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Water column dynamics of dissolved inorganic carbon (DIC), nitrogen and O_2 on Georges Bank during April, 1990

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Abstract—We measured dissolved inorganic carbon (DIC), combined inorganic nitrogen, O_2, chlorophyll *a* (Chl *a*), particulate carbon and nitrogen (PCN) along with selected additional parameters on Georges Bank during April. Summer conditions were developing in the region as reflected by elevated biological production at the margins of the Bank (Chl *a* and O_2 levels >16 mg m^{-3} and >109% saturated respectively) and nitrate depletion on mid-Bank. Oxygen supersaturations were maintained in the regions of low NO_3 concentration, suggesting that a rapid supply of NO_3 was occurring horizontally from deeper waters. The productive region was propagating into deeper waters as daylight increased but was not yet associated with the tidally mixed front on the western flank. Changes in DIC and O_2 suggested net community production (NCP) of 0.24–0.42 g C m^{-2} day^{-1} on the flank. A collaborative purposeful tracer experiment on mid-Bank permitted a time series of net biological activity to be made and changes in both DIC and O_2 indicated similarly large net respiration was occurring there (NCP = −1.4 g C m^{-2} day^{-1}). A budget of particulate carbon and nitrogen suggested the biological character of the mid-Bank seston changed from autotrophy to heterotrophy and most of the remaining suspended particulates were detrital. Thus, the prolonged residence time of shelf water on the Bank contributes to efficient respiration of much of the organic matter formed locally and diminishes the Bank's role as a source of organic matter for off-shelf or down-shelf export. Based on an analysis that accounted for mixing effects between different water masses on the Bank, the ratio of DIC to NO_3 consumption was significantly greater than the Redfield ratio of 6.6. Thus, in such eutrophic regions, estimates of NCP derived from new (nitrate) production may be low by as much as 40%.

INTRODUCTION

DESPITE its importance among the major nutrients for phytoplankton growth, measurements of dissolved inorganic carbon (DIC) have not been common in studies of surface water nutrient dynamics. However, available measurements indicate that the DIC system can be altered dramatically by biological production in eutrophic continental shelf areas and it is possible to record the net consumption of DIC during spring blooms with relatively imprecise techniques (COOPER, 1933). More extensive and modern measurements demonstrated that the net changes in DIC could be used to follow both the net production and respiration of organic matter during the linked physical–biological dynamics of bloom periods (CODISPOTI *et al.*, 1986). Using a more precise technique for the analysis of DIC in sea water (JOHNSON *et al.*, 1985), we report the results of DIC measurements made during April, 1990 (R. V. *Cape Hatteras*, Cruise 0390) on Georges Bank, a hydrographically complex and productive area on the outer continental shelf of the northeast U.S. Our goals were to test earlier conceptualizations of the spatial pattern

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of productivity and recycling that have been proposed for this region as well as to explicitly determine the relationship among DIC, oxygen and nitrogen, all of which have been assumed to provide analogous information on production–respiration processes.

Georges Bank is a shallow (<60m) region between the North Atlantic and the Gulf of Maine whose biological productivity has been studied for over 60 years (BIGELOW, 1926). The Bank is part of a larger three-dimensional circulation that results in the net movement of surface water from the Gulf of Maine across the area (HOPKINS and GARFIELD, 1981) and in the input of nutrient laden subsurface water from both the Gulf of Maine and the slope water from the south (LODER *et al.*, 1982). The pattern of nutrient utilization in surface waters is closely associated with the regional hydrography. The Bank crest is mixed vertically to the bottom throughout the year by a combination of tidal and wind energies (FLAGG, 1987). In spring and summer, a tidal front separates the mixed waters of the Bank from deeper, vertically stratified waters. On the southern flank, the tidal front is augmented by a shelf-break front, a consistent feature along the eastern North American coast (CSANADY and MAGNELL, 1987). Tidally mixed fronts typically are associated with elevated productivity because they allow deeper, nutrient rich water access to the surface throughout the summer (PINGREE *et al.*, 1978; BISHOP *et al.*, 1980). This also is true in the Georges Bank fronts, in which an effective upwelling rate of 10^{-1} cm s^{-1} due to tides (FALKOWSKI, 1983) maintains elevated chlorophyll levels throughout the summer (O'REILLY, *et al.*, 1987). Much of the production at the fronts is fueled by nitrate, and new production rates here are greater than in either the mid-Bank or deeper stratified waters (HORNE *et al.*, 1989). Thus, the fronts appear to intercept much of the nutrient flux from deeper waters before it reaches mid-Bank. However, in terms of total carbon productivity, the mid-Bank also remains highly productive throughout the summer, suggesting that much of the phytoplankton growth in this region is fueled by regenerated nutrients (WALSH *et al.*, 1987).

Direct DIC measurements provide an alternative means to quantify carbon flux from surface waters that is independent from both particle trap studies (e.g. MARTIN *et al.*, 1987) and incubation productivity measurements (EPPLEY and PETERSON, 1979). The DIC system represents a common ground on which to relate other, perhaps less direct estimates, of carbon export from surface waters. Theoretically, the cycling of surface water macronutrients like carbon and nitrogen are constrained by the observed oxidative stoichiometry of ocean thermocline waters as specified by REDFIELD *et al.* (1963). In ocean thermocline waters, the Redfield ratios have been shown to be remarkably consistent, although a revision to account for the oxidation of hydrogen has been made (TAKAHASHI *et al.*, 1985). This stoichiometry allows the net production of plankton systems to be modeled as a nutrient limited process and the new production paradigm of DUGDALE and GOERING (1967) has been widely used for this purpose [e.g. EPPLEY *et al.* (1983); JENKINS and GOLDMAN (1985); MINAS *et al.* (1986); CHAVEZ and BARBER (1987)]. The widespread use of thermocline nutrient ratios in biogeochemical analyses makes it critical that the dynamics of the surface water DIC system are verified quantitatively relative to the other important bio-active substances.

METHODS

Measurements of total dissolved inorganic carbon (DIC) were made by coulometric titration (JOHNSON *et al.*, 1985). Briefly, a precisely measured volume of seawater (20 ml) is introduced to a stripping chamber where it is acidified and purged with an inert carrier gas. Thus, any carbonates in the original sample are also converted to CO_2. The resulting CO_2 is absorbed in the cathode compartment of a coulometer cell containing ethanolamine. The hydroxyethylcarbamic acid formed shifts the pH of the cathode solution which is then titrated to the initial pH coulometrically. The coulombs required for this titration are thus stoichiometrically related to the amount of CO_2 initially absorbed by the cell. The coulometer used was a commercial instrument (UIC Inc., Joliet, IL) that was stable under field conditions. Based on triplicate measurements made during the cruise, the reported values have a precision of $\pm 2.7\ \mu M$ (1 standard deviation). The coulometer was calibrated at sea using an injection loop containing a known amount of pure CO_2. There was no detectable drift in the instrument response over the 12 day cruise. Subsequent laboratory calibration of the instrument with seawater on which DIC was measured manometrically by Dr C.D. Keeling of Scripps Institute of Oceanography, indicated that the Cape Hatteras 0390 values may be low by 0.1%. However, the data in this report have not been adjusted by this factor.

Oxygen was determined on-board by the modified Winkler method described by CARRIT and CARPENTER (1966) with the exception that 40 ml aliquots were titrated. KNAPP *et al.*, (1991) have shown that the aliquot method introduces no significant error as long as the thiosulfate standardization mimics the handling of seawater samples. The aliquot method offers the considerable advantage of eliminating the need for calibrated sample bottles and permits replicate analyses on a single sample. In order to increase analytical precision the end-point was detected amperometrically (CULBERSON and HUANG, 1987). Precision of the O_2 analysis under shipboard conditions was $0.3\ \mu M$. Analyses of NO_3 and NH_4 concentrations were done on-board by standard wet chemical methods (PARSONS *et al.*, 1984). Chl *a* was measured fluorometrically on acetone extracts (LORENZEN, 1966). Underway surface fluorescence was measured with a Turner Designs series 10 fluorometer equipped with a flow cell. Surface fluorescence was converted to chl *a* by regression against extracted pigment samples. The standard error of the regression was 1.9 mg Chl *a* m^{-3}. An ENDECO® oxygen sensor was used for the underway O_2 measurements. An isolation amplifier (Analog Devices AD284J) was used to isolate the O_2 sensor from the ship's ground. The profiling *in vivo* fluorometer was calibrated on shore, and we made additional comparisons with extracted Chl *a* samples at sea to ensure that the response had not changed during the cruise. Additionally, surface PAR, wind velocity and direction, temperature, salinity, and position were logged every 5 min and stored digitally on the ship-board data collection system of the R.V. *Cape Hatteras*.

Our biological sampling on the Bank was guided by a contemporaneous purposeful tracer experiment (WANNINKHOF *et al.*, in press). The tracer SF_6 was injected into the water column at the middle of the Bank at the beginning of our experiment (Fig. 1). The compound SF_6 is an inert gas but can be detected in minute quantities through electron capture detection after gas chromatography (WANNINKHOF *et al.*, 1985). Thus, we were able to follow the dispersion of the original water mass for the complete 10 day sampling period based on the on-board measurements of SF_6. The purposeful tracer work also will provide detailed information on gas exchange rates during our experiment (WANNINKHOF *et al.*, in press). Its importance to the present work was that it provided a rare opportunity to construct a biological and chemical time series in an off-shore environment.

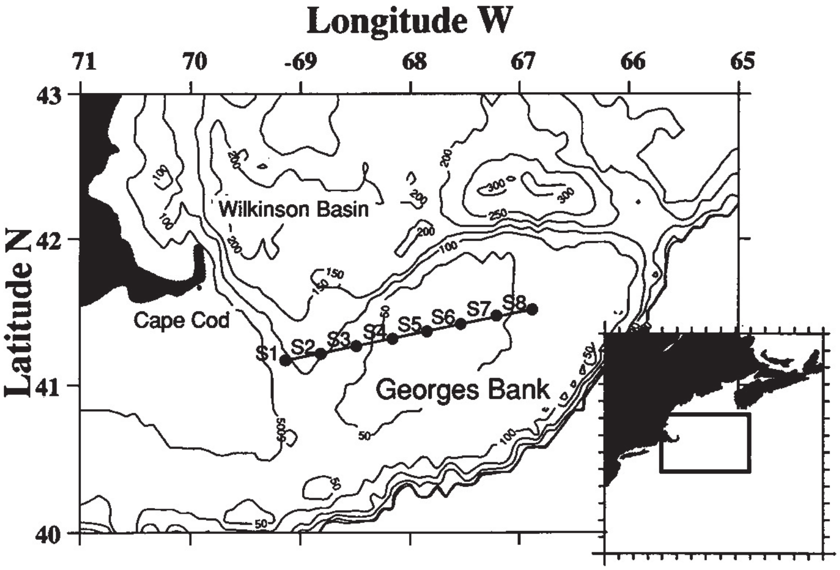

Fig. 1. Bathymetric map of study area (in m) showing the location of the stations on the main section. The time series (SF_6 patch) stations were sampled on mid-Bank in the vicinity of Sta. 5.

RESULTS

Cross-Bank sections

Hydrographic surveys were conducted across the Bank from Great South Channel to the northeastern flank on 6 and 16 April (Fig. 1). Eight stations at 15 km spacing were occupied on 6 April and on 16 April the six western most stations were resampled. In addition to standard bottle casts at each station, surface distributions of temperature, salinity, O_2 and chlorophyll fluorescence were mapped continuously. Surface water temperatures varied from 5.6°C on the Bank to 5.1°C at deeper stations on 6 April and were 0.5°C warmer when sampled 10 days later. This warming produced slight stratification of surface water in off-Bank regions that likely occurred in the few days prior to the 16 April section (winds were 10–20 m s^{-1} throughout most of the first week and diminished to less than 7 m s^{-1} during the few days prior to the 16 April section). However, more heating was needed to produce the conditions usually observed in summer, when the temperature of the vertically well mixed mid-Bank water is cooler than surrounding stratified regions (YENTSCH and GARFIELD, 1981).

Salinity varied from 32.91 to 33.46 ppt [Fig. 2(a)–(c)] and like temperature, was similar to previously reported Bank values at this time of year (HOPKINS and GARFIELD, 1981). The freshest water was found on the western side of the Bank, in water columns of 40–55 m depth. Possible origins of this low salinity water include Wilkerson Basin Water (WBW) and/or Scotian Shelf Water (SSW) and in either case this water probably was brought to the region by the anticyclonic circulation around the Bank (HOPKINS and GARFIELD, 1981). The underway salinity measurements on 6 April [Fig. 2(a)] suggest that the low salinity region was not as wide as the bottle data in Fig. 2(b) suggest, but was restricted to a narrow region between 40 and 60 km. This low salinity water was observed farther up the Bank in the later section [Fig. 2(c)] and may have been mixed horizontally over the 10 day period. Also, salinities in deeper parts of the Great South Channel decreased slightly between the two sections.

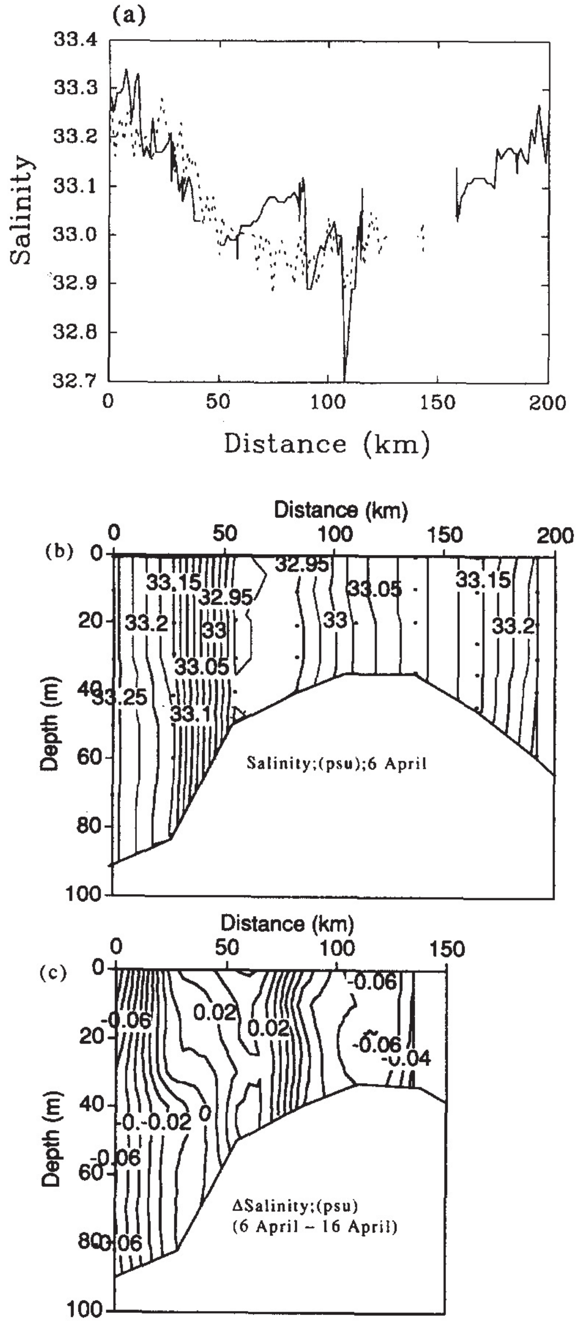

Fig. 2. (a) Surface salinity (psu) from underway measurements during the 6 April section (solid line) and 16 April section (broken line). Abscissa indicates distance from western-most station; (b) contour of the salinity values recorded at depth on 6 April (dots indicate data values used in contouring); (c) contour of the difference between the salinity measured on 16 April and 6 April (positive values indicate that salinity increased between the two sections).

Tidal fronts typically are associated with enhanced productivity throughout the summer PINGREE *et al.*, (1978) although in our April sampling, these conditions were not yet fully developed. Chlorophyll *a* levels were greatest at stations between the 40 and 50 m contours on either side of the Bank [Fig. 3(a) and (b)]. However, the stratified water on the seaward side of this elevated production had not yet formed. Chlorophyll *a* concentrations greater than $10\,\mu g\,l^{-1}$ were recorded on both sections in the western front, although mid-Bank Chl *a* decreased by more than 50% during the 10 day period [Fig. 3(c)]. Like Chl *a*, the greatest O_2 concentrations were consistently found within the 40–50 m isobaths on both sections and in both cases were well above saturation [Fig. 4(a)]. On 6 April mid-Bank waters were supersaturated with O_2 throughout the water column [Fig. 4(b)], but on 16 April mid-Bank waters were undersaturated with O_2 at depth [Fig. 4(c)].

DIC values varied from over $2120\,\mu M$ in deeper Great South Channel water to $100\,\mu M$ less on mid-Bank [Fig. 5(a)]. Although minimum concentrations of DIC were found on mid-Bank in both sections, a large increase (10–$30\,\mu M$) was observed in the DIC content of Bank waters between the two sections, particularly at depth [Fig. 5(b)]. In contrast, there was a significant decrease in surface DIC concentrations on the western flank of the Bank associated with the increased thermal stratification there [Fig. 5(b)]. The nitrate distribution was similar to that of DIC and minimum nitrate concentrations ($<1\,\mu M$) were found on mid-Bank [Fig. 6(a) and (b)]. Thus by our April sampling, new production on mid-Bank had consumed most of the 6–$8\,\mu M$ NO_3 that builds up on the Bank during winter (PASTUSZAK *et al.*, 1982). Continued new production on mid-Bank therefore, would be dependent on the horizontal supply of deeper surrounding waters to the Bank after this time. Relative changes in nitrate between the two sections also were similar to those observed in DIC in that nitrate increased slightly on mid-Bank and decreased on the western flank [Fig. 6(b)]. Consumption of both DIC and NO_3 was greatest between salinities of 32.95 and 33.10 ppt (Fig. 7). This salinity range corresponds to the elevated Chl *a* and mid-Bank regions [Fig. 2(b)].

Mid-Bank time series

We acquired a time series of chemical and biological changes on mid-Bank between 7 April and 16 April. Or sampling was based on underway measurements of SF_6 that had been injected into Bank waters during the 6 April section between Stas 5 and 6 to measure gas exchange rates (WANNINKHOF *et al.*, in press); (Fig. 1). This sampling area is referred to hereafter as the patch. The diameter of the SF_6 patch approximately doubled from its initial ~8 km length during the 10 day period following 6 April. The reliability of the purposeful tracer approach as a guide to our biological time series was reflected in the consistency of temperature and salinity measured in the patch (Fig. 8). Temperature increased linearly at a rate of $0.065°C\ day^{-1}$ ($r^2 = 0.92$). This rate is similar to the average seasonal heating rate derived from historical data and can be attributed mainly to local heating (HOPKINS and GARFIELD, 1981). In contrast to temperature, patch salinity exhibited no significant net change from an average value of 33.02 ($r^2 = 0.07$). The observed fluctuations in salinity can be reasonably accounted for by precipitation in that the salinity decrease observed between 11 and 13 April corresponded to an input of 4 cm of rain.

Collectively, the time series measurements suggested that there was continued net production of organic matter during the first few days, followed by net respiration after 11

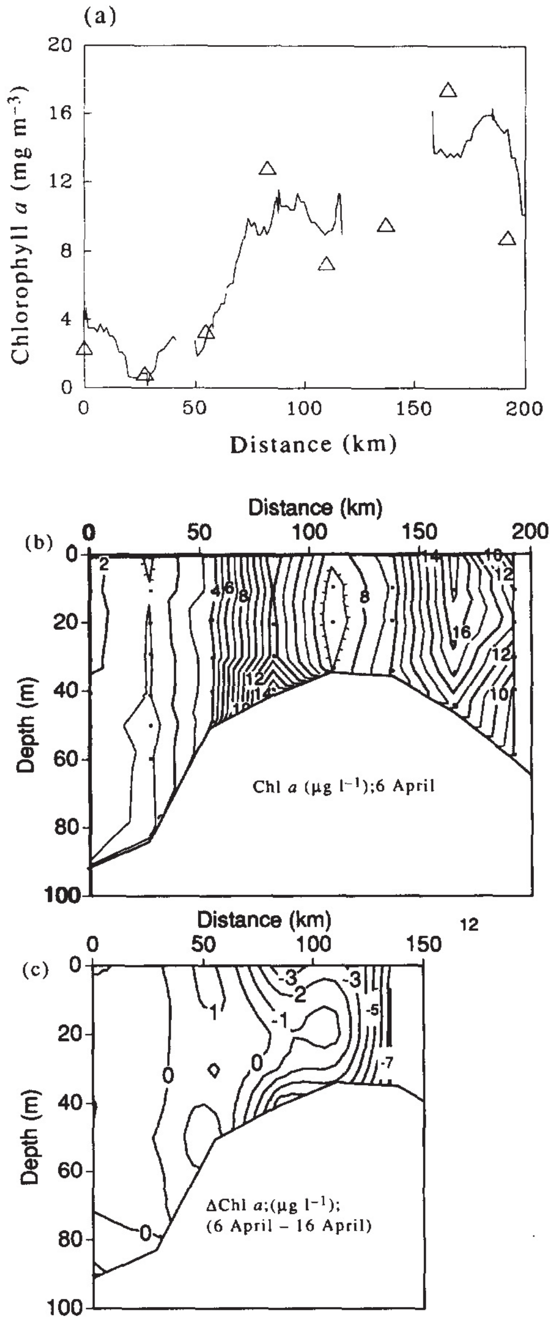

Fig. 3. (a) Surface Chl *a* concentrations from underway measurements during the 6 April section. The triangles are discrete surface samples taken for extracted Chl *a* determinations; (b) contour of Chl *a* concentrations recorded at depth on 6 April; (c) contour of the difference between Chl *a* concentrations measured on 16 April and 6 April (positive values indicate that Chl *a* increased between the two sections).

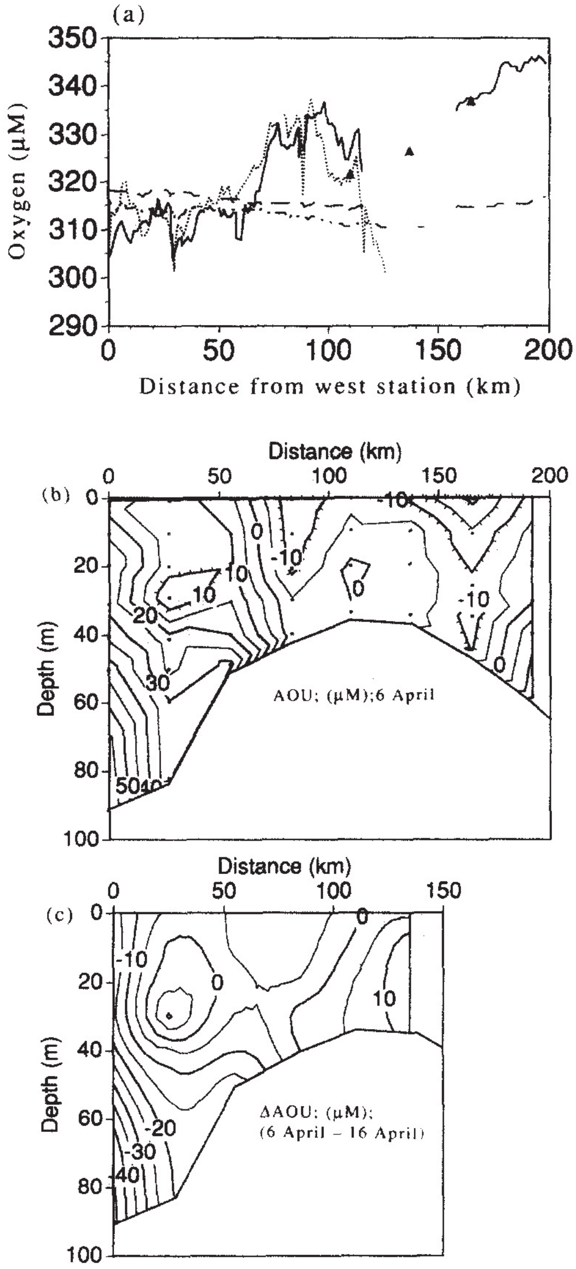

Fig. 4. (a) Surface O_2 concentrations (μM) from underway measurements during the 6 April section (solid line) and 16 April section (dotted line). The dashed line and the alternating dash-dot line are the saturation concentrations on 6 April and 16 April respectively; (b) contour of the apparent O_2 utilization (AOU) values recorded at depth on 6 April; (c) contour of the difference between AOU values on 16 April and 6 April (positive values indicate that AOU increased between the two sections).

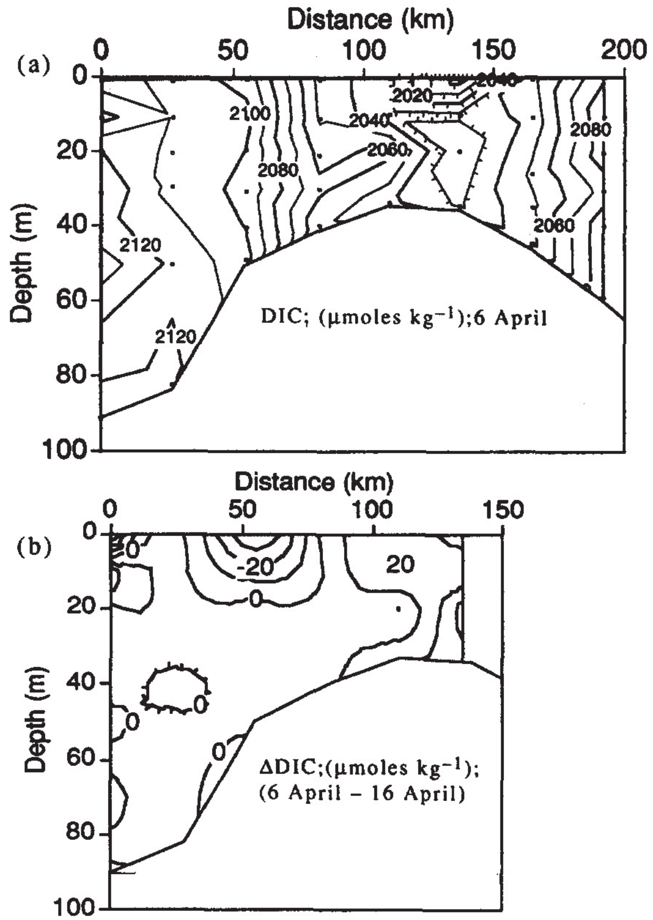

Fig. 5. (a) Contour of DIC (μmoles kg^{-1}) on 6 April; (b) contour of the difference between DIC measured on 16 April and 6 April (positive values indicate that DIC increased between the two sections).

April. Fluorescence values increased from 6–8 μg l^{-1} during the first 4 days, although all of the measurements that reflected particle abundance decreased thereafter (Fig. 9). The decrease was most dramatic in Chl *a* fluorescence (>70%), although we also recorded significant decreases in particulate carbon (PC) and particulate nitrogen (PN). DIC concentrations decreased slightly during the first few days and thereafter increased significantly (Fig. 10). Dissolved O_2 measurements did not reflect the increase in Chl *a* levels during the first few days (Fig. 10), although O_2 concentrations decreased after 11 April. Nitrate concentrations in the patch decreased approx. 0.4 μM at the start of the time series (Fig. 11), and were generally lower at the end of our sampling. Nitrite concentrations did not exhibit a clear trend, although ammonium concentrations increased during the last 4 days of our sampling (Fig. 11).

DISCUSSION

Nutrient and O_2 changes on the western flank of Georges Bank

During summer in coastal regions, tidally mixed fronts typically coincide with elevated productivity, particularly in steeply sloped regions such as northeast Georges Bank

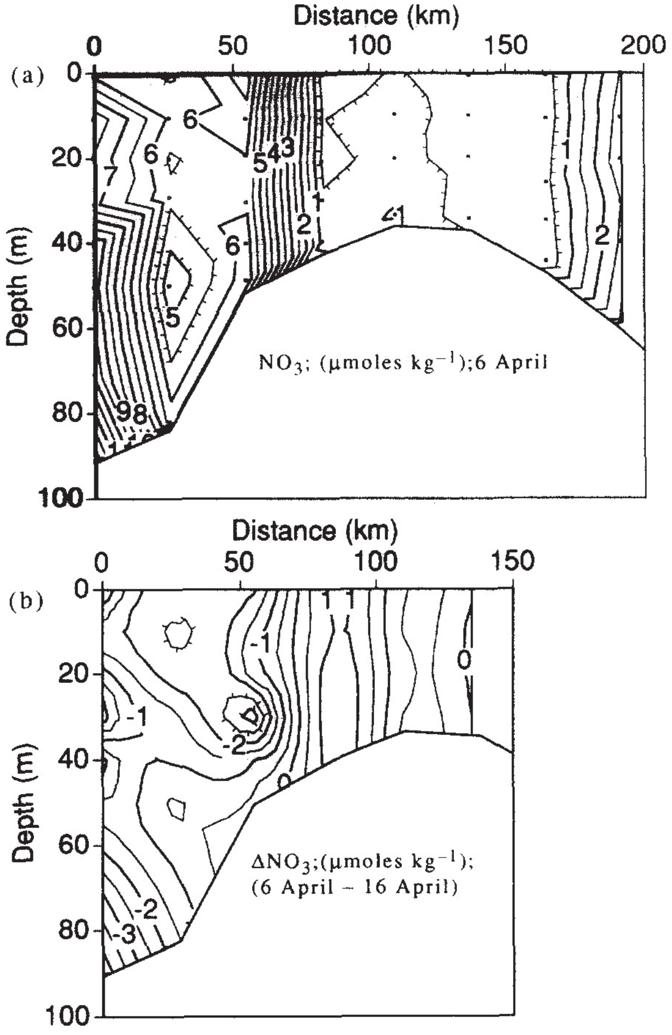

Fig. 6. (a) Contour of NO_3 (μmoles kg^{-1}) on 6 April; (b) contour of the difference between NO_3 measured on 16 April and 6 April (positive values indicate that NO_3 increased between the two sections).

(HORNE *et al.*, 1989). However, the initial development of the elevated Chl *a* region on the western Bank was not dependent on the position of the tidally mixed front and likely developed mainly in response to increasing daily light levels. The elevated Chl *a* region therefore would propagate into deeper water as daily light increased, a movement suggested by the changes in Chl *a* between 6 and 16 April [Fig. 3(c)] as well as the off-Bank shift observed in the O_2 maximum region [Fig. 4(a)]. Thus, the position of the tidally mixed front and the elevated Chl *a* region may coincide later in the season on the western Bank in response to increases in their respective forcing mechanisms (heat buoyancy and photosynthetically available radiation).

There is no quantitative information on advection and mixing in the western Bank region to isolate biological rates from the net changes we observed. However, in several instances, the changes appear to be closely associated with biology as illustrated by the changes recorded in the surface water (here defined as the isothermal layers on April 16; Table 1). For example, DIC decreased at the edge of the Chl *a* maximum (near Sta. 3) as

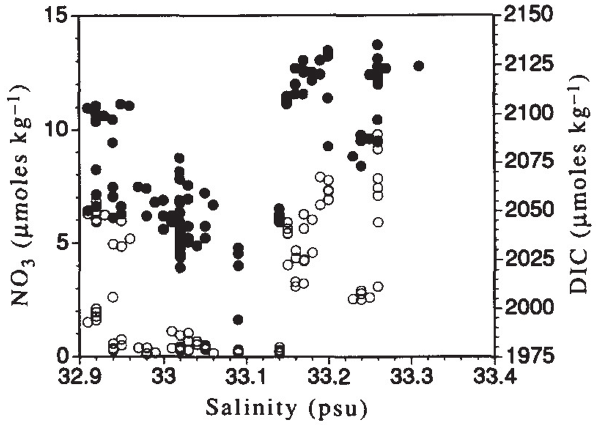

Fig. 7. Relationship of NO_3 (open circles) and DIC (closed circles) to salinity during the Georges Bank cruise.

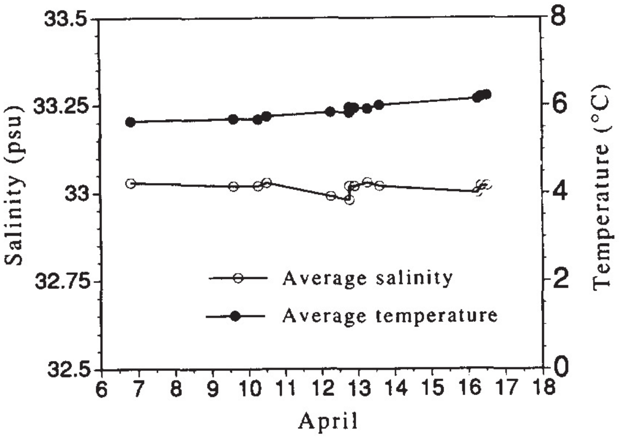

Fig. 8. Time series of salinity (open circles) and temperature (solid circles) in the patch water column. Values are water column averages (integrated amount/depth).

the band of productive water surrounding the Bank advanced into deeper regions. Similarly, the NO_3 decreases suggested that new production was greater in the peripheral Bank regions than on the mid-Bank that was NO_3 depleted by this time. The NO_3 decreases observed at the deeper stations approach new production values measured in similar (although more productive) tidally mixed frontal regions (Table 2). However, with the exception of Sta. 3, there was no similar decrease in DIC at these stations, confirming that advection and mixing prevent the biological changes from being isolated quantitatively. Even at Sta. 3, the change in DIC suggests a net community productivity (NCP) of 0.42 g C m^{-2} day^{-1} much less than the ^{14}C productivity measured in the northeast frontal region (Table 2). However, some of this discrepancy may be due to the nature of ^{14}C productivity [that measures somewhere between net and gross production (PETERSON, 1978)] and in part to the greater productivity of the northeast front. The ^{15}N data in Table 2 suggest that tidally mixed frontal regions are sites of active new production with nitrogen *f*-ratios of approximately 0.5. If the ratio of net/gross carbon production is similar, gross carbon production based on the observed DIC changes at Sta. 3 would be ~0.84 g C m^{-2}

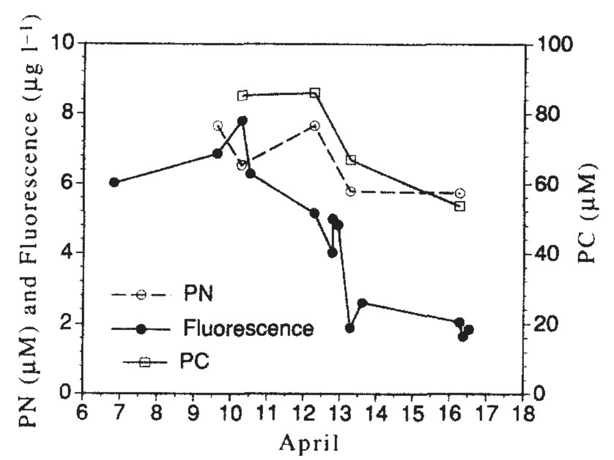

Fig. 9. Time series of particulate nitrogen (PN; open circles), particulate carbon (PC; open squares) and fluorescence (as Chl *a*; solid circles) in the patch water column. Values are averages for the water column.

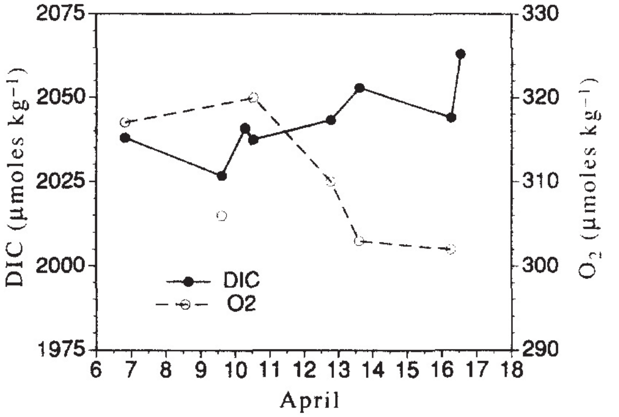

Fig. 10. Time series of DIC (closed circles) and O_2 (open circles) in the patch water column. The O_2 value on 9 April was anomalously low with respect to other parameters on this day. The estimate of NCP from O_2 was based on the values after 10 April. Values are averages for the water column.

day^{-1}, a rate that approaches the average ^{14}C rates measures on the Bank in April. Additional complications to isolating NCP from net DIC changes include the invasion of atmospheric CO_2 that takes place during productive periods (Watson *et al.*, 1991), as well as the loss of DIC due to the formation of carbonates (Karl *et al.*, 1991). The influx of atmospheric CO_2 and the precipitation of $CaCO_3$ have opposite effects on a surface carbon budget during productive periods and are roughly equal if $CaCO_3$ precipitation is not large (Chipman *et al.*, 1993).

The O_2 budget in Table 1 includes the estimated air–sea O_2 exchange in addition to the local change. At the observed surface temperature (~5.8°C) and mean wind speed (8.6 m s^{-1}) during the cruise, the O_2 exchange rate during this time would have been approx. 3.9 m day^{-1} (Wanninkhof *et al.*, 1985). This term often accounted for much of the O_2 change and thus constitutes an additional uncertainty in estimating NCP from the section O_2 data.

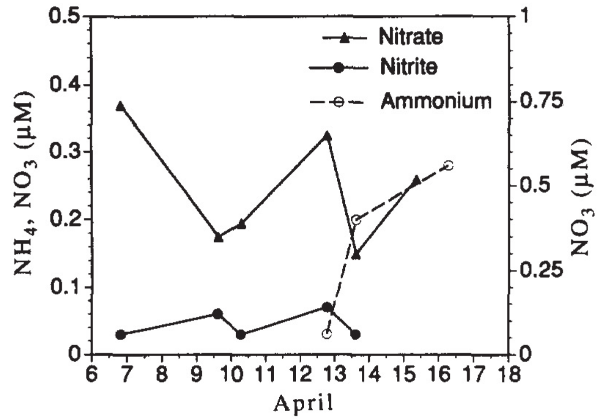

Fig. 11. Time series of NO_3 (solid triangles), NO_2 (solid circles) and NH_4 (open circles) in the patch water column. Values are averages for the water column.

Table 1. Local rates of change in Chl a, *NO_3, DIC and O_2 between* 6 *April and* 16 *April at the section stations. The estimated air–sea gas exchange has been added to the observed O_2 change*

			ΔNO_3	ΔDIC	ΔO_2 + gas exchange
Station	Depth of comparison (m)	ΔChl *a* mg m^{-2} day^{-1}	mmoles m^{-2} day^{-1}		
1	20	−1.2	−2.3	34.2	−1.3
2	20	−1.0	−4.8	4.2	−55.8
3	20	2.1	−3.2	−35.4	−0.4
4	20	−4.0	2.4	3.9	28.2
5	35	−5.7	−2.2	64.1	28.3
6	35	−28	−0.4	95.9	−104.5

Table 2. New ($^{15}NO_3$), regenerated ($^{15}NH_4$) and total (^{14}C) productivity measurements from comparable tidally mixed frontal regimes

Georges Bank, northeastern front/July–August*	
^{14}C	3.18 (±0.45) g C m^{-2} day^{-1}
$^{15}NO_3$	15.6 (±6.0) mmoles m^{-2} day^{-1}
$^{15}NH_4$	13.3 (±4.3) mmoles m^{-2} day^{-1}
Southeast Bering Sea, tidal front/April–May†	
^{14}C	1.46 (0.45–4.12) g C m^{-2} day^{-1}; (n=9)
$^{15}NO_3$	7.57 (4.59–10.55) mmoles m^{-2} day^{-1}; (n=2)
$^{15}NH_4$	9.42 (4.65–14.19) mmoles m^{-2} day^{-1}; (n=2)

*HORNE *et al.*, (1989); assuming 12 h day for NO_3 and 14 h day for NH_4.

†NIEBAUER *et al.*, (1982).

For example, the net O_2 evolution at Stas 4 and 5 coincides with elevated Chl *a* as well as a surface oxygen supersaturation of 17 mmole O_2 m^{-3} (little of which was due to temperature effects). However, the NCP estimate from the O_2 budget at these Stas (approx. 0.24 g C m^{-2} day^{-1} assuming a photosynthetic quotient (PQ) of 1.4 (LAWS, 1991) is small relative to the large phytoplankton biomass there. This may be due in part to the low NO_3 levels at these stations and the dominance of regenerated production, particularly if ammonium concentrations were large (SMITH and HARRISON, 1991). At Sta. 6 on the mid-Bank, both O_2 and DIC provide a similar estimate of NCP. This large respiration is discussed in more detail in the following section.

Although we did not measure net changes on a day to day basis in the off-Bank region, based on the observed wind speed and daily light, growth conditions probably improved significantly after 12 April (from 13 to 16 April average wind = 4.8 m s^{-1} and average irradiance = 42.3 quanta m^{-2} day^{-1}; from 6 to 12 April average wind = 10.5 m s^{-1} and average daily irradiance = 38.6 quanta m^{-2} day^{-1}). Therefore, much of the nitrate uptake at the Great South Channel stations probably occurred after the 12 April respite from wind mixing in association with the thermal stratification because new production is highly dependent on stable upper water conditions SAMBROTTO *et al.*, (1986). Analogously, the net consumption of DIC at Sta. 3 was likely less than the average value of 0.42 g C m^{-2} day^{-1} before 12 April, and significantly greater thereafter.

Net production in the mid-Bank time series

The collaborative purposeful SF_6 tracer study enabled us to make a robust estimate of NCP from the local changes in DIC and O_2 in the mid-Bank time series. Previous analyses of the heat budget on mid-Bank (<43 m) have estimated that despite the energetic mixing regime on the Bank, horizontal dispersion rates for a scalar are less than 0.03 day^{-1} after the development of the tidally mixed fronts (LODER *et al.*, 1982). The changes in SF_6 concentration with time during our April study also suggested slow dispersion rates. The most rapid mixing of the SF_6 resulted from an elongation of the original patch as some of the SF_6 was mixed into the shoal areas to the northwest of the injection area. This mixing was due mainly to the residual tidal circulation on the Bank that has a long axis oriented north northwest–south southeast and an excursion of approximately 11 km (HAIGHT, 1942). The major water mass mixing onto the Bank is the Wilkerson Basin Water (WBW) that lowers the salinity of Bank waters through spring and summer (HOPKINS and GARFIELD, 1981). WBW was evident in the frontal region during our sampling by its low salinity [Fig. 2(b)]. However, judging from the constancy of patch salinity (Fig. 8), there was no significant penetration of this water into the SF_6 patch. Therefore, the net concentration changes observed during our patch study mainly reflect local (within patch) processes.

The nutrient and O_2 changes in the patch suggest that unlike the western flank, respiration was the dominant process occurring on the mid-Bank, particularly after 10 April. The results of linear models fit to the temporal changes in the particulate and dissolved pools on the mid-Bank from 9 to 16 April are summarized in Table 3. The observed DIC increase (3.22 μM day^{-1}) in the 35 m water column of the patch stations corresponded to a NCP of -1.35 g C m^{-2} day^{-1} during this period. In the O_2 system, the addition of a 16.5 mmoles O_2 m^{-2} day^{-1} influx to the local rate of change in Table 3 suggested that NCP was -1.45 g C m^{-2} day^{-1}. The time series estimates of NCP are

Table 3. *Rates of change of particulate and dissolved pools measured in the patch water column from* 10 *April to* 16 *April based on the data in Figs* 9–11. *All rates are based on a least squares fit to a linear model*

Pool	Particulate pools rate of change (day^{-1})	r^2	Pool	Dissolved pools rate of change (day^{-1})	r^2
PC	$-5.75\,\mu M$	0.85	DIC	$3.22\,\mu M$	0.63
PN	$-0.25\,\mu M$	0.48	NO_3	N.S.	—
Chl *a*	$-0.87\,\mu g\,l^{-1}$	0.81	NO_2	N.S.	—
			NH_4	$0.06\,\mu M$	0.77
			O_2	$-2.95\,\mu M$	0.79

16–17% larger than those derived from the net 10 day changes on mid-Bank (Table 1) mainly because Table 1 included a period in which Chl *a* concentrations were still increasing, while the regressions in Table 3 focused on the period 10–16 April in which respiration clearly exceeded production. The rapid loss of particulates from the water column after 12 April (Fig. 9) coincides with the decrease in winds from >10 to <6 m s^{-1} and thus the net change in water column particulates (-2.4 g C m^{-2} day^{-1}) may be largely due to sinking. A large sinking flux also is compatible with the increase in AOU and DIC in deeper mid-Bank waters [Figs 4(b) and 5(a)] and suggests that particle destruction on the Bank is facilitated by resuspension that takes place consistently in shallow regions (Bothner *et al.*, 1981). Also, the respiratory demands of the zooplankton (Dagg and Turner, 1982) and the benthos (Florek and Rowe, 1983) are reflected in the DIC and O_2 changes, although likely to a lesser extent than microbial respiration. The fraction of respiration due to the oxidation of dissolved organic matter (DOM) may be large because previous measurements indicated that approximately 20% of total organic carbon production on the Bank is in dissolved form O'Reilly *et al.*, (1987) and bacteria on the Bank are elevated relative to surrounding waters (Hobbie *et al.*, 1987).

The present results support previous speculation Walsh *et al.*, (1987) that after the initial end-of-winter nutrients are exhausted (apparently this occurred just before our April sampling), continued eutrophic conditions on the Bank are maintained largely by regenerated nutrients. Of the observed decrease in patch particulate nitrogen (Table 3; 8 mmoles m^{-2} day^{-1}), less than one third could be accounted for in the dissolved inorganic pool (mainly in ammonium). Therefore, the local change suggested a regenerated nitrogen productivity of ~5.4 mmoles m^{-2} day^{-1}. This rate is only half of that measured by Horne *et al.*, (1989) on the mid-Bank and similarly low in comparison to estimates based on the nitrogen *f*-ratio (Loder *et al.*, 1982) and total carbon productivity (O'Reilly *et al.*, 1987). Two major reasons for this discrepancy are: (1) dissolved organic nitrogen (DON) also may be a significant source of regenerated nitrogen for phytoplankton growth; and (2) the turnover times of regenerated nitrogen pools can be rapid [<1 day; Gilbert (1982); Probyn (1987)] and thus local changes in ammonium are conservative estimates of the actual regenerated production.

New production on Georges Bank is available both to support local higher trophic levels or to be exported from the region. These fates are largely mutually exclusive and the observed productivity of local fisheries attests to the importance of the former (Schlitz and Cohen, 1984; Sissenwine *et al.*, 1984). However, the precision of such trophic analyses is not sufficient to accurately constrain the amount of organic matter that may be exported from the Bank. Significant cross-shelf export of organic material would provide a mechanism to sequester atmospheric carbon in slope sediments and/or deeper waters where it is isolated from the atmosphere (WALSH *et al.*, 1981; WALSH, 1983). Also, the dominant shelf circulation pattern that transports water from the Scotian shelf to the mid-Atlantic Bight (CHAPMAN and BEARDSLEY, 1989) may transport organic material from Georges Bank to downstream regions as has been suggested for other productive shelf locations (MALONE *et al.*, 1983). However, the large rates of respiration we recorded on the Bank suggest that it is not a major source of organic carbon to downshelf areas. The rate of net production on mid-Bank was similar in absolute value but opposite in sign to the productivity rates in the surrounding frontal regions (Tables 1 and 2). Also, the area of the mid-Bank (<45 m; 5×10^3 km^2) is slightly greater than that of the frontal area (45–55 m; 4×10^3 km^2; HOPKINS and GARFIELD, 1981). Thus, the mid-Bank has the capacity to respire all of the organic material produced at both the mid-Bank and frontal regions. Apparently, the physical retention of the organic matter produced on the Bank that has been suggested as an important factor leading to the rich fisheries there, (MOUNTAIN and SCHLITZ, 1987), also enhances the local respiration of this material before it can be exported. Therefore, despite its eutrophic character, Georges Bank probably exhibits a similar relationship to the adjacent slope as that found on the shelf to the south of this region, in which only a small amount of refractory organic carbon reaches the slope sediments (ANDERSON *et al.*, in press).

Inferred food web changes in the patch

The steady decrease in Chl *a* after 11 April and the low concentration of NO_3 on the mid-Bank, suggested that the patch time series recorded the end of a more productive period. The observed changes in the suspended particulate material during the patch time series were used to estimate the relative changes among particle types during this post-bloom period. For this analysis, particulate material was assumed to be composed of three broad types; phytoplankton, heterotrophs and detritus, each with a characteristic N/C ratio. Two simple mass balance relationships were then established in terms of carbon and nitrogen respectively:

$$C_P + C_H + C_D = C_T \tag{1}$$

$$C_P\left(\frac{N}{C}\right)_P + C_H\left(\frac{N}{C}\right)_H + C_D\left(\frac{N}{C}\right)_D = C_T\left(\frac{N}{C}\right)_T \tag{2}$$

in which the subscripts *P*, *H*, *D* and *T* represent the phytoplankton, heterotrophic, non-living (detrital and carbonate) and total particulate pools respectively. Both C_T and N/C_T were measured directly (Fig. 9). Phytoplankton carbon (C_P) was estimated from measured Chl *a* levels using a C/Chl *a* ratio (mg/mg) of 50 (LANGDON, 1987). Literature values were used for the N/C ratios of the three subgroups. For example, 0.14 (mole/mole) was used for $(N/C)_P$ of the diatom dominated phytoplankton assemblage we observed (CLEVELAND and PERRY, 1987) and $(C/N)_H$ was based on values typical of heterotrophic organisms within the microbial loop (~0.22; GOLDMAN *et al.*, 1987; HOPKINSON *et al.*, 1989). Thus, the analysis explicitly excluded the larger zooplankton that were not adequately sampled in our particulate measurements. Although the N/C ratio of a

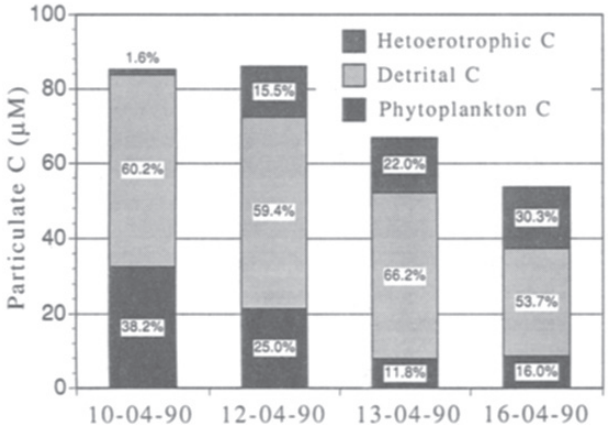

Fig. 12. Results of a mass balance model of particulate carbon (PC) changes during the patch time series (see text). Bar heights represent measured total PC levels and the shaded areas represent our estimates of selected particle group sizes.

heterogeneous pool such as detrital material is likely not constant, detrital material is relatively N depleted (Banse, 1974). Therefore, a value of 0.033 was used for $(N/C)_D$. This value is within a reasonable range for bacterial substrates (Hopkinson *et al.*, 1989) and provides a *N*-poor end member for our comparative analysis. This leaves two unknowns (C_H and C_D) in equations 1 and 2 so that the relative change in the three particle groups during the time series on the Bank could be estimated (Fig. 12).

The relative changes predicted by this simple model are compatible with the expected trophic changes during the post-bloom period as well as with seston composition estimated from cell counts in other coastal areas (Holligan *et al.*, 1984). For example, phytoplankton carbon declined most dramatically in the suspended material and this decrease was partly compensated for by an initial increase in heterotrophic biomass, although the heterotrophic carbon pool was fairly constant over the last samplings in the patch (*ca* 15–16 μM). The detrital pool did not increase as the phytoplankton declined, which suggests that the phytoplankton were largely sinking to the bottom and/or that the detrital pool was the substrate for most of the respiration we observed. The respiration of the detrital carbon pool is compatible with two observations from our sampling: (1) the decrease in total particulate C/N ratio during the time series from 12.2 to 8.9; and (2) the significant non-zero intercept of the PC/PN relationship (*ca* 27 μM; Fig. 13). This intercept is similar to the 28 μM of detrital C predicted by the mass balance model in patch waters at the end of the cruise and thus both suggest that a significant proportion of the particulate matter was detrital.

The estimated redistribution of carbon among particle groups during our time series was similar to the distributional differences (Holligan *et al.*, 1984) found between a productive front and a vertically mixed region in the English Channel (their Table 4). For example, the proportion of phytoplankton in the seston decreased between productive frontal regions and the less productive vertically mixed areas in the English Channel while heterotrophic and detrital carbon increased. The large intercept on the PC to PN regression from Georges Bank (Fig. 13) also was similar to that found in the English Channel. The successional changes we observed on Georges Bank seston therefore, mark a transition to summer conditions in which over 80% of the filterable particulates are detritus and heterotrophic organisms in the tidally mixed regions.

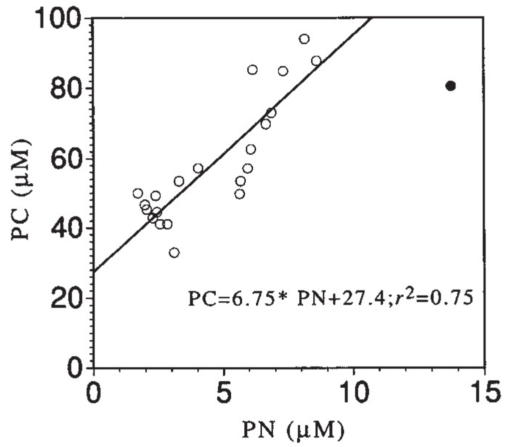

Fig. 13. Relationship between particulate carbon (PC) and particulate nitrogen (PN) on Georges Bank during April, 1990. The solid symbol was not included in the regression analysis shown on the chart.

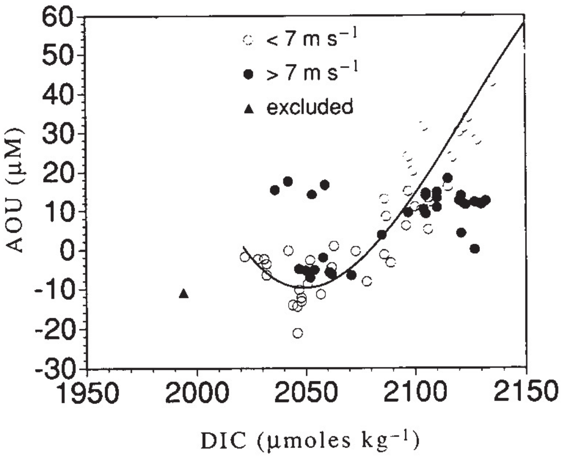

Fig. 14. The relationship between AOU and DIC. The data were subdivided into a low wind group (those with an average previous 24 h wind speed less than 7 m s^{-1}; open circles) and a high wind group (those with an average previous 24 hr wind speed greater than 7 m s^{-1}; solid circles). The polynomial fit was based only on the low wind speed data and the data point below 2000 μmoles kg^{-1} DIC was excluded.

Relative changes in DIC, NO_3 and O_2

The relationship between AOU and DIC was difficult to discern, largely because of the influence of gas exchange on the O_2 pool (Fig. 14). The gas exchange rate during the Georges Bank study (~4 m day^{-1}) suggested that the e-folding time for surface O_2 concentrations (essentially the biological memory of a given O_2 measurement) was approximately 4 days. In the case of DIC and NO_3, air–sea exchange is either a much smaller factor (i.e. gaseous CO_2 is only *ca* 1% of the DIC pool), or negligible (as in the case of an ionic nutrient like NO_3). Thus, for comparisons involving AOU, the data have been

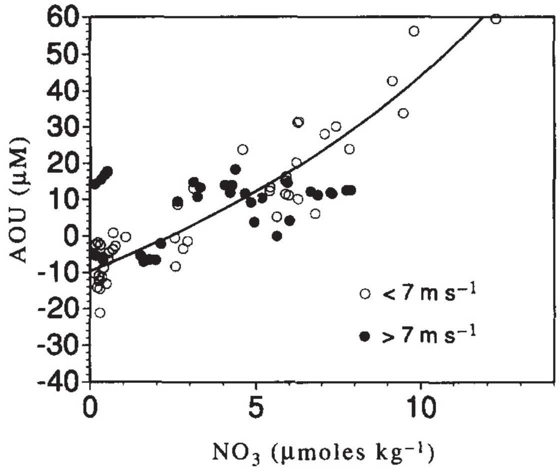

Fig. 15. The relationship between AOU and NO_3. The data were subdivided and analyzed as in Fig. 16.

separated into low and high wind regimes based on the average wind speeds during the previous 24 h to minimize the effect of gas exchange on O_2. A 7 m s^{-1} cut-off between the two regimes was chosen because this is the global average wind speed over the ocean. Although, as expected, there was no relationship for the strong wind group, the relationship of AOU to DIC gave a reasonable PQ (approx. 1) for the light wind group at DIC concentrations greater than 2080 μM (Fig. 14). This suggests that the changes in O_2 and DIC associated with NCP are similar to those expected from Redfield ratios. The maximum in net water column O_2 production (most negative AOU values) at approximately 2050 μM DIC corresponded closely to the region in which NO_3 became depleted on the western flank (Figs 5 and 6) and suggests that there was a close relationship between new (nitrate) production and net production in terms of either O_2 or DIC. The DIC values less than 2040 μM in Fig. 14 are associated with low NO_3 on mid-Bank, and here rapid gas exchange in these well mixed waters maintain O_2 concentrations near saturation.

The AOU–NO_3 relationship also exhibits a slope (~8) approximating the Redfield value for large NO_3 concentrations (>5 μM) at low wind speeds (Fig. 15). Oxygen supersaturations were measured repeatedly in association with NO_3 levels below 0.5 μM. Most of these low NO_3 values are from the mid-Bank stations in which NH_4 concentrations approached those of NO_3 (Fig. 11). Under such conditions, new production rates are expected to be low, due to both concentration dependent limitation and the inhibitory effects of ammonium (Wheeler and Kokkinakis, 1990). Thus, the maintenance of O_2 supersaturation in low NO_3 regions is unexpected if new and net production are biologically equivalent processes (Platt *et al.*, 1989). The evolution of O_2 may be supported by a rapid horizontal flux of NO_3 onto the Bank that is not reflected in the ambient concentration measurements (Horne *et al.*, 1989) as well as by the memory of previous new production in situations in which NO_3 had been recently depleted. The mid-Bank O_2 results therefore, provide another case in which additional NO_3 supply must be invoked to balance observed O_2 changes when Redfield conversions between the two systems are used (Jenkins, 1988; Platt *et al.*, 1989).

To compare the relative biological consumption of DIC and NO_3, the effects of mixing and fresh water exchange due to precipitation–evaporation (P–E) were considered (Fig.

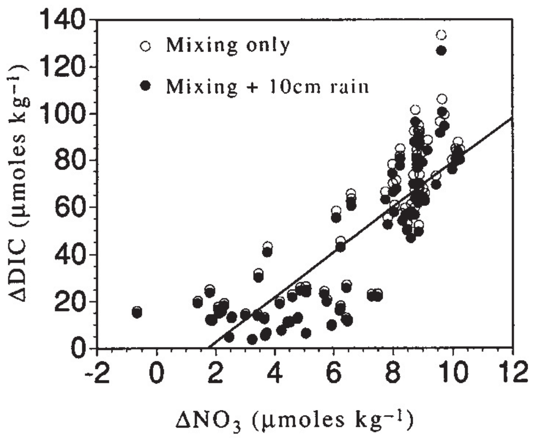

Fig. 16. Relationship between DIC and NO_3 expressed as the difference between the value expected from mixing of two end member water masses (WBW and uSW) and the observed value (open circles), similar to the diagram analysis of MINAS *et al.* (1986). The solid circles include an estimate of the effect of precipitation–evaporation (specified as a net input of 10 cm of freshwater). The linear regression model was based on the latter values ($\Delta DIC = 9.56^* \Delta NO_3 + 16.59$; $r^2 = 0.70$; $n = 91$).

16). The former was addressed with the diagram analysis approach of MINAS *et al.*, (1986). The NO_3 and DIC concentrations expected from mixing alone were estimated using the low salinity [nominally Wilkerson Basin Water (WBW): 32.9 psu; 8 μM NO_3; 2115 μM DIC] and the high salinity [nominally upper Slope Water (uSW): 33.4 psu; 13 μM NO_3; 2150 μM DIC] water as end members (Fig. 7). The relationship between the differences from these estimated values of DIC and NO_3 and the actual measurements therefore were largely free from water mass mixing effects (Fig. 16; open circles) and the results were not sensitive to moderate changes in the choice of end-member characteristics. The effect of rainfall was assessed by adjusting the measured values of DIC and NO_3 for dilution such that:

$$C_{\text{dil.}} = C_{\text{meas.}} \times \left[1 + \frac{(P\text{–}E) \times \dfrac{\Delta}{\Delta_{\max}}}{Z}\right] \tag{3}$$

In which $C_{\text{dil.}}$ is the dilution adjusted value; $C_{\text{meas.}}$ is the measured value; Δ is the concentration change between the mixing line and the measured value; $\Delta_{\max}$ is the maximum observed difference and Z is stratum thickness. The ratio $\Delta/\Delta_{\max}$ increases the dilution effects for values with a large Δ because both dilution and nutrient uptake are surface and time dependent processes. The thickness (Z) was set at 35 m, the depth at mid-Bank and a reasonable approximation of the mixed layer in deeper waters.

The linear regression model shown in Fig. 16 was based on values adjusted to a P–E of 10 cm (slope = 9.56; $r^2 = 0.70$; $n = 91$). This slope was significantly greater than the Redfield C/N ratio of 6.6 ($P < 0.001$; REDFIELD *et al.*, 1963) that has been the standard assumption regarding the interaction of these two nutrients in surface waters. A P–E value of over 60 cm was required to decrease the slope to 6.6 and thus it is unlikely that the $\Delta DIC/\Delta NO_3$ relationship can be attributed to either water mass mixing or precipitation. An exponential fit to the data in Fig. 16 does not provide a better fit, although as a subgroup, the large delta values in Fig. 16 (mainly from the mid-Bank region) have a greater slope than the total

Table 4. Comparison of the observed changes in DIC (based on the changes recorded in Fig. 9) with the changes predicted from the observed NO_3 consumption scaled by the Redfield C/N ratio of 6.6

Source water	Initial DIC	Initial NO_3 (μM)	Redfield est. of DIC loss ($\Delta NO_3 \times 6.6$) (μM)	Observed DIC loss (μM)	% underestimate by Redfield
Low salinity (WBW)	2100	8.0	53	90	41
High salinity (uSW)	2150	13.0	86	125	31

data set. These results suggest that although the stoichiometry between DIC and NO_3 is fairly consistent in the ocean thermocline (TAKAHASHI *et al.*, 1985), the relative behavior of these nutrients is significantly different in eutrophic surface waters over moderate (~1 month) time scales. This discrepancy also can be illustrated by a simple comparison between the observed consumption of DIC on the Bank and that expected on the basis of NO_3 consumption and the Redfield C/N ratio (Table 4). Starting from either the low or high salinity source water NO_3 concentration, the minimum DIC observed on the Bank (2025 μM) was significantly lower than expected. Also, our results are similar to previous reports of surface DIC/NO_3 consumption greater than expected from the Redfield ratio in the eastern Bering Sea (CODISPOTI *et al.*, 1986) and in the Southern Ocean (KARL *et al.*, 1991) during eutrophic periods.

It is not possible to calculate the contribution of carbonate production on the Bank to the observed non-Redfield behavior because contemporaneous measurements of alkalinity (or one of the other carbonate system parameters such as pCO_2 that would allow alkalinity to be calculated) were not made. Measured alkalinity changes in Gerlache Strait suggested that no appreciable $CaCO_3$ production took place there during the spring bloom and the observed DIC/NO_3 relationship was similar to that found on Georges Bank (*ca* 12; KARL *et al.*, 1991). However, in coccolithophore blooms, $CaCO_3$ production would be significant and such blooms may occur in the Georges Bank region during summer (ACKLESON and HOLLIGAN, 1989). Coccolithophores were not observed in fresh samples we examined from Georges Bank in April. The fixation of N_2 was likely not a major source for new nitrogen in the eutrophic region we sampled as it can be in more oligotrophic, oceanic regions (CARPENTER and ROMANS, 1991). The efflux of CO_2 from surface waters would increase the observed DIC/NO_3 slope. However, productive waters such as those on Georges Bank typically are undersaturated in CO_2 with respect to air (WATSON *et al.*, 1991) and the influx of atmospheric CO_2 would cause the observed decrease in surface water DIC to be a conservative estimate of net consumption.

Based on these observations, the most likely explanation for the observed DIC/NO_3 ratio is the production of carbon rich organic matter with a C/N ratio >12 and the particulate material on Georges Bank had a C/N ratio in this range. However, much of the phytoplankton was produced either earlier on mid-Bank or on the western flank where there were large concentrations of nitrate. Thus, it is unlikely that nutrient limitation caused the phytoplankton to have an elevated C/N ratio. Also, by mid-April the particulate C/N ratio was decreasing (Fig. 10), inferring that the net mineralization flux from this pool was relatively enriched in DIC. DOM production was suggested as a factor in the elevated DIC/NO_3 ratio observed in the Bransfield Strait region (KARL *et al.*, 1991) as well as an important vehicle for carbon flux generally (TOGGWEILER, 1989). One of the major advantages in using direct measurements of DIC to quantify organic carbon production and export is that these changes reflect both dissolved and particulate production unlike standard particle production techniques like ^{14}C, or particle interceptor traps, that usually reflect only the growth and export of the particulate pool. Thus, although we cannot differentiate DOC from POC production, our results suggest that a smaller amount of new (nitrate) production is needed to produce a given NCP signal than conversions from Redfield ratios predict. Biogeochemical budgets based on surface ocean NO_3 should therefore be considered as minimum estimates of organic matter export from plankton systems.

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