Nitrogen limitation of secondary production on Georges Bank

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Abstract. Springtime distributions of phytoplankton chlorophyll *a* and nitrate + nitrite on Georges Bank were analyzed for three survey cruises: 17–26 May 1993, 7–15 April 1994 and 12–20 May 1994. Results showed that nutrients become depleted over much of the Bank inside the 60 m isobath as a result of the spring phytoplankton bloom, after which relatively high nutrient concentrations were confined to the frontal regions around the periphery of the Bank. Highest nutrient concentrations and horizontal gradients occurred along the northern edge and the Northeast Peak, where cross-frontal, on-bank fluxes of new nitrogen onto the Bank were most pronounced. These data, and earlier observations by others that show (i) high rates of primary production on the central Bank despite low nutrients, (ii) low f-ratios on the central Bank, (iii) anomalously low secondary production as compared with rates of primary production and (iv) average distributions of zooplankton and gadid spawning areas on the Bank, are interpreted in the context of nitrogen limitation of secondary production. Calculations of cross-bank nutrient fluxes suggest that Georges Bank is too large a geographical feature to function efficiently on nutrients delivered via fluxes from deeper waters around its periphery and therefore much of the primary production is recycled. Thus, it follows that production of higher trophic level biomass, from zooplankton to fish, is limited by the frequency and intensity of processes that drive fluxes of deep-water nitrogen onto the Bank.

Introduction

Georges Bank is a shallow submarine bank on the east coast of North America, situated between Cape Cod, Massachusetts and Nova Scotia (Figure 1). It is among the most physically energetic and biologically productive areas of the world ocean, and has for more than two centuries supported an important commercial fishery (Backus, 1987). The Bank is a relatively large geographical feature, encompassing 34 000 km^2 of waters shallower than 100 m, and 14 000 km^2 shallower than 60 m.

A principal physical oceanographic feature of Georges Bank is the vigorous mixing of its relatively shallow waters by tidal currents. After deep convective mixing during winter, the upper water column of the Gulf of Maine and surrounding waters stratify each spring in response to inflows of relatively fresh water and an increase in solar insolation. In contrast, the central waters over the shallow Bank, especially inside the 60 m isobath, remain vertically homogeneous under the influence of tidal mixing.

The intensity of vertical mixing due to tidal currents varies inversely with water depth. The steep topography along the edges of the Bank thus gives rise to strong lateral gradients in the density and pressure distributions and associated anticyclonic geostrophic currents (see Townsend and Pettigrew, 1996). In addition to producing density-driven currents, the developing density stratification has the second, indirect effect of augmenting the Georges Bank gyre through a reduction of bottom friction. This frictional reduction affects both the density-driven component and the tidally rectified component (Loder, 1980) which is generally accepted to be the principal cause of the mean annual anticyclonic circulation
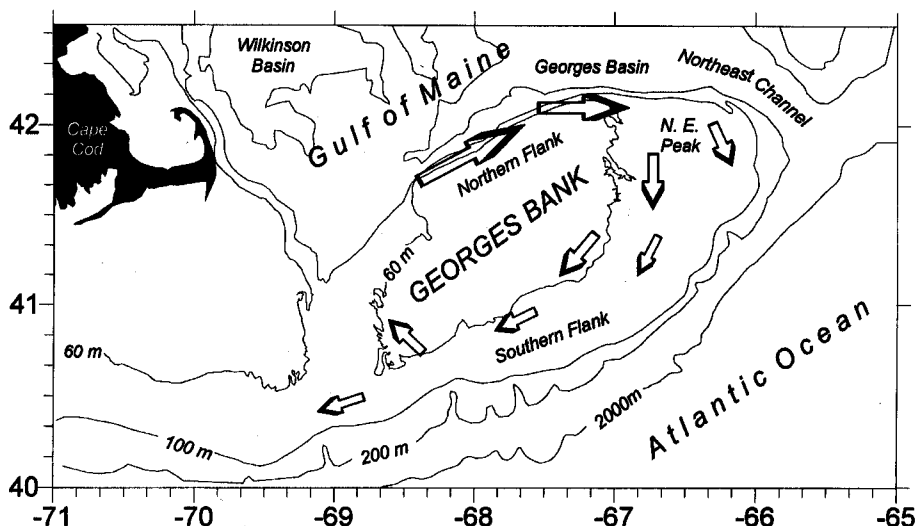
Fig. 1. Map of the Georges Bank region, showing major basins north of the Bank in the Gulf of Maine, and the Northeast Channel, through which new nitrogen (NO_3) in deep waters enters the Gulf from the Atlantic Ocean. Degrees north latitude and west longitude are given on the axes. Cape Cod, Massachusetts, and the 60, 100, 200 and 2000 m isobaths are indicated. Residual currents are represented schematically by arrows, with approximate relative velocity indicated by size.

around Georges Bank (Figure 1). As shown by the model of Loder and Wright (1985), the reduction of friction is especially effective at increasing the tidally rectified currents on the Northern Flank of the Bank.

Based on analysis of satellite imagery, Yentsch and Garfield (1981) concluded that the location of the front generally corresponds with the 60 m isobath. Hydrographic data in the present study support this finding. Once the front has been established, it becomes an important constraint upon the exchange of properties (including nutrients) between the mixed top of the Bank and its stratified surroundings. Thus, the processes of across-frontal transport of scalar properties become of central importance to any discussion of the ecology of the mixed region on top of Georges Bank as well as other analogous submarine features located throughout the world's oceans. While Yentsch and Garfield (1981) reasoned that the high rates of primary production were the result of the vigorous tidal mixing and accompanying cross-frontal fluxes of new nutrients to Georges Bank, we will argue that the exchange across the 60 m isobath is in fact limited. The result of this situation is that primary production on the central portion of the Bank is based on regenerated nutrients, and that secondary production is nitrogen limited.

Primary production and nutrients

Phytoplankton primary production on Georges Bank is among the highest of any region in the world's oceans, with annual production exceeding 450 g C m^{-2} year^{-1}

in the central portion (O'Reilly *et al.*, 1987). The Bank typically exhibits a pronounced late winter–early spring phytoplankton bloom (Riley, 1941) which, based on limited nutrient data presented in Walsh *et al.* (1987), appears to deplete available dissolved inorganic nitrogen over the top of the Bank (inside the 60 m isobath) from winter values of ~7 μM NO_3 to nearly undetectable levels by early May. Primary production remains high throughout the summer and fall, with daily production rates of 1–2 g C m^{-2} day^{-1} in summer (O'Reilly *et al.*, 1987). With nitrate depleted throughout the late spring and continuing through early fall, the nutrient requirement for primary production must be supplied by some combination of on-bank fluxes of 'new' nitrate (*sensu* Dugdale and Goering, 1967; Eppley and Peterson, 1979) along the edges of the Bank, and nitrogen that is recycled 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). As discussed above, cross-isobath mixing and/or nutrient injections onto Georges Bank appear to be most important along the Northern Flank, where the nutrient concentrations and gradients are most pronounced (Pastuszak *et al.*, 1982). Whatever the dominant cross-frontal mechanism is, the nutrient flux will be roughly proportional to the nutrient gradient and one would expect a relatively greater flux of nutrients to the northern edge.

Pastuszak *et al.* (1982) reported data collected on nine survey cruises between July of 1975 and August of 1976; station spacing was variable among cruises, and data were grouped for analysis by date and depth interval, and position on the Bank. In general, they found that nutrient levels in summer fell to near zero over much of the Bank, and that significant nutrient concentrations during the warmer months of the year were found only along the Bank's edges, especially the northern edge and Northeast Peak.

Despite the very high rates of primary production, the ratio of secondary production of zooplankton and benthos to primary production by phytoplankton on Georges Bank is lower than would normally be expected when it is compared with other marine areas (Cohen and Grosslein, 1987; Sherman *et al.*, 1987). Reasons proposed by earlier workers to explain this discrepancy between primary and secondary production have dealt primarily with advective losses of zooplankton from the Bank (Cohen and Grosslein, 1987; Mountain and Schlitz, 1987). We discuss that discrepancy here, based on new survey cruise results on springtime nutrient and chlorophyll distributions over most of the Bank, as well as other lines of evidence from the literature, and suggest that the relatively low secondary production on the Bank is more likely the result of nitrogen limitation.

Method

Hydrographic data presented here were collected during three research cruises on Georges Bank aboard the R/V 'Columbus Iselin': 17–26 May 1993, and 7–15 April and 12–20 May 1994. Standard CTD (conductivity, temperature, depth recorder) casts were made at each station shown in Figure 2 using a Neil Brown MKIII CTD and rosette sampler with SeaTech *in situ* fluorometer. Water samples were collected for fluorometric determination of chlorophyll *a* by filtering 100 ml onto a

GF/F filter and extracting in 90% acetone for at least 12 h at $-18°C$ in the dark (Parsons *et al.*, 1984). Those data were used to calibrate the *in situ* fluorometer. Nitrate + nitrite concentrations were measured at sea using a semi-automated analyzer and standard methods (Parsons *et al.*, 1984) on water samples that had been previously frozen. Portions of the hydrographic data, including the temperature and salinity fields, have been published in Townsend and Pettigrew (1996).

Results

Areal distributions of surface chlorophyll *a* and nitrate + nitrite for each cruise are given in Figures 2 and 3. Those distributions demonstrate that high winter concentrations of nutrients on the top of Georges Bank (inside the 60 m isobath) are depleted by the early spring phytoplankton bloom, which appears to begin in March–April and thus does not depend upon vertical stratification and water column stability (*sensu* Townsend *et al.*, 1994). The water column in April of 1994 was vertically well mixed inside the 60 m isobath, and there was only a slight indication of vernal warming of surface waters around the Bank's edges. Some of the increased vertical stability beyond the edges resulted from intrusions of warmer or fresher surface water masses (Townsend and Pettigrew, 1996). Surface nitrate + nitrite concentrations in April 1994 were <1.0 μM at the central Bank stations (Figure 3), while concentrations between 60 and 100 m isobaths were much higher. Surface phytoplankton chlorophyll *a* concentrations at the central Bank stations were still >5.0 $\mu g\,l^{-1}$, which suggests that we had arrived for our April survey while the spring bloom was still under way over the central Bank region (Figure 2). Following the spring bloom, in late April–May, the highest phytoplankton chlorophyll concentrations were seen between the 60 and 100 m isobaths in the frontal features along the periphery of the Bank (Figure 2). In May of 1993, those phytoplankton populations were most concentrated on the Northeast Peak (Figure 2) and appear to have been supported by cross-frontal fluxes of new nutrients that upwell onto the Northern Flank and Northeast Peak, and then flow around the Bank toward the Southern Flank with the residual circulation. Although patches of relatively high chlorophyll concentrations are also found on the Southern Flank and on the top of the Bank in May of 1994, they are much lower than in May 1993; chlorophyll *a* in May 1994 was 1–3 $\mu g\,l^{-1}$ over most of the Bank, and >3 $\mu g\,l^{-1}$ only at two stations. On the other hand, nitrate + nitrite levels were higher in May 1994 than the previous year, especially on the northern edge and Northeast Peak where concentrations ranged from 3 to 6 μM versus only 0.5–2.0 μM in May 1993 (Figures 2 and 3).

Concentrations of nutrients were greater on the northern edge and Northeast Peak, in May of both 1993 and 1994, than the southern parts of the Bank (Figures 2–5). It is presumed that the cross-bank fluxes are also greater in these areas, as is consistent with the higher nutrient gradient. Cross-bank sections of nitrate + nitrite and chlorophyll concentrations on the Southern Flank in May 1993 (Figure 5) suggest that off-bank sources of new nitrogen (NO_3) there are quickly utilized by phytoplankton as those waters are entrained and upwelled onto the relatively broad and shallow southern flanks of the Bank, and those fluxes do not reach the
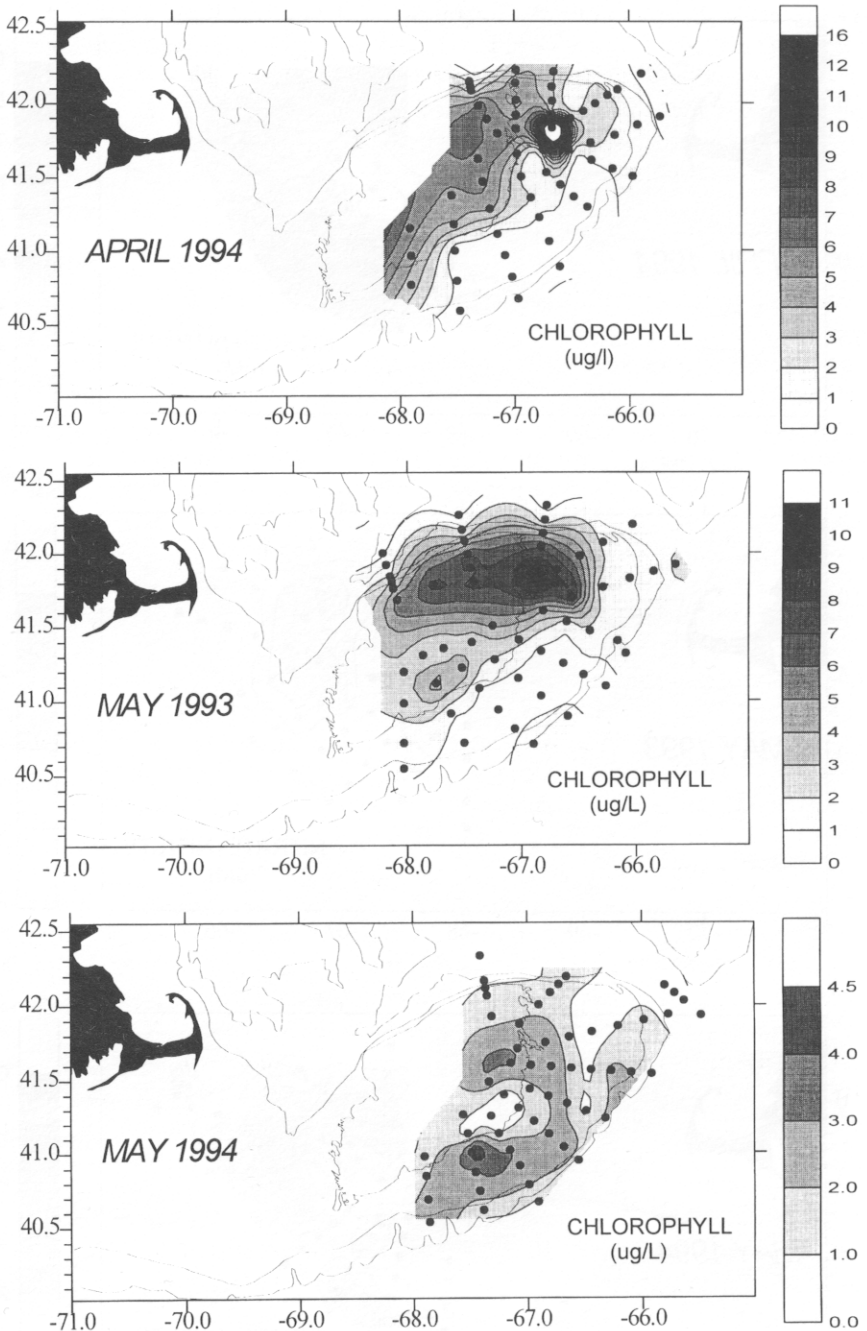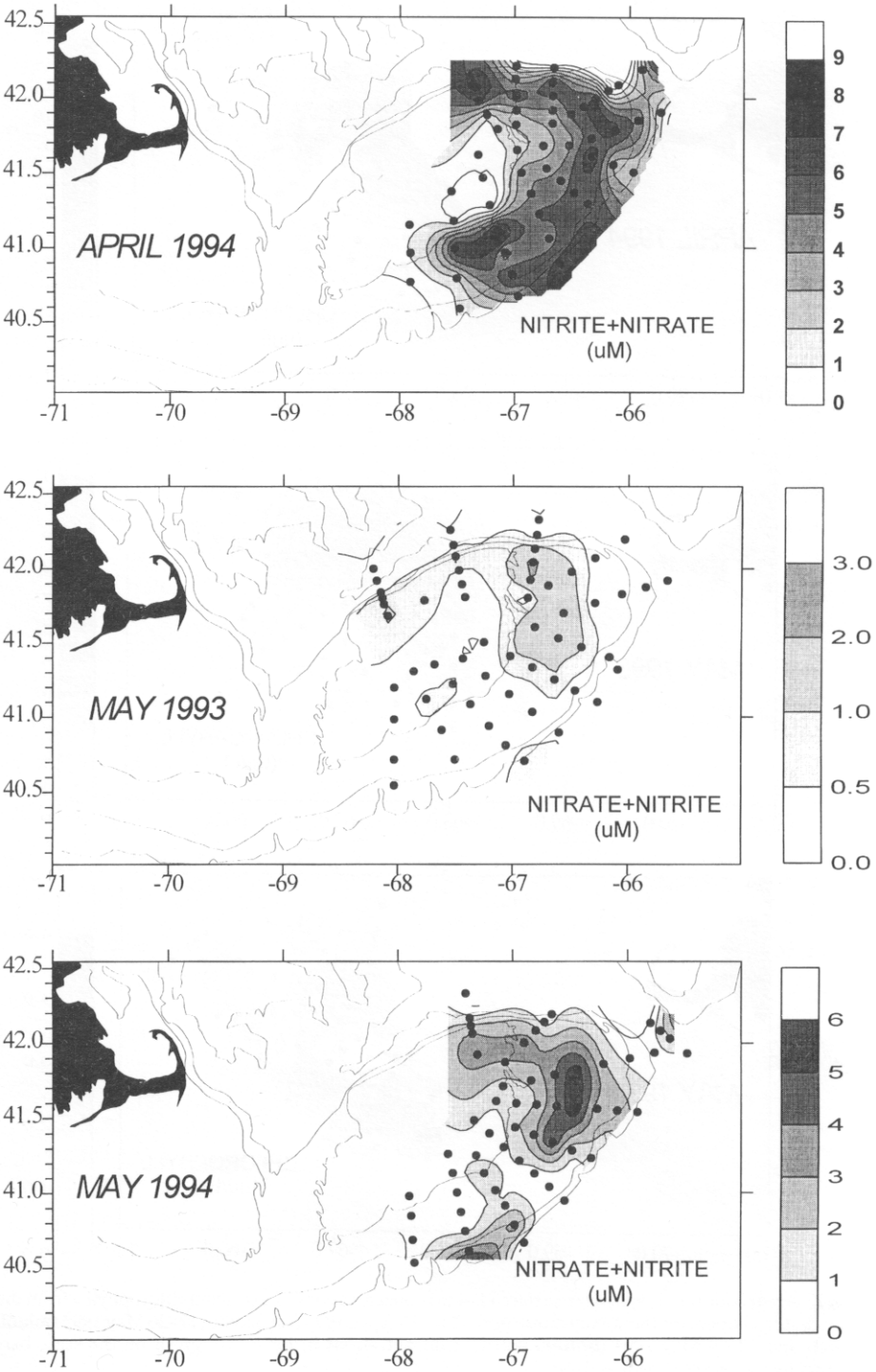
Fig. 2. Areal contour plots of near-surface (1–4 m) concentrations of extracted chlorophyll *a* from discrete water samples, for the survey cruise periods: 7–15 April 1994 (**top panel**), 17–26 May 1993 (**middle panel**) and 12–20 May 1994 (**bottom panel**). Concentrations in µg l⁻¹ are given on the scale bars. Station locations are shown as dots.

central portions of the Bank. Chlorophyll levels were between 2 and 6 μg l^{-1} on the Bank on the Southern Flank (Figure 5). On the northern edge, however, where the Bank edge is narrower and depth changes more abruptly than on the Southern Flank, the nitrogen gradients appear more intense, providing $NO_3 + NO_2$ concentrations between 2 and 3 μM on the northern edge. The resultant on-bank chlorophyll a concentrations were between 6 and 10 μg l^{-1} (Figure 4).

Discussion

Our survey cruise results suggest that nitrogen limits phytoplankton production shortly after the spring bloom, and that new production is confined mostly to the Northern Flank frontal region, as well as at some point downstream of nutrient injections, i.e. in the area of the Northeast Peak. This pattern, in general, agrees with earlier field observations of phytoplankton distributions (Cura, 1987). Cura (1987) showed that the northern edge and Northeast Peak were dominated by diatoms, which have affinities for new nitrate, through the summer, whereas the remainder of the Bank was composed mainly of dinoflagellates, which grow well in low-nitrate conditions and in the presence of recycled ammonium. The enriched diatom flora on these northern parts of the Bank produces a 10-fold higher total cell abundance during late spring to summer than on other parts of the Bank (Sears, 1941).

Nitrogen limitation of primary production

Nutrient limitation of phytoplankton productivity is well known, both for freshwaters, where phosphorus is the limiting nutrient, and for marine waters, where nitrogen is limiting (Hecky and Kilham, 1988; Doering et $al.$, 1995). In marine systems, there are two principal forms of inorganic nitrogen used by phytoplankton: nitrate (NO_3), which is also known as 'new nitrogen' because it is supplied to the euphotic zone from external sources, usually from deep waters, and ammonium (NH_4), which is a form of recycled nitrogen regenerated by heterotrophic activity and microbial decomposition of organic matter (Dugdale and Goering, 1967). The ratio of 'new' primary production, which utilizes the NO_3 form of nitrogen, to recycled primary production, which utilizes recycled nitrogen (NH_4), is termed the f-ratio (Eppley and Peterson, 1979) and represents the percentage of primary production that is fueled by new nitrogen (NO_3) fluxes. It must be pointed out that new nitrogen is not necessary to support high rates of primary production (carbon fixation) and, in theory, phytoplankton primary production could run forever on recycled nitrogen alone, provided that no nitrogen was exported, or passed upward to other trophic levels in the food chain (Dugdale and Goering, 1967). However, in nature, the f-ratios in nutrient-poor, oligotrophic regions of the world ocean are on the order of 0.05–0.2, meaning that nitrogen atoms are recycled as many as 19 times before being lost via export from the

Fig. 3. Areal contour plots of near-surface (1–4 m) concentrations of $NO_2 + NO_3$ for the survey cruise periods: 7–15 April 1994 (**top panel**), 17–26 May 1993 (**middle panel**) and 12–20 May 1994 (**bottom panel**). Concentrations in μmol l^{-1} (μM) are given on the scale bars. Station locations are shown as dots.
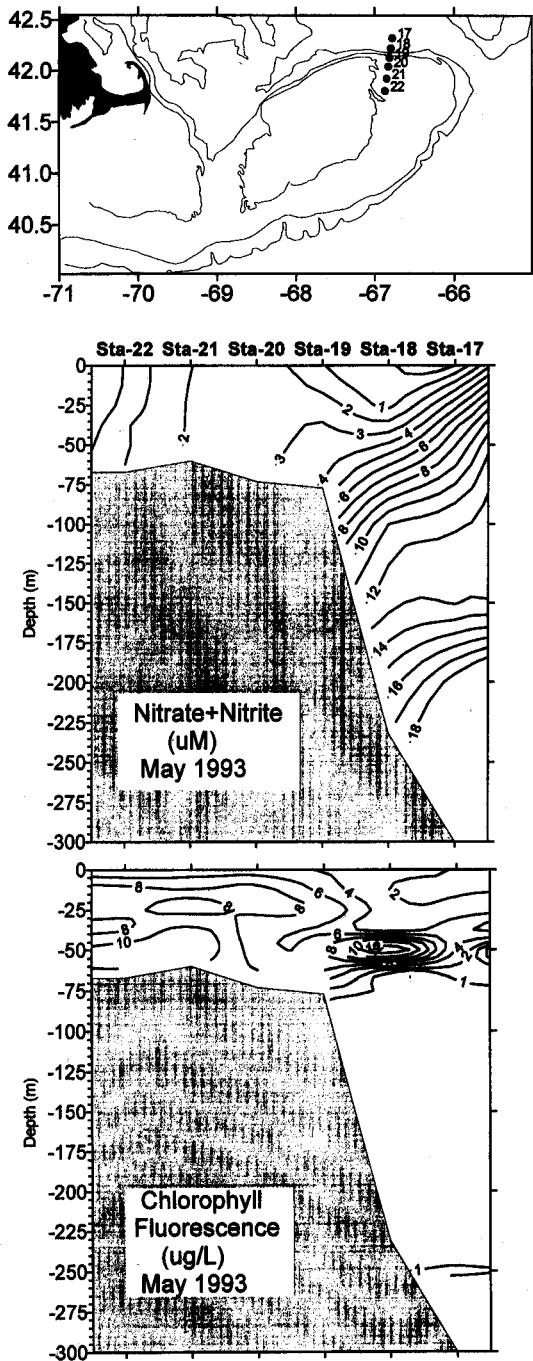
Fig. 4. Vertical section contour plots of $NO_2 + NO_3$ concentrations in μmol l^{-1} (μM) and continuous phytoplankton chlorophyll *a* concentrations, determined from *in situ* fluorescence calibrated against extracted chlorophyll *a*, along the transect of stations no. 17–22, shown in the top panel, in May 1993.
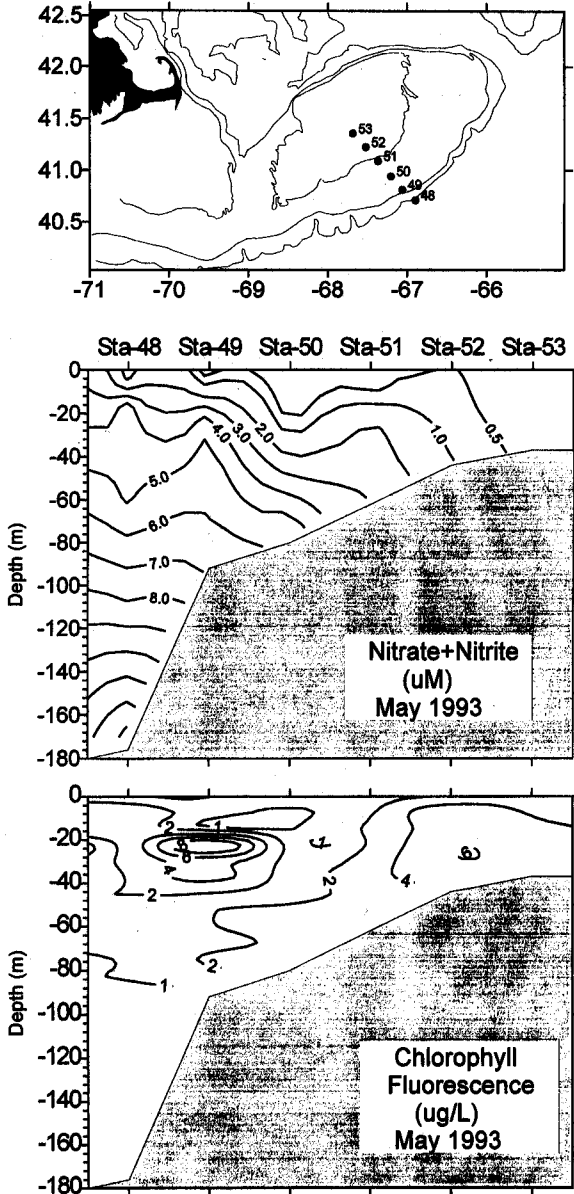
Fig. 5. As Figure 4, except for the transect of stations no. 48–53.

system, while the f-ratio in nutrient-rich, eutrophic waters is on the order of 0.5–0.8 (Eppley and Peterson, 1979).

The high concentrations of phytoplankton chlorophyll we observed on the northern part of Georges Bank are likely 'new' production, reflecting the more intense nitrate fluxes there, but on the southern and central parts of the Bank, however, the

production is more likely dependent on recycled nitrogen. The flux mechanisms are likely a combination of cross-frontal circulation (Loder and Wright, 1985) and lateral mixing (Garrett, 1983). Significant nitrate + nitrite fluxes do not reach the top of the Bank, and phytoplankton levels, while not as high as on the northern part, are still relatively high, and are likely the result of recycled primary production. Evidence in support of this interpretation of the data in Figures 2–5 is given by Harrison et al. (1990) and Loder et al. (1992) who used ^{15}N tracer techniques to measure f-ratios along a transect that ran from deep waters just north of Georges Bank to the tidally well-mixed waters on the Northeast Peak. They found that the f-ratio varies with location on Georges Bank, being as high as 0.7 in regions where nitrate is mixed upward and onto the Bank (e.g. the tidal front area around the edges of the Bank, and in a second area of turbulence just off the Bank's edges, which results from internal wave passages). Inside the frontal areas, and in the central well-mixed regions on top of the Bank, the f-ratios were on the order of 0.1–0.2. Thus, nitrate fluxes would appear to support the nitrogen requirements of ~70% of primary production along the Bank's edges, while recycled ammonium supports 80–90% of primary production on the Bank itself. Despite the high measured rates of primary production on the Bank itself (O'Reilly et al., 1987), the particulate nitrogen so formed is effectively unavailable to consumers. Consumers can meet their maintenance metabolism needs by consuming the fixed organic carbon so produced, but secondary production of new nitrogen-containing biomass will be nitrogen limited.

Estimates of on-bank fluxes of nitrogen help to illustrate our point. Loder and Platt (1985) computed a nitrogen demand on Georges Bank based on measured rates of primary production of 1–2 g C m^{-2} day^{-1} (O'Reilly and Busch, 1984) over the central well-mixed region of Georges Bank during the summer season. They assumed a Redfield ratio of carbon to nitrogen in their calculations and computed a corresponding nitrogen demand over the ~1.4×10^4 km^2 area of the Bank inside the 60 m isobath (Hopkins and Garfield, 1981) to be roughly $2–4 \times 10^6$ mg at N s^{-1}. Of this nitrogen demand, the proportion supplied by lateral mixing of new nitrogen from the stratified side of the tidal-mixing front can be explored using a simple diffusive conceptual model.

Loder et al. (1982) used a model of the temperature evolution over central Georges Bank to estimate a horizontal dispersion coefficient of 250 m^2 s^{-1}, with upper and lower bounds estimated to be 150 and 380 m^2 s^{-1}. These findings are consistent with earlier estimates (100–400 m^2 s^{-1}) based on drifter dispersion on Georges Bank (EG&G, 1979) and the slightly lower range of values (30–160 m^2 s^{-1}) obtained by Smith (1989) for Brown's Bank, also based on drifter dispersion.

When tidal excursions are much smaller than the length scale of the Bank residual circulation, horizontal tidal dispersion associated with a tidal random walk process may be estimated by scale analysis as:

$$K_{\mathrm{H}} \approx \frac{U^2 u_0}{\omega^2 L}$$

where U is the tidal velocity scale, u_0 is the residual velocity scale, ω is the angular frequency of the dominant tide and L is a characteristic length scale of the residual

circulation (see Smith, 1989). Using scale values of $U \approx 1$ m s^{-1}, $u_0 \approx 0.3$ m s^{-1}, $\omega \approx 0.3 \times 10^{-4}$ s^{-1} (the M2 tide) and $L \approx 100$ km (the minor axis of the Bank gyre), one calculates $K_H \approx 150$ m^2 s^{-1}.

The consistency of the above estimates arising from these varied approaches and data sets suggests that the value of 250 m^2 s^{-1} is a reasonably conservative estimate for the effective lateral dispersion coefficient over the central vertically mixed region of the Bank. Using this estimate of the lateral dispersion coefficient (250 m^2 s^{-1}) and vertically integrating nitrate + nitrite gradients observed across the 60 m isobath during our May 1993 cruise, we estimate representative new nitrogen fluxes for four quadrants about the 60 m isobath to be 2.9, 0.3, 0.8 and 0.3 mg at N s^{-1} m^{-1}, respectively, for the north, east, south and west sections of the Bank. Assigning to each of these fluxes one-quarter of the perimeter of a circle of area 1.4×10^4 km^2, we arrive at a total flux of roughly 4.8×10^5 mg at N s^{-1} into the vertically mixed region inside the 60 m isobath. This represents 12–24% of the nitrogen demand estimated by Loder and Platt (1985) based on primary production rates of 1–2 g C m^{-2} day^{-1} as discussed above. These rough calculations are consistent with the f-ratios reported by Harrison *et al.* (1990) and strongly suggest that the rate of cross-frontal mixing causes primary production in the central region of Georges Bank to be dependent on recycled nitrogen (which would be on the order of 76–88% of total primary production).

The nitrate fluxes we calculate here are a factor of 5–10 lower than those estimated for Georges Bank by Horne *et al.* (1989), which were comprised of two principal components: mean cross-frontal advection and 'skew' eddy fluxes. The moored measurements upon which they based their estimates were under-resolved. The mean across-frontal current profiles used in calculations of nitrate advection do not conserve mass, but rather result in a convergence within the 60 m isobath. The same lack of resolution may affect the estimated eddy fluxes. In addition, the 'skew' eddy nitrate fluxes should be considered overestimates since a portion of this flux does not actually transfer scalar properties down the gradient (Horne *et al.*, 1989).

We suggest that the flux estimates provided in Horne *et al.* (1989) may be significantly too high, and that nitrate fluxes along the frontal perimeter of the central well-mixed region of Georges Bank may only be sufficient to support 12–24% of the total estimated primary production. In effect, the ratio of frontal surface area-to-volume enclosed of Georges Bank is too small to allow 'full' production potential given the observed frontal gradients.

Nitrogen limitation of secondary production

The production of herbivorous zooplankton depends on food quantity and quality. Animals require not only a source of energy (carbon), but other foodstuffs such as nutrients [nitrogen (N) and phosphorus (P)], vitamins and various micronutrients. Without these other foodstuffs, there can be no growth in biomass of animal populations; this general notion of nutrient limitation of secondary production in marine and freshwaters is not new, and has been discussed by others. Checkley (1985) showed that copepods in the oligotrophic waters off California were food limited as compared with populations in more eutrophic waters nearer

shore, and through laboratory enrichment experiments he suggested that copepod feeding and egg production rates were limited by nitrogen. Hessen (1992) reported that freshwater *Daphnia* had much higher particulate phosphorus-to-carbon ratios than other sestonic particles, and showed in a regional survey of lakes that zooplankton biomass was better correlated with particulate P than phytoplankton biomass. Rothhaupt (1995) demonstrated in laboratory experiments with rotifers fed N- and P-limited phytoplankton that each nutrient element could limit growth rates, but not necessarily ingestion rates. It is very likely that, given several lines of evidence discussed here, the production of higher trophic level biomass in Georges Bank is similarly limited by the availability and flux rates of new nutrients onto the Bank.

The levels of zooplankton production on Georges Bank have been shown to be anomalously low when compared with the high rates of planktonic primary production (Sherman *et al.*, 1987). Total zooplankton production (sum of microzooplankton and macrozooplankton) on Georges Bank has been estimated at 18% of phytoplankton production, while in waters of the adjacent Gulf of Maine it is 26% (Cohen and Grosslein, 1987). We suspect that at least part of the reason for this difference — nutrient limitation of secondary production — is revealed in the temporal and spatial patterns of annual zooplankton abundance in each area. The annual cycle of copepods on Georges Bank exhibits a mid-spring peak, which follows the spring phytoplankton bloom, and then it abruptly declines to low summertime levels; this is in sharp contrast to the Gulf of Maine, where the decline in summer is far more gradual (Sherman *et al.*, 1987). That is, zooplankton production on Georges Bank is anomalously low in summer, and may be limited by the low post-bloom nitrogen concentrations, and flux rates, over most of the Bank's area. Despite the high rates of photosynthetic carbon fixation (O'Reilly *et al.*, 1987), the low f-ratios mean that this is mostly recycled primary production. Although that particulate nitrogen (in the form of phytoplankton) is consumed, it quickly passes through the consumers (and decomposers) and cannot be incorporated into new biomass at the next trophic level for very long, lest the system run down completely for lack of nitrogen altogether.

The same principle is reflected in the spatial distribution of zooplankton on the Bank as well. Mean zooplankton abundance after the spring bloom is generally greatest on the Southern Flank of Georges Bank (Davis, 1984), which is in keeping with the hypothesis of nitrogen limitation on top of the Bank and greater nitrate fluxes on the Northern Flank. That is, the maximum zooplankton densities are normally found downstream of the area of maximal nitrate fluxes onto the Bank and downstream of an area of high 'new' phytoplankton production on the Northern Flank and Northeast Peak (Cura, 1987). Zooplankton on the Southern Flank, then, are less likely to be nitrogen limited, and are most likely a delivered product of new production upstream. This conceptual framework also fits with our understanding of fish spawning strategies on Georges Bank. Generally speaking, cod and haddock spawn on the northern and northeastern parts of the Bank, and the residual circulation then carries the developing larvae to the Southern Flank (Mountain and Schlitz, 1987; Townsend and Pettigrew, 1996) where zooplankton abundances are greatest, and secondary production is less nitrogen limited.

Georges Bank is inefficient with respect to the production of higher trophic level biomass, which given the Bank's reputation as an important fishing ground, would seem paradoxical. The reason it is inefficient is that the Bank is simply too large a geographical feature. Since the ratio of nitrogen flux to nitrogen demand in a cylindrical water column varies as $1/r$, where r is the radius of the vertically mixed region, one can reasonably conclude that the well-mixed region on the top of Georges Bank is too large for photosynthesis to be fueled by across-front fluxes of new nitrogen. Thus, the primary production in this region is largely supported by recycled nitrogen. On the other hand, given the observed across-frontal nitrate gradients and the reported levels of primary production (1–2 g C m^{-2} day^{-1}), one calculates that if such production were 'new' primary production it could be supported by nitrate fluxes into mixed regions of radius 8–16 km. A bank of this size in the Gulf of Maine would then be able to support higher secondary production per unit area, resulting from trophic transfer of the 1–2 g C m^{-2} day^{-1}, which is supported by lateral mixing alone.

For submarine banks such as Georges Bank, nutrients necessary for the production of new consumer biomass must be distributed throughout its area after first being brought onto the Bank via fluxes of nutrient-rich deep waters from beyond its edges. In the case of Georges Bank, much of that new nitrogen flux is instead utilized locally in the frontal features and especially on the northern edge and Northeast Peak, as nutrient-rich waters are advected around the Bank with the residual circulation. New higher trophic level production is limited to those frontal and upstream (northern) areas, and is impeded throughout most of the remainder of the Bank. Should this hypothesis prove correct, it carries with it implications for interpreting fisheries dynamics in this important fishing ground. Standing stocks of higher trophic level species, including marketed and non-marketed species, are ultimately controlled by the dynamics of cross-bank nitrate fluxes, which in turn may vary among years, and in the future as one consequence of global climate change.

Acknowledgements

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