observed again in May at some stations (Fig. 6). This reappearance of silicate in May would at first seem to indicate an upwelling of deep-water nutrients into surface waters and subsequently onto the Bank. This process potentially could renew silicate and other nutrients to concentration levels seen in winter. However, we observed no concomitant signatures in nitrogen or in temperature and salinity as would be expected as a result of upwelling. Stations that exhibited elevated surface (and subsurface) silicate concentrations in May most often had nitrate + nitrite concentrations less than 1 μM (see Figs. 5 and 6). Rather than being a result of upwelling, we suggest that the patches of elevated silicate in May could have been produced by dissolution of diatom frustules that remained following the winter–spring bloom. It would follow that the dissolution of this particulate silica was most likely triggered by the warmer

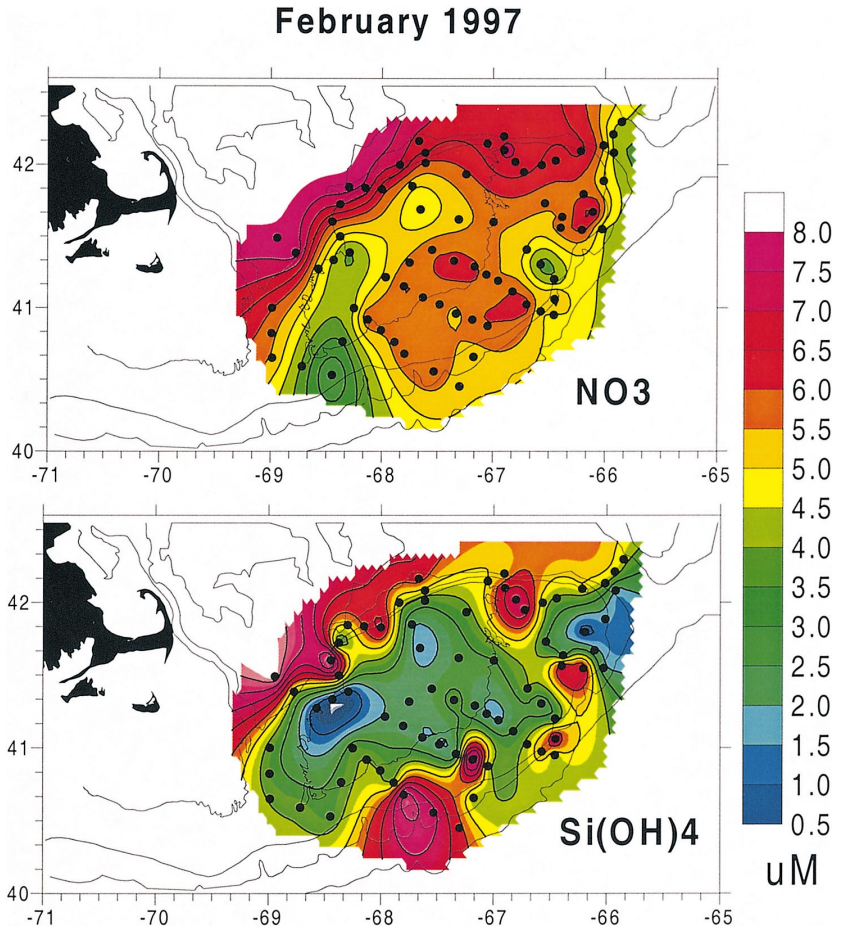

Fig. 10. Comparison of areal contour plots of surface nitrate + nitrite (μM) and silicate (μM) in February 1997.

water temperatures that became most pronounced in May. Interestingly, we saw this apparent recycling of silicate both at the shallower stations on top of Georges Bank as well as at some stations off the Bank in the deeper waters beyond the 200 m isobath in the Gulf of Maine and off the southern flank (Stations 29 and 16; Fig. 11). Surface silicate concentrations at these deep water stations were, like the shallower stations on the Bank, much higher than nitrate + nitrite. We would have expected a recycling of silicate in the shallower waters on the Bank itself where much of the primary production from diatom blooms likely sinks either as fecal pellets or as flocs and aggregates of diatom cells and/or diatom frustules. This would effectively strip the water column of dissolved silicate, and deposit it on the bottom in particulate form until such time as it is redissolved and recycled back to the water column as a result of tidal mixing. In the case of Station 16 south of the Bank (Fig. 11), it appears that we sampled Georges Bank water that had moved off the Bank via entrainment in a warm core eddy of the Gulf Stream. Both the eddy and the entrainment of cold Georges Bank water can be seen in the satellite image in Fig. 8. Likewise, it is

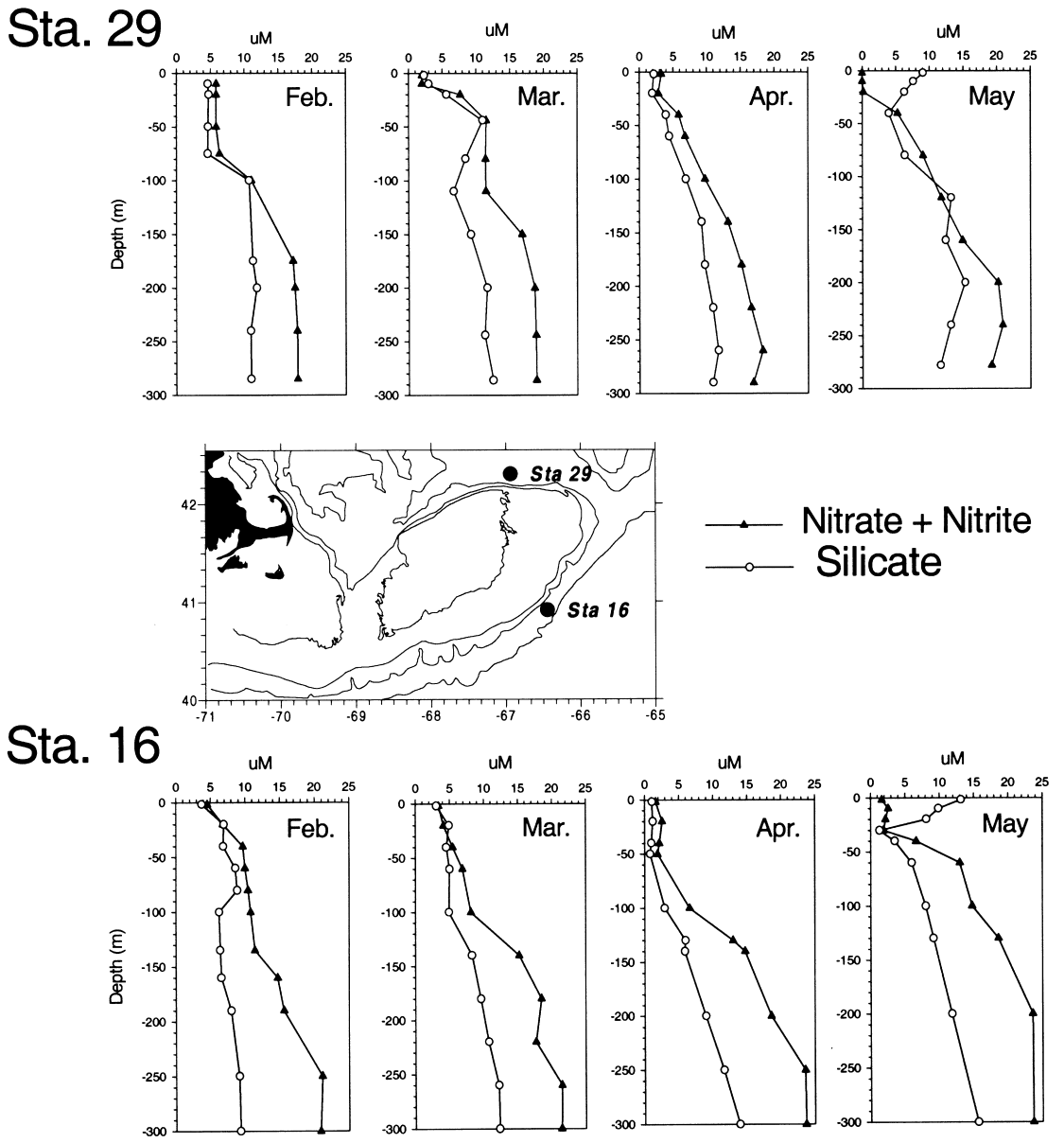

Fig. 11. Vertical profiles of nitrate + nitrite and silicate from February to March at Station 29, in the Georges Bains area of the Gulf of Maine, and Station 16, just beyond the 200 m isobath off the southern flank of Georges Bank.

possible that a similar phenomenon resulted in Georges Bank water being brought off the northern edge of the Bank in association with another mass of cold Scotian Shelf Water located nearby. That is, the high silicate in the surface waters beyond the Bank's edges reflects off-Bank fluxes of silicate-rich water.

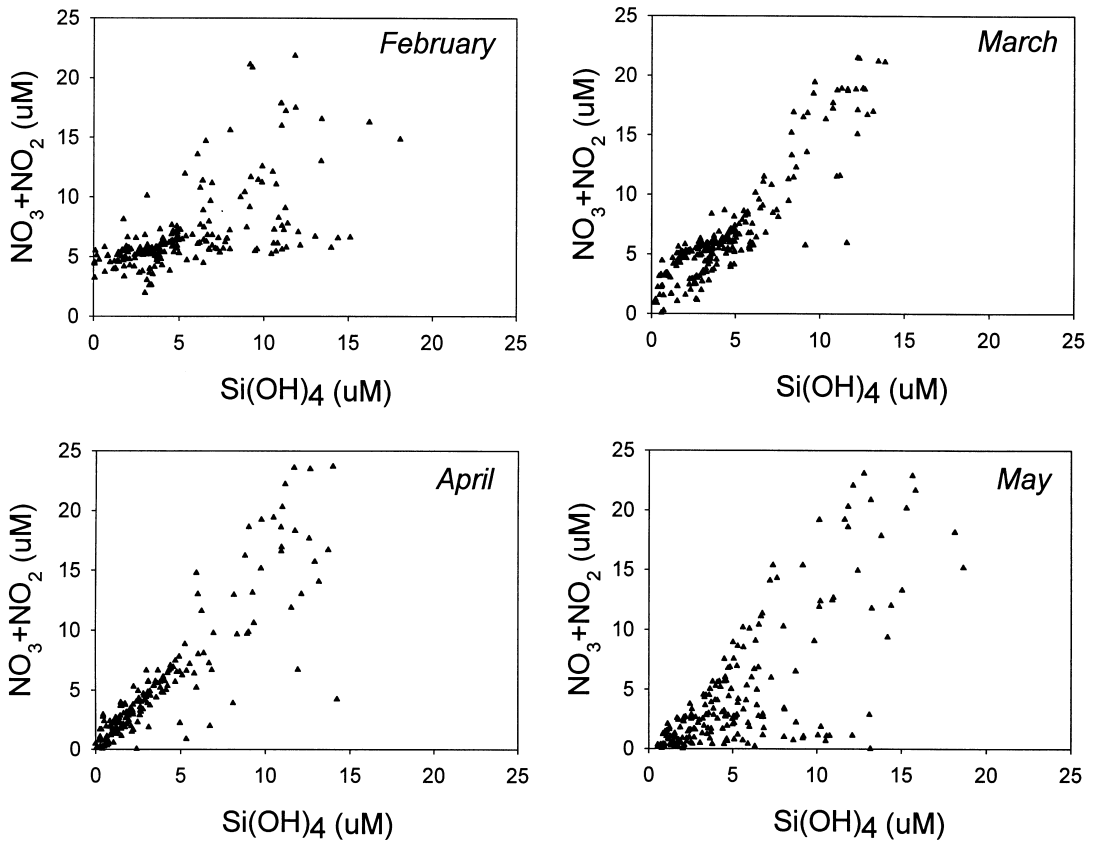

Fig. 12. Plots of nitrate + nitrite versus silicate for all depths sampled at all stations from February to May.

An examination of the ratios of nitrate + nitrite to silicate reveals the nature of the initial uptake of these two phytoplankton nutrients and their subsequent regeneration. These ratios, using all samples collected from all depths in the Georges Bank region from February to May, are shown in Fig. 12. The contour plots of surface nitrate + nitrite and silicate in February show silicate apparently more depleted than nitrogen (Fig. 10). We can see in Fig. 12 that this disparity may hold more so for the lower concentrations of both nutrients (e.g., corresponding to shallower and near surface waters) than for the higher nutrient concentrations normally sampled in deeper waters. In general, Fig. 12 shows that early in the winter–spring period there is more dissolved inorganic nitrogen present than silicate, especially at the lower concentrations ($<$ about 8 μM) we observed at the shallower stations on the top of the Bank. This difference between the two nutrients is not suggestive of a greater uptake of silicate than of nitrate, but rather reflects unequal winter concentrations prior to phytoplankton uptake. It is known that diatoms take up nitrogen and silicate in approximately equal proportions; the 4–5 μM nitrate + nitrite present when silicate is depleted (Fig. 10) would suggest that the initial nutrient concentrations immediately after winter mixing have more nitrogenous nutrients present than silicate. If the source of new nutrients to Georges Bank is the deep waters around the periphery, then it would be expected that those deeper

waters have unequal proportions of nitrate + nitrite and silicate. Indeed this is the case, as shown in Fig. 11. For each month (February to May), the deep-water nutrient concentrations at Stations 16 and 19 (selected to be representative of deep waters beyond the edges of the bank) are enriched with inorganic nitrogen relative to silicate. This also would imply that silicate limits phytoplankton production, not only on Georges bank, but throughout the region.

In summary, we observed that the winter–spring phytoplankton bloom in the Georges Bank region begins as early as February, and is initially silicate-limited. The bloom was augmented by an input of colder and fresher Scotian Shelf Water to the Bank in 1997, which brought with it an already-developed phytoplankton bloom. Later in the spring we saw nitrate + nitrite become limiting, which most likely reflected post-bloom production by flagellates. By May we began to see an increase in dissolved silicate concentrations that were probably the result of a temperature-dependent dissolution of diatom frustules produced during the earlier diatom bloom.

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