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Distribution, fluxes and biological utilization of inorganic nitrogen during a spring bloom in the New York Bight

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ABSTRACT

The utilization of ammonium (NH₄) and nitrate (NO₃) by natural phytoplankton communities was measured during a *Ceratium tripos*-dominated spring bloom in the New York Bight. During 6-8 hour uptake experiments, the inshore phytoplankton communities that were typically located at depths $\geqslant$ 25 m were characterized by NH₄ and NO₃ uptake rates that were less light-dependent than those of the more uniformly distributed communities at the shelf break. Measurements of NH₄ utilization, as a percentage of NH₄ plus NO₃ utilization, yielded values of 59% inshore and 70% at the shelf break. High biomass of zooplankton at the shelf break suggested they could account for ~62% of the regenerated production (i.e., based on NH₄), while inshore, estimates of regenerated NH₄ from zooplankton, benthos and bacterioplankton could account for 38 to 53% of the phytoplankton requirements. In the cross-shelf distribution, the ambient concentrations of NH₄ and NO₃ in the surface water were ~0.4 and ~0.1 μmol L^{-1}, respectively; however at depths between 25 and 50 m, concentrations of ~2 and ~4 μmol L^{-1} were observed.

1. Introduction

The New York Bight is bounded by Long Island on the north, New Jersey on the west, and the 100 fathom contour line seaward. An estuarine circulation characterizes the inner waters of the bight, with surface waters moving generally seaward and bottom waters generally landward (Beardsley *et al.*, 1976; Gordon *et al.*, 1976).

After stratification of the water column in the spring (April-May), the concentration of dissolved inorganic nitrogen (DIN) in the euphotic zone is maintained at a low level (<3 μmol L^{-1}; Walsh *et al.*, 1978) by phytoplankton utilization. Without a source of additional ammonium (NH₄) and nitrate (NO₃) to the euphotic zone, the DIN would be depleted in a few days. The renewal of nitrate to the euphotic

zone occurs primarily through vertical advective and diffusive processes. If a concentration gradient exists across the pycnocline, advection and diffusion can also be important processes supplying ammonium to the euphotic zone (Riley, 1967); however the primary processes are biological and include (1) herbivore excretion, (2) bacterial regeneration, and (3) benthic regeneration (in shallow waters). The rapid regeneration and recycling of NH_4 within the euphotic zone can result in primary production that is more dependent on NH_4 than NO_3 (e.g., Dugdale and Goering, 1967).

Ryther and Dunstan (1971), using nutrient enrichment-bioassay techniques, characterized the bight as a nitrogen-limited system in terms of phytoplankton growth, but field measurements of DIN utilization by phytoplankton have not been previously reported for this region.

The purpose of the present study was to characterize the DIN dynamics of the New York Bight by determining the maximal utilization rates of DIN by natural phytoplankton communities and comparing these rates to the distribution and fluxes of DIN within the water column.

2. Materials and methods

This field study was conducted during a U.S. Energy Research and Development Administration (ERDA) cruise to the New York Bight in April and May 1976. The maximal utilization rate of DIN by phytoplankton was determined at 11 stations (Fig. 1). Water samples were taken from five light depths (100, 50, 30, 15 and 1%), corresponding to the percent penetration of surface light intensity as determined by a Lambda quantum meter. The water was passed through a 253-μm Nitex mesh to remove large zooplankton and placed in 2- or 4-L bottles fitted with the appropriate neutral-density light screens. The samples were enriched with ~15 μmol L^{-1} of ^{15}N-labelled NH_4 or NO_3 and incubated under natural light for 6 to 8 h, 0900 to 1700 h local time, in plexiglass tanks cooled by surface seawater. In addition to the ^{15}N samples described above, ^{15}N incubations were completed using (1) a dark bottle (taped to prevent light penetration) containing water from the 50% light depth (all stations), (2) a 50% light-screened and a dark bottle, both containing water from the 0.1% light depth (all stations), (3) bottles screened for 18, 9, 5, 3, and 0.2% of the incident radiation and containing water from the chlorophyll maximum (31 m, station 77), and (4) bottles incubated for 6 and 24 h to determine diel variations in the uptake rates (stations 62 and 91).

After incubation with the stable isotope ^{15}N, the method of Pavlou et al. (1974) and the modified combustion technique of Gunther et al. (1966) were used to analyze for the ^{15}N/^{14}N ratio in the phytoplankton. The biological transport rate of NH_4 was calculated from the equation:

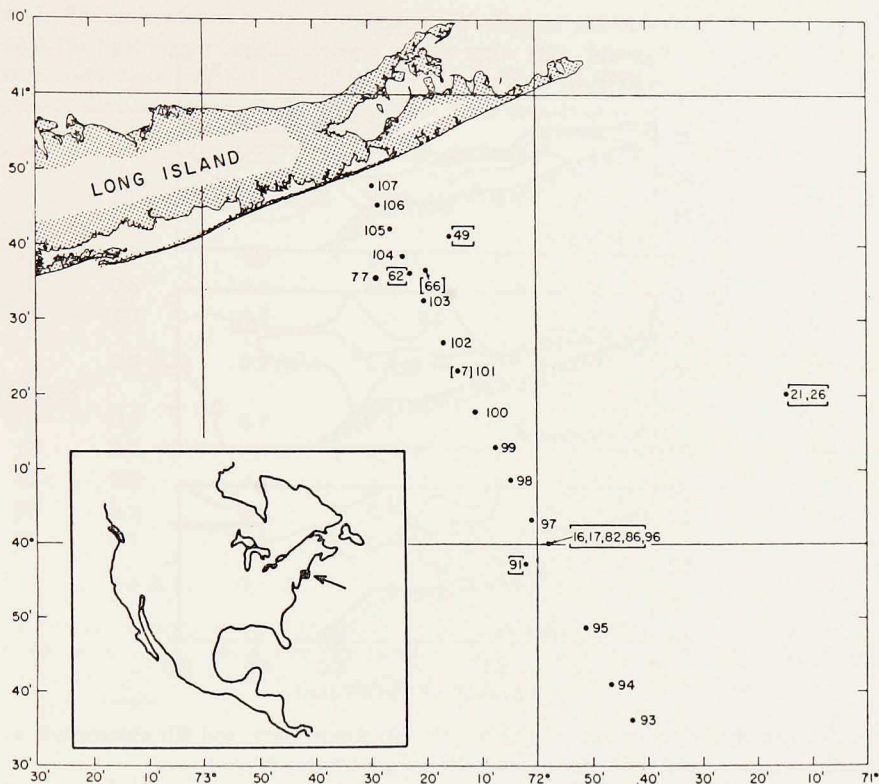$$\rho NH_4 = V_{NH_4} \cdot PN, \tag{1}$$

Figure 1. Sampling locations off Long Island with approximate location shown by arrow in insert. Productivity stations are enclosed in brackets.

where V_{NH_4} is the specific uptake rate of NH_4 (h^{-1}) and PN is the particulate organic N concentration (μmol L^{-1}) determined at the end of the experiment. The resulting units of transport are μmol of N untilized per liter per hour. The total biological transport rate (T_N) of DIN into the phytoplankton community is:

$$T_N = \rho NH_4 + \rho NO_3, \qquad (2)$$

where ρNH_4 and ρNO_3 are the biological transport rates of NH_4 and NO_3 and assuming that the utilization of nitrite is negligible.

The ambient concentrations of $NO_3 + NO_2$ and NH_4 were determined with an AutoAnalyzer, using the methods described by Armstrong *et al.* (1967) and Friedrich and Whitledge (1972).

In this study the maximal or potential uptake rate of DIN by natural phytoplankton communities was measured instead of estimating the *in situ* rate (e.g., Dugdale and Goering, 1967) because (1) the maximal utilization rate of NH_4 can be realized at ambient concentrations ≥ 0.1 μmol L^{-1} for N-starved populations (Conway and
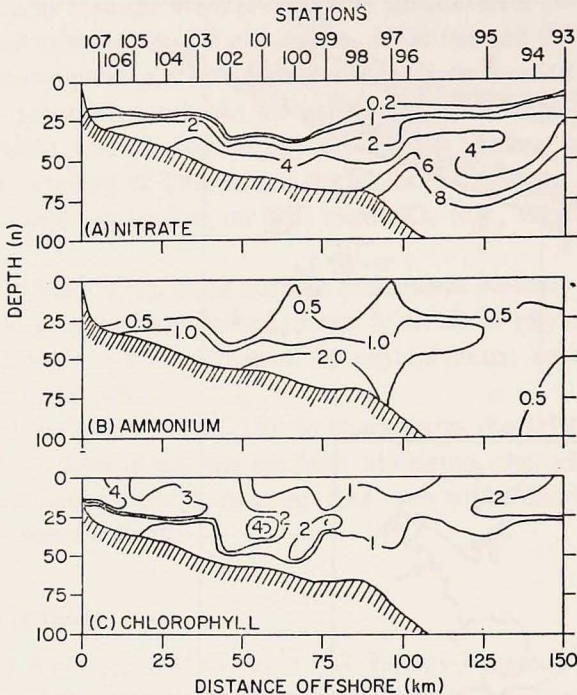
Figure 2. Cross-shelf distributions of (A) Nitrate, (B) Ammonium, and (C) chlorophyll *a*. The isopleths units are μmoles L^{-1} for (A) and (B) and $\mu g\ L^{-1}$ for (C).

Harrison, 1977), (2) the maximal utilization rate of NH_4 or NO_3 can be maintained at ambient concentrations $\geqslant 1.0$ μmol L^{-1} for N-limited populations (Conway and Harrison, 1977; Q. Dortch, pers. commun.), and (3) even a small increase ~ 0.5 μmol L^{-1}) in the ambient NH_4 concentration can result in a perturbed NH_4 uptake rate (Harrison and Conway, unpubl. ms.).

3. Results and discussion

In presenting the results of this study, we have concentrated on the transect that included 9 of the 11 productivity stations (Fig. 1). These productivity stations were classified as inshore (49, 62, 66; $Z<50$ m) or shelf break stations (16, 17, 82, 86, 91). The exception was station 7 which was located between the two station groupings. On the first transect of the present study, diatoms were predominant at shelf break locations (stations 16, 17), but *Ceratium tripos* (a dinoflagellate) dominated at all depths when that location was reoccupied (stations 82, 86, 91) 9 days later. Inshore, the *C. tripos* community was typically located between the 0.3 and 3% light depths (~ 20-40 m) but at the shelf break it was more uniformly distributed as indicated by the chlorophyll distribution (Fig. 2c).

Table 1. The ratio of dark to light uptake rates (V_D/V_L) for phytoplankton taken from the 50% and 0.1% light depths and the ratio of uptake under 50% light conditions for phytoplankton taken from these two light depths at the inshore and shelf-break stations. The mean and standard deviation (in parentheses) are found at the bottom of each column.

Station	V_D/V_L (NH$_4$)*		V_D/V_L (NO$_3$)*		$\dfrac{V_{NH_4} (50\%)^{**}}{V_{NH_4} (0.1\%)}$	$\dfrac{V_{NO_3} (50\%)^{**}}{V_{NO_3} (0.1\%)}$
	50% LD	0.1% LD	50% LD	0.1% LD		
Inshore						
49	0.7	1.0	0.8	0.6	1.2	1.0
62	0.8	0.8	0.8	0.8	0.7	0.6
66	1.3	0.9	1.0	0.8	0.4	0.5
	0.9 (0.3)	0.9 (0.1)	0.9 (0.1)	0.7 (0.1)	0.8 (0.4)	0.7 (0.3)
Shelf break						
16	0.6	0.7	0.7	0.9	6.3	3.8
17	0.7	0.4	0.5	n.a.	2.2	n.a.
82	0.5	0.4	n.a.	0.3	2.0	2.2
86	n.a.	0.7	0.3	0.7	6.8	10.0
91	0.6	0.5	n.a.	0.2	1.6	4.3
	0.6 (0.1)	0.5 (0.1)	0.5 (0.2)	0.5 (0.3)	3.8 (2.5)	5.1 (3.4)

* Defined as (uptake rate in dark)/(uptake rate in 50% light).
** Defined as (uptake rate in 50% light bottles of phytoplankton taken from the 50% light depth)/(uptake rate in 50% light bottles of phytoplankton taken from the 0.1% light depth).
n.a. = not available.

a. *Biological utilization of NH$_4$ and NO$_3$.* The results of DIN uptake experiments in dark bottles and in 50% light-screened bottles were expressed as a ratio of the specific uptake rates (V_D/V_L). This ratio was used as a measure of the light dependence of DIN utilization by natural phytoplankton communities. Within each station grouping (inshore or shelf break), the ratios were not significantly different (*t*-test at the 95% confidence level) for either light depth (50% vs. 0.1%) or nitrogen species (NH$_4$ vs. NO$_3$) (Table 1). Therefore the ratios were pooled for the inshore stations as well as for the shelf break stations and resulted in mean values with ±95% confidence limits of 0.9 ± 0.1 ($n = 12$) and 0.5 ± 0.1 ($n = 16$), respectively. These data show a slight light dependence at the inshore stations, compared with the stronger light-dependent utilization of DIN at the shelf break.

Dark uptake of NH$_4$ and NO$_3$ has been observed in laboratory studies with the coccolithophore *Coccolithus huxleyi* (Eppley *et al.*, 1971), the diatom *Ditylum brightwelli* (Eppley and Coatsworth, 1968; Eppley and Rogers, 1970), and the dinoflagellates *Pyrocystis noctiluca* and *Dissodinium lunula* (Bhovichitra and Swift, 1977). Dark uptake has also been observed in natural populations (e.g., Dugdale and Goering, 1967; MacIsaac and Dugdale, 1972). In the laboratory studies cited above, V_D/V_L ranged from 0.4 to 1.0 for NH$_4$ and 0.3 to 0.9 for NO$_3$. The field experiments of Dugdale and Goering (1967) yielded V_D/V_L values for NH$_4$ and

NO_3 of 0.2 and 0.1 in temperate waters and 0.6 and 0.3 in tropical waters. Working in a dinoflagellate/diatom-dominated upwelling region off Baja California, Nelson and Conway (unpubl. ms.) found mean values of 0.5 and 0.2 for the V_D/V_L rations of NH_4 and NO_3 uptake, respectively. In contrast to the field results of Dugdale and Goering (1967), Nelson and Conway (1979) and Nelson and Conway (unpubl. ms.), our V_D/V_L values for NO_3 were comparable to those of NH_4. Also the V_D/V_L values for NO_3 showed less light dependence than was observed in the field studies cited above. Harrison (1976) has shown that N-starvation enhances the uptake of NO_3 by *Gonyaulax polyhedra* to a greater degree in the dark than in the light. However the difference in the V_D/V_L ratios between the inshore and shelf break communities could not be explained by a gradient in N deficiency since there was no significant difference in ambient DIN concentration between the two areas (see below).

Another indication of reduced light dependence for DIN utilization by the inshore communities is the ratio of uptake rates in the light for phytoplankton taken from the 50% and 0.1% light depths (Table 1). The ratios were not significantly different (*t*-test at 95% confidence level) for NH_4 versus NO_3 uptake; therefore the ratios were pooled for the inshore stations and also for the shelf break stations and resulted in mean values with 95% confidence limits of 0.7 ± 0.3 (n = 6) and 4.4 ± 2.2 (n = 9), respectively. These ratios show that the inshore uptake rate potential at the 0.1% light depth was greater than that at the 50% light depth; however, the opposite was true at the shelf break.

The thermocline was shallower than the 1% light depth during the first part of the cruise (stations 7, 16, 17, 21, 26), but it was deeper during the middle and latter parts (stations 49, 62, 66, 82, 86, 91). From the combined data of all productivity stations, we observed no significant differences between the depth of the thermocline and the 1% light depth (*t*-test at 95% confidence level) and there was no trend in the data as far as inshore vs. shelf break stations were concerned. Therefore, the depth of physical mixing in relation to the lower boundaries of the euphotic zone cannot be used to explain the differences in light dependency between the inshore and shelf-break communities.

An important factor influencing the reduced light dependence of DIN utilization by the inshore *C. tripos* community was the location of the majority of the community in the disphotic zone. Based on chlorophyll *a* values, ~80% of the total inshore *C. tripos* community was found at depths >25 m. This community did not undergo vertical migration and chlorophyll *a*/particulate carbon ratios indicate that they were shade adapted (W. Esaisas, unpubl. ms.). The results of the low-light experiment at station 77 tend to support the idea of shade adaptation, e.g., it indicated a high potential for DIN utilization and only marginal light limitation, even at 0.2% of the surface intensity (Fig. 3).

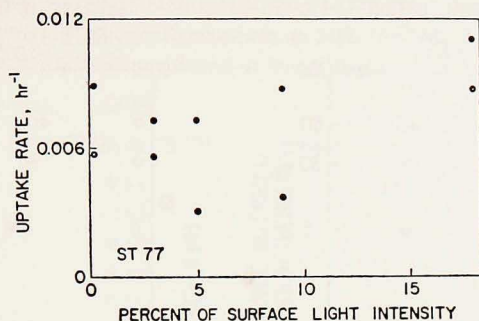If *in situ* growth is responsible for the cencentrated populations at depth, then

Figure 3. The uptake rates of NH_4 (●) and NO_3 (○) as a function of the percent of surface light intensity for the *C. tripos*-dominated community at 31 m (chlorophyll maximum layer).

one possible advantage associated with the location of the inshore *C. tripos* community in the disphotic zone is that it may derive essential trace elements and organic compounds from adjacent sediments (Iwasaki, 1973; Honjo, 1974; Maclean, 1977). Also the higher ambient DIN concentration at depth (Fig. 2) may favor the phytoplankton located there by providing more DIN for growth than could be obtained in the euphotic zone. Alternately, some advective mechanism may have played a role in the high concentrations of cells observed at depth.

Representative depth profiles of V_{NH_4} and V_{NO_3}, together with the ambient concentrations of NH_4 and NO_3, are shown for the inshore and shelf break regions in Figure 4. In general, the inshore communities exhibited less light-dependent DIN utilization than the phytoplankton at the shelf break; e.g., the DIN utilization rate at the 1% light depth inshore was comparable to the rates measured at the 100 and 50% light depths. However at the shelf break the uptake rate at the 1% light depth was substantially lower than the surface values.

The biological transport of NH_4 into the phytoplankton communities was greater than NO_3 at all stations taken (Table 2). The integrated value of T_N was 0.7 mmol $N \cdot m^{-2}h^{-1}$ and NH_4 utilization accounted for 68% of the total (e.g., %-$NH_4 = \rho NH_4 \cdot 100/T_N$). There was no significant difference (*t*-test at 95% confidence level) between the mean T_N value inshore vs. at the shelf break; however there was a significant difference (*t*-test at 95% confidence level) between the dependency on NH_4 (%-NH_4) inshore (59%) vs. at the shelf break (70%). The values of T_N (~0.7 mmol $N \cdot m^{-2}h^{-1}$) and %-NH_4 (68%) were similar to those observed during dinoflagellate domination in an upwelling area off Baja California, Mexico (Conway and Harmon, unpubl. ms.). However, during diatom domination off Baja California, values of 2.8 mmol $N \cdot m^{-2}h^{-1}$ and 35% were observed for T_N and %-NH_4 (Conway and Harmon, unpubl. ms.), in contrast to the values of ~0.9 mmol $N \cdot m^{-2}h^{-1}$ and 75% that were observed at the diatom-dominated, shelf-break stations (16, 17) in our study. Mean nitrate concentrations in the euphotic zone at the shelf break
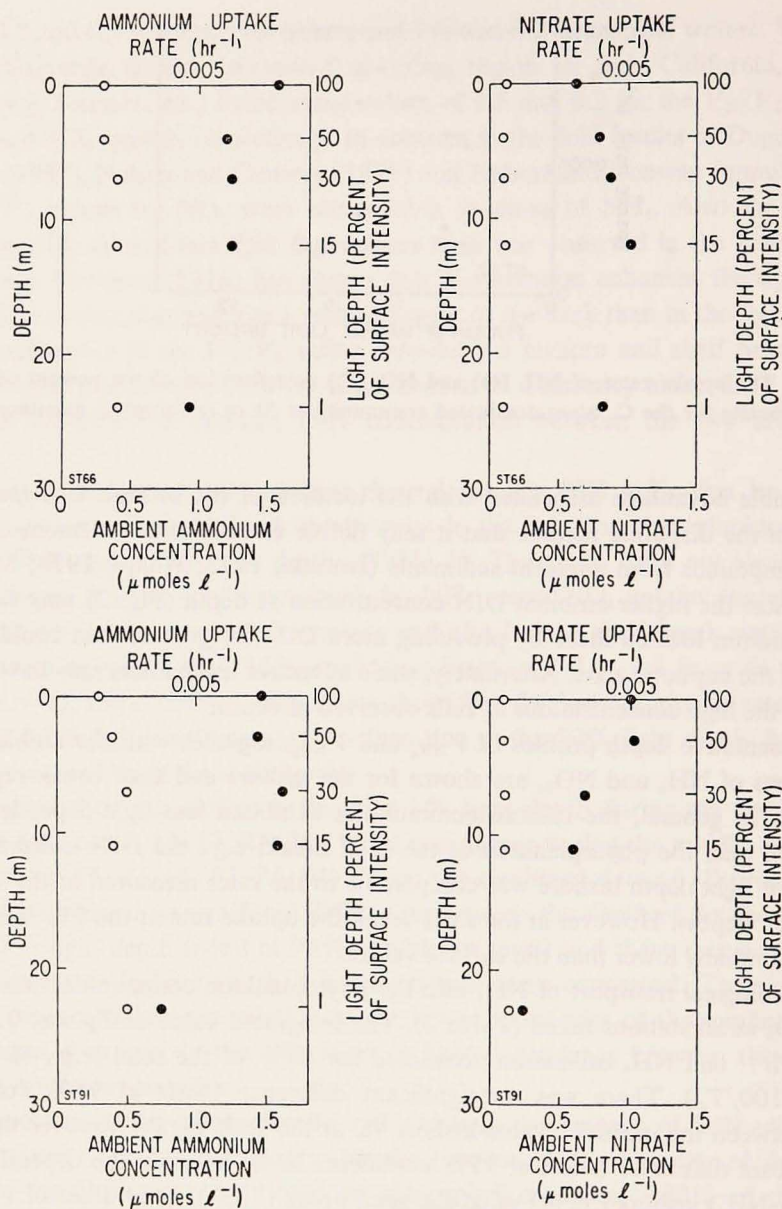
Figure 4. Representative depth profiles of the uptake rates of NH_4 and NO_3 (●), together with their respective concentrations (○), at stations 66 and 91.

off Long Island were approximately 10 percent of those off Baja California and this may have diminished the uptake potential of the diatom communities in the bight, while it had little effect on the *C. tripos* communities. Other ^{15}N studies, mostly located in the Pacific Ocean and the Mediterranean Sea, yielded values of either

Table 2. The biological transport of NH_4 (ρNH_4) and NO_3 (ρNO_3), integrated over the euphotic zone, and the corresponding percent dependence on NH_4 ($\%$-NH_4). The mean values and corresponding 95% confidence limits are found at the bottom of each column.

Station	ρNH_4 (mmol NH_4 $m^{-2}h^{-1}$)	ρNO_3 (mmol NO_3 $m^{-2}h^{-1}$)	$\%$-$_{NH_4}$*
7	0.51	0.15	77
16	0.65	0.22	75
17	0.62	0.22	74
21	0.44	0.22	66
26	0.36	0.13	73
49	0.34	0.24	59
62	0.42	0.23	64
66	0.52	0.42	55
82	0.28	0.16	61
86	0.75	0.31	70
91	0.56	0.22	71
	0.50 ± 0.10	0.23 ± 0.05	68 ± 5

* $\%$-$NH_4 = \rho NH_4 \cdot 100/T_N$.

V_{NH_4} as a percentage of $V_{NH_4} + V_{NO_3}$ or ρNH_4 as a percentage of T_N, that ranged from 50 to 100% (Dugdale and Goering, 1967; MacIsaac and Dugdale, 1972; Eppley *et al.*, 1973; Hattori and Wada, 1974). The strong dependence on NH_4 for primary production is a manifestation of the preferential utilization of NH_4 over NO_3 by marine phytoplankton, a preference that has been documented in numerous studies (e.g., Eppley *et al.*, 1969; Strickland *et al.*, 1969; MacIsaac and Dugdale, 1972; Conway, 1977; McCarthy *et al.*, 1977).

b. *Cross-shelf distribution of NH_4 and NO_3.* The $NO_3 + NO_2$ concentration was generally very low in the upper 20 m with a mean value, $\pm 95\%$ confidence limits, of 0.12 ± 0.02 μmol L^{-1}. In the offshore region higher NO_3 concentrations were found within 15 m of the surface but the upper layer always exhibited low concentrations (Fig. 2a). The upward displacement of the NO_3 isopleths at the seaward end of the section may have been the result of increased mixing at the shelf break, similar to that discussed by Gordon *et al.* (1976). Onshore flow along the bottom resulted in increased NO_3 concentrations in the bottom waters at the shelf break and inshore stations (Walsh *et al.*, 1979). However, no noticeable increase in NO_3 concentration was observed in the euphotic zone on any of the five cross-shelf transects, suggesting that the NO_3 input may have been utilized by the *C. tripos* communities residing at depth.

In the cross-shelf distribution, the NH_4 concentration was ~3 times higher than NO_3 in the upper 20 m with a mean concentration, $\pm 95\%$ confidence limits, of 0.37 ± 0.03 μmol L^{-1}. Elevated NH_4 concentrations were measured in bottom waters from midshelf to the shelf break. These observations indicate that shelf-water

NH_4 may originate in the sediments, as suggested by Rowe and Smith (1977), as well as from pelagic zooplankton and bacterial populations. In the offshore region there was a slight increase in the NH_4 concentration that corresponded to increased NO_3 concentrations (Fig. 2b). This increase in NH_4 was probably due to increased zooplankton abundance in that area (see below).

Integrated NH_4 and NO_3 concentrations were determined for the top 20-30 m at 59 inshore stations and for 37 shelf break and offshore stations. Inshore, the mean values, ±95% confidence limits, for NH_4 and NO_3 were 11.81 ± 1.30 mmol m^{-2} and 2.51 ± 0.33 mmol m^{-2}. At the shelf break (and offshore) they were 10.05 ± 1.00 mmol m^{-2} and 3.73 ± 0.66 mmol m^{-2}. The surface waters, therefore, contained 3 (shelf break) to 5 (inshore) times more NH_4 than NO_3, which in turn resulted in a greater utilization of NH_4 by the phytoplankton communities (Table 2).

c. Biological regeneration of NH_4. Zooplankton species and abundance were determined on a cross-shelf transect using 60 cm bongo nets with a 223 μm mesh, Wirick (pers. commun.). The inshore zooplankton at station 103 was sparse, with a mean dry weight of 1.0 g m^{-2} in a 50 m water column. At midshelf, the numbers of copepods and pteropods increased markedly and near the shelf break at station 98, copepods were by far the largest component with a mean biomass of 7.6 g dry wt m^{-2} in a 65 m water column. These values are representative of the zooplankton biomass across the shelf. Some contamination of *C. tripos* was evident in the bongo samples but serious contamination was probably not a problem because the highest zooplankton biomass was obtained offshore where the relative concentration of *C. tripos* was the lowest. The greater zooplankton biomass at the shelf break (~8 times), compared to the inshore region, corresponded to an increased utilization of NH_4 by phytoplankton. The estimated NH_4 regeneration rates of the inshore and shelf break zooplankton are 0.6 and 6.4 mmol N • m^{-2}d^{-1}, respectively (excretion rates were calculated using the values of Smith and Whitledge (1976) and corrected for the lower temperatures observed off Long Island). The observed NH_4 utilization rates were 7.7 inshore and 10.3 mmol N • m^{-2}d^{-1} at the shelf break (values corrected for diurnal changes in N utilization rates based on 6-h vs. 24-h observations); therefore, the zooplankton were contributing about 8% of the daily regenerated production inshore and 62% at the shelf break. This relatively large input at the shelf break was the result of a higher biomass of small zooplankton, which in turn have higher NH_4 excretion rates. The greater biomass and greater excretion rates (~120% larger) resulted in an estimated regeneration rate at the shelf break which is an order of magnitude larger than inshore. In the inshore water, benthic regeneration could provide an additional NH_4 input of about 1.6 mmol N • m^{-2}d^{-1}, as estimated from sediment fluxes (Rowe *et al.*, 1975). The bacterioplankton conversion of amino N into NH_4 could possibly add another 0.65 to 1.85 mmol N • m^{-2}d^{-1} (Barvenik, pers. commun.). The combined inshore NH_4 input from pelagic regenera-

tion and benthic processes ranges from 2.9 to 4.1 mmol $m^{-2}d^{-1}$ which is 38 to 53% of the phytoplankton utilization potential.

Additional unmeasured sources of regenerated NH_4 are microzooplankton (<223 μm), fish, and other grazers too fast to be captured by the zooplankton net. Therefore, the regeneration rates presented are probably minimal estimates. Similarly, the maximal uptake rates that were measured in this study using saturating substrate concentrations may be overestimates of the *in situ* utilization of NH_4 by the phytoplankton communities. In any event, the rates involving sources and sinks of DIN presented in this paper should be considered as estimates which may be substantiated or revised as a result of additional studies in this area.

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