YALE
PEABODY
MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research,* one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.

This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
https://creativecommons.org/licenses/by-nc-sa/4.0/

Journal of Marine Research, 48, 641–660, 1990

Nitrogen recycling in coastal waters of southeastern U.S. during summer 1986

by R. B. Hanson[1], C. Y. Robertson[1], J. A. Yoder[1,2], P. G. Verity[1] and S. S. Bishop[1]

ABSTRACT

Summer-time pelagic nitrogen recycling using an $^{15}NH_4^+$ tracer technique was studied for important biological pathways, sinks, and residence times in the microbial food web of coastal Georgia, U.S.A. Results showed that estimated rates of NH_4^+ regeneration by a variety of microheterotrophs and microzooplankton balanced rates of NH_4^+ assimilation by the microbial community, i.e., phytoplankton, bacteria and other microheterotrophs, in surface waters. In bottom water below the 1% light level, NH_4^+ regeneration exceeded community NH_4^+ assimilation by 3.5 times. However, over a period of 2 weeks, high NH_4^+ concentrations rarely occurred in bottom waters, and this was attributed to rapid mixing of the water column by winds and tides. Estimated mixing times from time-dependent numerical models were on the order of NH_4^+ turnover times of 5 to 10 hours. Overall, rates of community NH_4^+ assimilation exceeded rate estimates of phytoplankton N demand by 1.8 to 2.7 fold, which were made from rates of $^{14}CO_2$ incorporation into proteins. In bottom samples where phytoplankton were light limited, rates of NH_4^+ assimilation exceeded the phytoplankton N demand by 3.6 to 11.1 fold. Calculations concerning the role of dissolved organic nitrogen in N cycling suggest that only 10% is recycled to NH_4^+ daily. This N could support 12 to 29% of the estimated phytoplankton N demand. Residence times of particulate nitrogen pools, based on rates of NH_4^+ regeneration, were on the order of 3–10 days. During summer-time hydrographic conditions and despite other losses, particulate nitrogen could recycle as often as 100 times before autumn removal processes occur off southeastern U.S.

1. Introduction

Coastal waters off the southeastern U.S. receive inputs of particulate matter and nutrients from eight major rivers and salt-marshes (Dunstan and Atkinson, 1976; Haines, 1979; Imberger *et al.,* 1983; Dame *et al.,* 1986; Whiting *et al.,* 1987). Other studies have shown decreasing gradients of particulate and dissolved organic material, plankton production and biomass with distance offshore (cf. Remsen *et al.,* 1972; Gardner and Stephens, 1978; Turner, 1981; Yoder *et al.,* 1981; Hanson and Robertson, 1988). Estimates of net total nitrogen (NH_4^+, NO_3^-, NO_2^-, PON, DON) exported from these estuaries to coastal waters are of the order of 40 g N/m^2 of salt

1. Skidaway Institute of Oceanography, P. O. Box 13687, Savannah, Georgia, 31416, U.S.A.
2. Present address: Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, 02882, U.S.A.

marsh-estuarine surface area per year (Kjerfve and McKellar, 1989; Whiting *et al.*, 1987). This rate, when combined with an estimate of total southeastern U.S. salt marsh area, implies a total N flux representing only 17% of the N required to support the annual productivity of inner shelf waters (0–20 m isobaths) (Yoder, 1985). More than 90% of this "new" N exported to coastal waters is either DON or PON (Bishop *et al.*, 1984; Dame *et al.*, 1986), which are sources of N generally not readily available to phytoplankton. Nitrogen sources which are readily available to support phytoplankton production (e.g., NO_3^-, NO_2^-, NH_4^+, urea and other low molecular weight organic compounds) account for far less than 10% of the coastal phytoplankton N requirement. The results of these previous studies lead to the obvious hypothesis that N recycling is a key process affecting plankton dynamics. These calculations are obviously rough approximations of potential nitrogen sources for coastal phytoplankton. However, they demonstrate our lack of general understanding of time-space scales of nitrogen sources and availability, nitrogen uptake and regeneration, and autotrophic and microheterotrophic interactions in the microbial food web off southeastern U.S.

Coastal pelagic ecosystems support high year-round productivity because of their proximity to anthropogenic inputs of "new" nutrients, to recycled nutrients from shelf sediments, to upwelling of nutrient-rich oceanic water, and to internal recycling of nitrogen within pelagic-benthic food webs. It is often accepted that marine food webs are nitrogen-limited without rigorous proof of nitrogen limitation at all organizational levels (Hecky and Kilham, 1988). Therefore, a better understanding of phytoplankton production in coastal ecosystems requires information on biogeochemical pathways, sinks and residence times of various nitrogen species. Our objective in this study was to examine phytoplankton and microheterotrophic assimilation of regenerated NH_4^+ during a period when growth rates and biomass of both functional groups are at seasonally high levels. The relationships among measured biological pathways, pools of organic and inorganic nitrogen, and biomasses of functional groups provided some information on important rate processes within each functional group, phytoplankton nitrogen limitation, organic nitrogen availability, and the residence times of various nitrogen species off southeastern U.S.

2. Methods

a. Study sites. Over a two week period in July 1986, the magnitude of nitrogen (NH_4^+) assimilation and regeneration in phytoplankton and microbial communities was examined in estuarine and coastal waters of Georgia, U.S.A. (Fig. 1). An estuarine station (#3) was chosen at the mouth of Wassaw Sound and a coastal station (#7) at the 10 meter isobath off Wassaw Island, 5–10 km inshore of the coastal frontal zone (Blanton *et al.*, 1984). Water samples from 1 meter below the surface and 1 meter above the bottom were collected with 5-liter Niskin Bottles from the R/V *Blue Fin.*

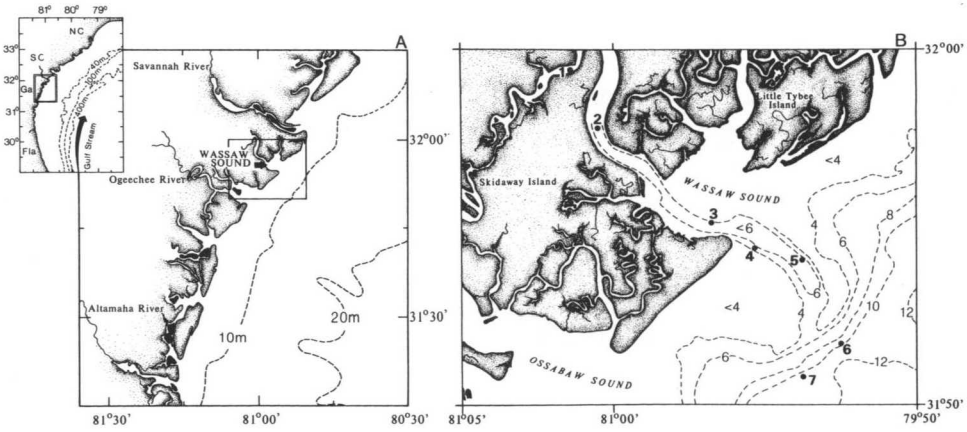

Figure 1. Location of study area on the southeastern U.S. coastline and sample sites in the waters of Wassaw Sound and coastal waters of Wassaw Island.

b. Nutrient and biomass measurements. Dissolved inorganic and organic nitrogen were analyzed after water samples were filtered through combusted (450°C for 2 hours), glass-fiber filters (Whatman GF/F). The filters were retained for particulate analyses (below). Filtered water was dispensed in acid-cleaned polypropylene bottles. Samples for dissolved NH_4^+ were fixed with a phenol-ethanol solution on ship and refrigerated until analyzed the next day (Solorzano, 1969). Ammonia samples were taken immediately before and after tracers were added to each experimental bottle and again at the termination of the experiment. Samples for total dissolved nitrogen were stored frozen until analyzed by the persulfate oxidation method (Solorzano and Sharp, 1980). Nitrate was undetectable in nearly every sample analyzed. NH_4^+ and nitrate were analyzed using a Technicon Auto Analyzer II, with precision of 0.03 and 0.1 μmoles/l, respectively.

Particulate matter on glass-fiber filters was analyzed for C and N, chlorophyll *a* and ATP. Particulate C and N on oven-dried (60°C) filters were determined with a Perkin-Elmer 240 C elemental analyzer. The coefficient of variation (C. V.) averaged 4% for a known carbon and nitrogen standard. Filters for chlorophyll *a* analysis were prepared as described by Strickland and Parsons (1972), wrapped in aluminum foil, and stored frozen at −20°C until analyzed. Chlorophyll *a* (Chl *a*) and chlorophyll *a* + phaeopigments (Chl *a* + pheo) were determined (C. V. = 10–15%) with a Turner Designs fluorometer using the fluorometric method of Yentsch and Menzel, (1963). Chlorophyll *a* fluorescence, near-surface temperature and salinity were continuously measured from water pumped from a depth of about 1 meter along the transect. Fluorescence measurements were converted to estimates of Chl *a* + pheo concentrations by comparing fluorescence with Chl *a* + pheo extracted (see above) from water samples collected every 30 minutes along the transect. Samples for ATP analysis were immediately extracted in boiling Tris buffer at pH 7.8 (Sutcliffe *et al.*, 1976). Extracts

were stored frozen at −20°C, and ATP concentrations were determined (C.V. = 5–10%) with a Chem Glow Photometer. Water samples were also preserved with 0.2 micron filtered, 10% formaldehyde (saturated with carbonate chips), and bacteria were counted (C.V. = 4–7%) according to Hobbie *et al.* (1977).

c. Rate measurements for primary production. For measurements of phytoplankton primary production and rate of protein synthesis, water samples were dispensed into 250-ml polycarbonate bottles that were previously acid-cleaned. Duplicate bottles were spiked with 5 μCi of ^{14}C-bicarbonate (Amersham) and incubated in deck incubators. Neutral density screens were used to simulate irradiance levels at the 50% isolume for incubation of near-surface samples or the 1% isolume for incubations of near-bottom samples.

Following incubation periods of 4 hours, the acid bubbling method was used to prepare production samples for liquid scintillation counting (Wessels and Birnbaum, 1979). The method of DiTullio and Laws (1983) was used to measure ^{14}C incorporation into proteins. From the same incubation bottles used for primary production measurements, 25-ml subsamples were filtered onto 25 mm Whatman GF/F glass-fiber filters and processed according to the TCA extraction procedure (DiTullio and Laws, 1983).

d. Rate measurements for NH_4^+ recycling. Estimates of NH_4^+ assimilation and regeneration were made following $^{15}NH_4^+$ tracer procedures described earlier (Hanson and Robertson, 1988). Briefly, water samples were spiked with 0.05 μmoles/L $^{15}NH_4^+$ (99% atom enrichment) in 21 acid-cleaned polycarbonate bottles. Incubation conditions were the same as described above for the measurement of primary production. Water samples (500 ml) for $^{15}N/^{14}N$ analysis and concentration determination of dissolved NH_4^+ and particulate N were collected at time 0 and 2 hours. Particulate nitrogen samples were filtered onto Whatman GF/F glass-fiber filters, rinsed with filtered seawater using a separate filtration manifold, dried at 90°C, and stored under vacuum. To facilitate $^{15}NH_4^+$ distillation, filtrates were spiked with NH_4Cl (10 μmoles) and 5 ml NaOH-borate solution, and 100 ml of distillate was collected in acid. Distillates were evaporated on Whatman 934 AH filters and stored under vacuum. All ^{15}N filters were ground with Cuprox plus platinum catalyst, placed in discharge tubes with CaO, evacuated to <4 microns of Hg, and sealed with a torch. Tubes were combusted at 500°C and later analyzed for $^{15}N/^{14}N$ on a Jasco NIA-1 emission spectrometer (Fiedler and Proksch, 1975). The analytical model of Laws (1985) was used to estimate NH_4^+ recycling rates. Laws' (1985) model provides an estimate of NH_4^+ regeneration (R) and distinguishes actual NH_4^+ assimilation (A) into PN from NH_4^+ uptake (U), which simply reflects the loss of NH_4^+ from the dissolved pool and ignores alternate pathways. R:A ratios were calculated for each sample and provide an

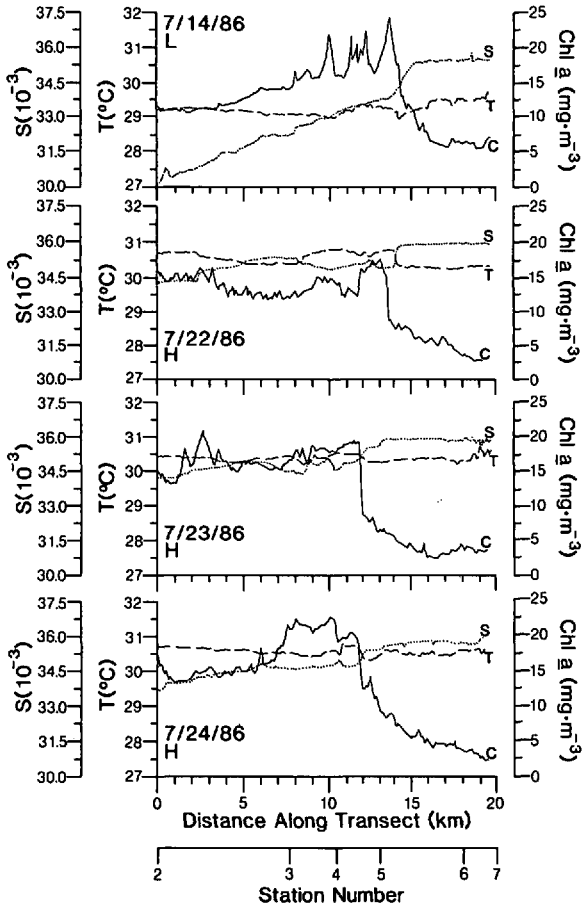

Figure 2. Near-surface distributions of salinity (S), temperature (T) and chlorophyll *a* (C) from stations 2–7 (see Fig. 1) on 4 different dates and tides (high, H; low, L) during the study period of July 1986.

estimate of the NH_4^+ balance. In addition, Laws' (1985) model provides an estimate of the net assimilation rate of N species other than NH_4^+ (a). We felt this model would yield realistic estimates of nitrogen transformation rates.

3. Results

a. Physical setting. Figure 2 shows the distribution of surface temperature, salinity and Chl *a* + pheo along 4 transects (3 at high tide and 1 at low tide) extending through Wassaw Sound and out to the 10 meter isobath (see Fig. 1). Rates of plankton processes were measured at station 3, located within the estuary containing high phytoplankton biomass and particulate matter, and station 7, located in coastal waters characterized by lower phytoplankton and particulate matter concentrations. A salin-

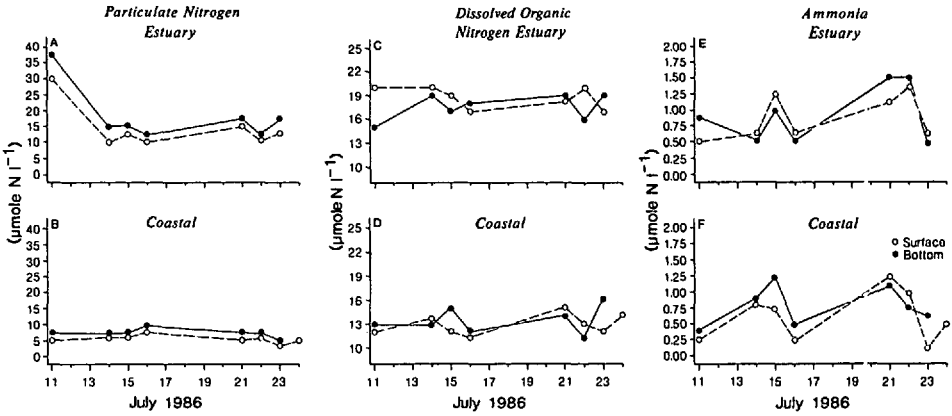

Figure 3. Particulate nitrogen (A and B), dissolved organic nitrogen (C and D), and ammonia (E and F) concentrations in waters of Wassaw Sound and coastal waters off Wassaw Island, Georgia, July 1986.

ity front which defined the boundary between estuarine and coastal waters, fluctuated around station 5 (Fig. 2) (Bishop *et al.*, 1980; Yoder, 1985).

Subsurface irradiance was measured on days when rates of plankton processes were determined. At station 3, the 1% irradiance level ranged between 2.5–6.0 meters and averaged 4.1 meters (n = 7). At station 7, the 1% irradiance level ranged between 7–10 meters and averaged 8.3 meters (n = 6).

b. Nitrogen and carbon distribution. Particulate nitrogen (PN) concentrations in the estuary were slightly, but not significantly, higher in bottom waters than in surface waters (Fig. 3, Table 1). In coastal waters, PN was higher in near-bottom waters; however, concentrations were only 40% of those measured in the estuary. Likewise, coastal dissolved organic nitrogen and ammonia were 73 and 75%, respectively, of that measured in the estuary (Table 1).

Particulate carbon (PC) concentrations showed site distribution patterns similar to those of PN (Fig. 4; Table 2). The C:N ratio of 8–9:1 for particulate matter suggests a mixture of nonliving and living carbon (assuming biological carbon has C:N close to the Redfield ratio of 6.6:1). All estimates of biomass were highest in the estuary; however, only PC and Chl *a* concentrations were significantly different between sites ($P < 0.001$; Table 2). Correlation analysis showed that estimates of biomass correlated significantly ($P < 0.01$) with PN and PC in surface and bottom waters (Chl *a*, $r = 0.72$ and 0.72; ATP, $r = 0.61$ and 0.81). Bacteria were not correlated with estimates of biomass, particulate nitrogen or particulate carbon.

c. Ammonia assimilation and regeneration. Rates of $^{15}NH_4^+$ assimilation by surface and bottom plankton showed significant differences between sites (Fig. 5). Excluding a bottom sample collected on 11 July with a PN concentration of 38 μmoles N l^{-1} and a

Table 1. Concentrations of particulate nitrogen, dissolved organic nitrogen, NH_4^+, and particulate molar C:N ratios in southeastern U.S. coastal surface and bottom waters during July 1986. All values are expressed as means ± standard error (S.E.), and overall averages are given for each site. Letter pairs indicate mean values that are significantly different: A, $P < 0.10$; B, $P < 0.05$; C, $P < 0.01$; D, $P < 0.001$.

A. Estuarine Water

	Particulate Nitrogen (μmoles/l)	Dissolved Organic Nitrogen (μmoles/l)	Ammonia (μmoles/l)	Particulate Carbon:Nitrogen Ratio (molar)
Surface	14.65 ± 2.56 B	18.77 ± 0.59	0.93 ± 0.17	8.03 ± 0.37
Bottom	18.33 ± 3.50 B	17.44 ± 0.60	0.88 ± 0.14	9.19 ± 0.71
Average	16.49 ± 2.14 D	18.11 ± 0.44 D	0.91 ± 0.11	8.61 ± 0.42

B. Coastal Water

Surface	5.87 ± 0.40 B	13.04 ± 0.42	0.62 ± 0.15	9.46 ± 0.73
Bottom	7.50 ± 0.64 B	13.56 ± 0.66	0.77 ± 0.11	8.10 ± 0.63
Average	6.63 ± 0.41 D	13.28 ± 0.37 D	0.69 ± 0.09	8.83 ± 0.50

calculated rate of 2.01 μmoles N $l^{-1}h^{-1}$ (not plotted), NH_4^+ assimilation ranged between 0.011 and 0.169 μmoles N $l^{-1}h^{-1}$ (Fig. 5). The median rate was 0.0985 μmoles N $l^{-1}h^{-1}$. Significant differences between surface and bottom rates were only found in coastal waters (Table 3, *t*-Test, $P < 0.05$). Overall, NH_4^+ assimilation was not correlated ($r = 0.19$, $P > 0.1$) with photosynthesis in surface waters. In bottom waters, NH_4^+ assimilation correlated with ATP ($r = 0.84$, $P < 0.002$), PC ($r = 0.85$, $P < 0.001$), and Chl *a* ($r = 0.68$, $P < 0.02$) concentrations.

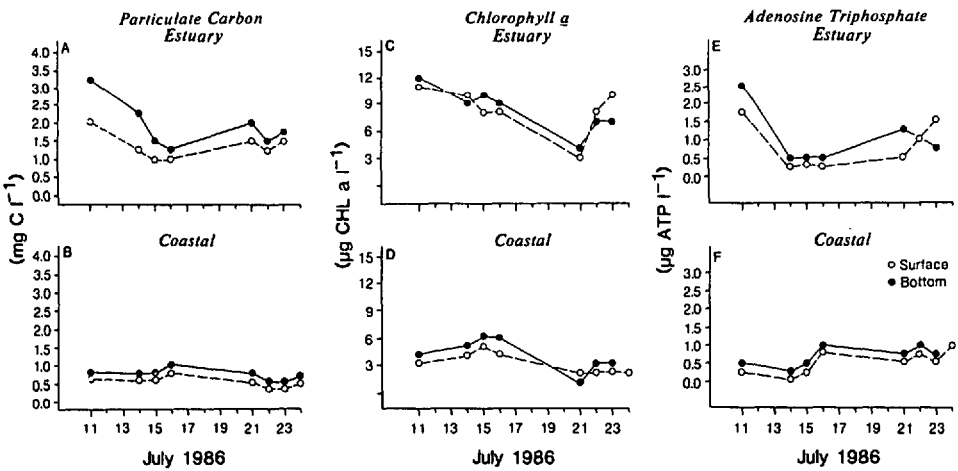

Figure 4. Particulate carbon (A and B), chlorophyll *a* (C and D) and ATP (E and F) concentrations in waters of Wassaw Sound and coastal waters off Wassaw Island, Georgia, July 1986.

Table 2. Mean and standard error (S.E.) of particulate carbon, chlorophyll *a*, adenosine triphosphate, and bacteria for surface and bottom waters, and overall average (mean ± S.E.) at each site, July 1986. Letter pairs indicate mean values that are significantly different as in Table 1.

	Particulate Carbon (mg/l)	Chlorophyll *a* (μg/l)	Adenosine Triphosphate (μg/l)	Bacteria (10^9/l)
A. Estuarine Water				
Surface	1.34 ± 0.139 A	8.13 ± 0.94	0.85 ± 0.21	3.25 ± 0.85
Bottom	1.93 ± 0.264	8.30 ± 1.02	1.01 ± 0.34	3.15 ± 0.36
Average	1.63 ± 0.164 D	8.21 ± 0.67 D	0.93 ± 0.19	3.20 ± 0.41
B. Coastal Water				
Surface	0.65 ± 0.049 A	3.01 ± 0.42	0.64 ± 0.12	2.52 ± 0.32
Bottom	0.71 ± 0.060	3.98 ± 0.62	0.68 ± 0.11	2.39 ± 0.86
Average	0.68 ± 0.038 D	3.46 ± 0.37 D	0.66 ± 0.08	2.45 ± 0.41

Regeneration rates of NH_4^+ in the estuary were significantly ($P < 0.01$) faster by 2 fold than rates measured in coastal waters (Fig. 5). Rates measured near the surface waters were similar to rates measured near the bottom at either site (Fig. 5, Table 3). Overall, rates of NH_4^+ regeneration correlated with dissolved organic nitrogen

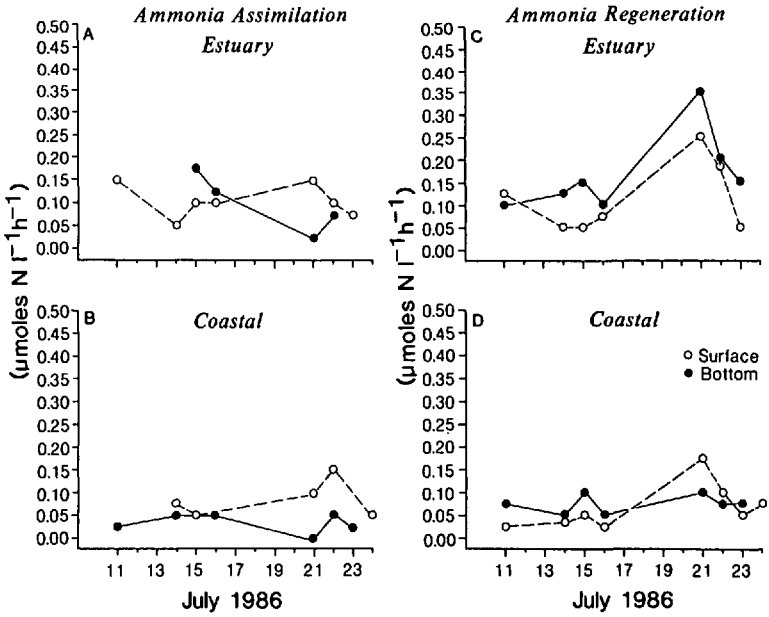

Figure 5. Assimilation (A and B) and regeneration (C and D) of NH_4^+ (N-15) in waters of Wassaw Sound and coastal waters off Wassaw Island, Georgia, July 1986.

Table 3. Mean and standard error (S.E.) of NH_4^+ assimilation (A), and regeneration (R), assimilation of other nitrogen species (a), NH_4^+ turnover times, and R:A ratios for surface and bottom waters, and overall average value (mean ± S.E.) at each site, July 1986. Each mean R:A ratio was calculated from the R:A ratio of each sample. Letter pairs indicate mean values that are significantly different as in Table 1.

A. Estuarine Water

	Ammonia Assimiliation (μmoles/l)	Ammonia Regeneration (μmoles N/l/h)	Assimiliation of other Nitrogen Species (μmoles/N/l/h)	Ammonia Turnover Time (h)	R:A Ratio
Surface	0.100 ± 0.015	0.115 ± 0.030	0.009 ± 0.025	9.62 ± 1.52 B	1.12 ± 0.22
Bottom	0.481 ± 0.383	0.164 ± 0.033	−0.305 ± 0.408	5.73 ± 0.63 B	3.44 ± 2.40
Average	0.259 ± 0.160	0.139 ± 0.023 C	−0.122 ± 0.166	7.67 ± 0.96	2.08 ± 1.00
B. Coastal Water					
Surface	0.084 ± 0.017 B	0.073 ± 0.018	0.012 ± 0.023	8.72 ± 1.34	1.18 ± 0.22
Bottom	0.036 ± 0.010 B	0.073 ± 0.008	0.034 ± 0.017	10.90 ± 1.32	3.55 ± 1.40
Average	0.058 ± 0.012	0.073 ± 0.0010 C	0.024 ± 0.014	9.74 ± 0.96	2.48 ± 0.82

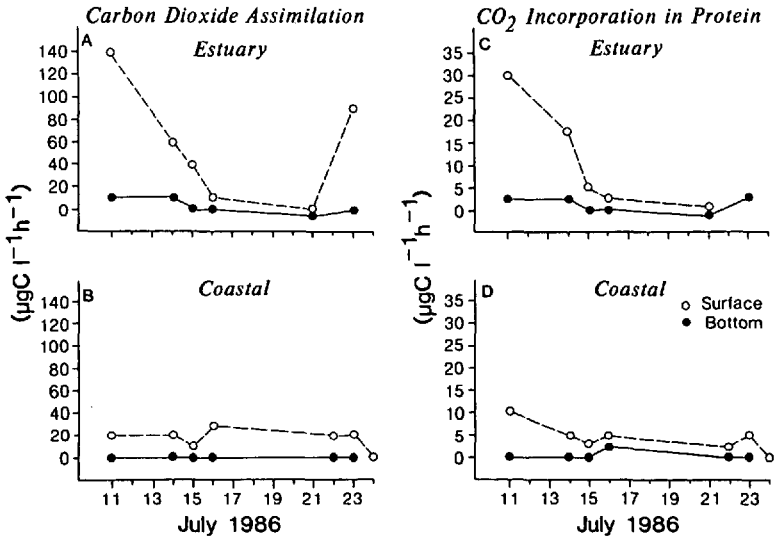

Figure 6. Autotrophic uptake of $^{14}CO_2$ (A and B) and incorporation into proteins (C and D) in waters of Wassaw Sound and coastal waters off Wassaw Island, Georgia, July 1986.

($r = 0.51$, $P < 0.005$), particulate carbon ($r = 0.38$, $P < 0.04$) and particulate nitrogen ($r = 0.32$, $P < 0.1$) concentrations. Estuarine estimates of NH_4^+ regeneration did not correlate with DON concentrations ($r = 0.16$, $P > 0.5$), whereas coastal rates of regeneration did correlate with DON ($r = 0.73$, $P < 0.001$). The model parameter for the assimilation or excretion of alternative nitrogen species (a) showed that there was no major alternative source or loss of nitrogen in the estuarine. Rates of NH_4^+ regeneration balanced NH_4^+ assimilation by surface plankton in both estuary and coastal waters. Calculated NH_4^+ regeneration to assimilation (R:A) ratios suggest that rates were nearly balanced (1.06:1) for surface waters, but uncoupled (3.5 ± 1.9: 1) in bottom waters (Table 3).

d. Carbon dioxide assimilation and incorporation into proteins. Rates of surface $^{14}CO_2$ uptake and incorporation into proteins showed significant site differences (Fig. 6; Table 4). Highest rates occurred in the estuary, but varied by a factor of 7 over the study period. In bottom waters, rates were significantly ($P < 0.05$) reduced at the 1% light level (Table 4). Although the mean rates in bottom waters at both sites were low (Table 4), rates were significantly greater than zero (univariate analysis, $P < 0.01$). Surface rates of CO_2 uptake were significantly ($P < 0.05$) correlated with particulate carbon ($r = 0.81$ and 0.95) and nitrogen ($r = 0.0.83$ and 0.94), Chl *a* ($r = 0.0.79$ and 0.77), and ATP ($r = 0.69$ and 0.78) concentrations.

Highest rates of $^{14}CO_2$ incorporation into proteins also occurred in estuarine waters (Fig. 6). Incorporation rates into proteins by surface and bottom plankton were highly correlated with $^{14}CO_2$ uptake ($r = 0.82$ and 0.95, $P < 0.001$), even though rates were

Table 4. Mean and standard error (S.E.) of CO_2 assimilation and incorporation into proteins, percent incorporation in proteins, and estimated C:N assimilation ratio for surface and bottom waters, and overall average value (mean ± S.E.) at each site, July 1986. Letter pairs indicate mean values that are significantly different as in Table 1.

	$^{14}CO_2$ Assimilation (μg C/l/h)	$^{14}CO_2$ Incorporation In Proteins (μg C/l/h)	Incorporation In Proteins (%)	C:N Assimilation Ratio (Molar)
A. Estuarine Water				
Surface	57.18 ± 20.52 C	10.43 ± 4.83	19.94 ± 3.69 D	31.40 ± 11.95 A
Bottom	4.96 ± 1.31 C	1.98 ± 0.42	41.94 ± 2.95 D	8.04 ± 0.55 A
Average	33.45 ± 13.52 A	6.59 ± 2.86	29.94 ± 4.16	20.79 ± 7.25
B. Coastal Water				
Surface	17.23 ± 3.04 D	4.27 ± 1.23 B	24.09 ± 4.49 B	19.17 ± 5.74
Bottom	1.83 ± 0.38 D	0.80 ± 0.23 B	42.22 ± 7.40 B	9.23 ± 1.75
Average	10.12 ± 2.72 A	2.67 ± 0.82	32.46 ± 4.77	14.58 ± 3.39

significantly suppressed due to little or no photosynthesis in bottom waters. The percent of $^{14}CO_2$ incorporated into proteins to total $^{14}CO_2$ uptake by surface plankton was 19.9 to 24.1%, while the range for bottom plankton (dark) was 41.9 to 42.2% (Table 4). The percent incorporation was not significantly different ($P > 0.1$) between sites (Table 1).

Nitrogen balance between phytoplankton and other community microheterotrophs can be evaluated by comparing phytoplankton N demand as described above and community N demand as estimated from $^{15}NH_4^+$ assimilation. Table 5 shows that the rates of community NH_4^+ assimilation (A) exceeded estimates of phytoplankton N demand by 1.8 to 2.7 times in surface waters, while in bottom samples rates of community NH_4^+ assimilation exceeded estimates of phytoplankton N demand at low light by 3.6 to 11.1 times. Similar calculations were also made for regeneration, and the

Table 5. Comparison of phytoplankton nitrogen demand (Pt, estimated from $^{14}CO_2$ incorporation into proteins), community NH_4^+ assimilation (A), and NH_4^+ regeneration (R) for surface and bottom waters, and overall average value (mean ± S.E.) at each site during July 1986.

	A/Pt	R/Pt
A. Estuarine Water		
Surface	1.81 ± 0.92	2.22 ± 1.50
Bottom	11.07 ± 6.20	2.92 ± 0.64
Average	4.89 ± 2.44	2.54 ± 0.84
B. Coastal Water		
Surface	2.67 ± 1.20	1.58 ± 0.80
Bottom	3.57 ± 2.05	5.83 ± 2.42
Average	3.17 ± 1.20	3.54 ± 1.29

results show that NH_4^+ regeneration exceeded phytoplankton N demand by 1.6 to 2.3 surface waters while in bottom waters regeneration exceeded estimates of phytoplankton N demand by 2.5 to 3.5.

4. Discussion

a. Mass balance of the $^{15}NH_4^+$ tracer technique. Dugdale and Wilkerson (1986) identified several analytical and experimental problems associated with ^{15}N-tracer techniques which limit the interpretation of field results. Most often, problems occur with samples collected from low-nutrient oceanic regions. However, even in nitrate-rich coastal bays and upwelling systems, several researchers have reported problems in obtaining ^{15}N mass balance (Gilbert *et al.*, 1982; Laws, 1984; Kokkinakis and Wheeler, 1987). Likewise, Hanson and Robertson (1988) found 1.5 times more $^{15}NH_4^+$ left the dissolved phase [uptake (U)] than was recovered in particulate components [assimilated (A)] in organic-rich waters off southeastern U.S. In this study ^{15}N balanced well within the estuary (1.06:1), but in coastal waters a large imbalance occurred (4.05:1). This imbalance was well within the range of 1.5 to 20:1 reported by others (Glibert *et al.*, 1982; Laws, 1984; Kokkinakis and Wheeler, 1987, Hanson and Robertson, 1988).

Many environmental and biological conditions have been identified for the ^{15}N mass imbalance (cf. Dugdale and Wilkerson, 1986). The results noted here and elsewhere suggest that nitrification and/or excretion of labeled dissolved organic nitrogen by phytoplankton or "sloppy grazing" by zooplankton influence mass balance. These possibilities, including small particles or organisms passing through filters, may have a significant effect on the loss of ^{15}N mass from the particulate nitrogen and dissolved nitrogen pools. If so, the ^{15}N-tracer technique may underestimate NH_4^+ assimilation and/or overestimate NH_4^+ regeneration. Laws' (1985) analytical nitrogen model includes a parameter for excretion or assimilation of other alternative nitrogen species (a) in the particulate nitrogen pool. Our results show that within analytical error of the technique, there was little or no release of labeled dissolved organic nitrogen during the assay. Anticipating the possibility of biological ^{15}N recycling, we kept the incubation periods as short as possible (2 h). Nevertheless, nitrification on hourly time scales may be important in the nitrogen metabolism of southeastern coastal waters (Whiting *et al.*, 1987). In Delaware Bay, nitrification has been identified as a major mechanism of NH_4^+ removal from the NH_4^+pool (Lipschultz *et al.*, 1986).

b. Assimilation and regeneration of NH_4^+. Many studies on regeneration and assimilation of NH_4^+ have shown that these processes are well balanced in most marine systems (Harrison, 1978; Caperon *et al.*, 1979; Glibert *et al.*, 1982; Harrison *et al.*, 1983). During this summer-time study, rates of regeneration also balanced the rates of assimilation in near-surface waters, and rates of regeneration in bottom water equaled regeneration rates measured in near-surface waters. However, when bottom samples

were collected below the 1% light level, regeneration exceeded assimilation by a factor of 3.5:1. These results suggest that ammonium assimilation by photoautotrophs can be uncoupled from heterotrophic regeneration in near-bottom waters. Such conditions probably occur whenever surface waters mix below the 1% light as well as after sunset (i.e., diel periodicity, Caperon *et al.*, 1979). Unfortunately, bottom samples were neither incubated in full sunlight (or surface samples incubated in the dark) nor taken after sunset. Although not at all examined here, it appears that the ratio between NH_4^+ regeneration and assimilation can potentially vary over a wide continuum of spatial-temporal scales in turbid southeastern coastal waters. As an example, in stratified waters of Chesapeake Bay, summer phytoplankton production was a consequence of nitrogen recycling during the previous spring (Malone *et al.*, 1988).

Although rates of NH_4^+ regeneration exceeded assimilation in bottom samples with an increase in NH_4^+ concentrations during the incubation, natural ammonium concentrations in bottom waters were not significantly different from those measured in surface waters. A simple explanation is that the water column was unstratified and presumably well-mixed during July, a theory also supported by similar concentrations of materials in surface and bottom waters and a time-dependent, mixing model for coastal Georgia (Blanton *et al.*, 1989). The turnover times for ammonium, derived from NH_4^+ concentrations and rates of NH_4^+ regeneration (Table 3), ranged from 5 to 10 hours and were on the time scale of tides. The response time of coastal waters to mixing, which is under control by local wind stress/direction, water depth and currents, also varies on the scale of 6 to 24 hours. Therefore, with summer plankton and nutrients continually mixing throughout the water column, a relatively constant NH_4^+ concentration can be maintained near bottom waters.

c. Assimilation balance of phytoplankton carbon and nitrogen synthesis. Laboratory cultures of phytoplankton growing under optimal conditions usually assimilate carbon and nitrogen close to the Redfield ratio of 6.63:1 by atom for marine organic matter. When rate processes of natural phytoplankton vary greatly from the Redfield ratio, nutrient limitation and unbalanced growth are usually discussed as possible causes (Goldman *et al.*, 1979). To assess summer-time C:N assimilation ratios and nitrogen demand of southeastern phytoplankton, the DiTullio and Laws (1983) procedure was used. The estimates of phytoplankton N demand are considered rough because it is assumed that the C:N ratio of phytoplankton protein is close to 3.33:1 by weight and 85% of phytoplankton N is protein N under nitrogen limitation (DiTullio and Laws, 1983, 1986). For example, previous C:N measurements of phytoplankton protein have shown that the ratio varies from about 3.1 to more than 30.1 with incubation time, nitrogen sources, shading, and light intensity (Fisher *et al.*, 1982; Laws *et al.*, 1985; Carpenter and Dunham, 1985; Paasche, 1988). However, the method works best when ambient inorganic N concentrations are low, which is characteristic of Georgia coastal waters.

Based on our experiments, summer-time phytoplankton assimilated carbon and nitrogen at a relative rate of 19 to 31:1 while in near-bottom samples relative rates ranged from 5 to 11:1. Large C:N assimilation ratios such as these are expected when phytoplankton cycle continually between high and low light conditions by synthesizing carbon and assimilating nitrogen when conditions permit (Eppley, 1981; Wheeler *et al.*, 1983; Cuhel *et al.*, 1984; DiTullio and Laws, 1986). Ratios greater than 10:1 may indicate nitrogen limitation during the incubation period. Therefore, if the DiTullio and Laws (1983) procedure accurately measures C and N assimilation by phytoplankton, then our results suggest that southeastern phytoplankton experience uncoupled rate processes and are possibly nitrogen limited in surface waters.

d. Nitrogen demand of phytoplankton and other microbes. Community NH_4^+ assimilation (A) is a conservative estimate of the community N demand as not only is NH_4^+ a major nitrogen source for both phytoplankton, bacteria, and other microheterotrophs (Wheeler and Kirchman, 1986; Goldman *et al.*, 1987), but bacteria and other microheterotrophs can use other combined nitrogen sources with dissolved-free amino acids being preferred over combined amino acids (Hollibaugh and Azam, 1983; Kirchman and Hodson, 1984). We suggest that a strong heterotrophic N demand exists in southeastern waters. Other estimates of the southeastern U.S. coastal ecosystem have also shown that pelagic community metabolism favors net heterotrophic respiration of organic matter over autotrophic production of organic matter (Hopkinson, 1985; Hopkinson *et al.*, 1989; Pomeroy and Wiebe, 1988; Griffith *et al.*, 1990).

e. Residence times of particulate and dissolved organic matter. In coastal southeastern U.S. waters, particulate material includes utilizable and refractory organic matter and living plankton. Based on estimates of phytoplankton and community biomass, nonliving organic matter accounts for most (70 to 85%) of the particulate matter in Georgia waters, calculated assuming 50 μg C/μg Chl *a* (Malone *et al.*, 1983) and 250 μg C/μg ATP (Sutcliffe *et al.*, 1976). The residence times of particulate matter can be calculated in terms of particulate mass divided by the sum of the production rate minus removal rate (Eppley *et al.*, 1983), although the source term is dominated by both phytoplankton and microheterotrophic production.

We calculated residence times of POC from rates of phytoplankton and community C production. Estimates of community C production were based on the mean rate of NH_4^+ assimilation (Table 3) and a Redfield C:N ratio of 6.6:1. Rates of carbon removal were estimated from NH_4^+ regeneration. Our estimates of community C production most likely error conservatively because other sources of particulate and dissolved organic nitrogen are known to contribute to heterotrophic growth. Thus, we caution strict interpretation of these estimates of residence time. The results are given in Table 6 with residence times of particulate carbon ranging from 1 to 31 days and

Table 6. Mean, minimum and maximum residence times (days) of particulate carbon and nitrogen in southeastern U.S. waters during July 1986. Estimates based on rates of carbon and nitrogen production (Pd) calculated from phytoplankton CO_2 uptake and community NH_4^+ assimilation, and rates of removal (Rv) calculated from NH_4^+ regeneration. Phytoplankton carbon estimated using 50 μg C/μg Chl *a* (Malone *et al.*, 1983) and microbial carbon estimated using 250 μg C/μg ATP (Sutcliffe *et al.*, 1976). Biomass and rates expressed in terms of carbon (C) and nitrogen (N) assuming a Redfield C:N ratio of 6.63:1.

	Phytoplankton		Microbes	
	Carbon $(Pd\text{-}Rv)_c$	Nitrogen $(Pd\text{-}Rv)_n$	Carbon $(Pd\text{-}Rv)_c$	Nitrogen $(Pd\text{-}Rv)_n$
MEAN	3.8	67.7	10.0	7.9
MIN	1.2	3.7	1.0	1.0
MAX	26.2	90.8	31.0	22.7

with mean residence times of 3.8 days and 10 days for phytoplankton and microbial biomass, respectively.

Residence times of particulate nitrogen can also be calculated based on community NH_4^+ assimilation. Calculated residence time for particulate nitrogen was 7.9 days, similar to residence time of particulate carbon. Again, this is probably a conservative estimate of residence time in southeastern waters. However, if nitrogen production is based on phytoplankton N demand, the mean residence time for particulate nitrogen was 67.7 days (Table 6). Thus, heterotrophic processes may account for a large fraction of community N production and recycling rates.

It has been shown previously that biogenic matter, e.g., fecal pellets from small salps and doliolids, disintegrate in 2 to 4 days, leaving behind the more recalcitrant matter (Pomeroy and Deibel, 1980; Pomeroy *et al.*, 1984). Residence time of this matter, possibly a lignocellulose component in fecal pellets, is probably much more than 2–4 days. Furthermore, respiratory rates of southeastern microheterotrophs confirm the short residence times (days) of the organic matter produced along this coast (Hopkinson *et al.*, 1989; Griffith *et al.*, 1990).

Most dissolved organic nitrogen (DON) in marine systems appears to be resistant to mineralization and unavailable to phytoplankton (Thomas *et al.*, 1971; Gardner and Stephens, 1978; Bishop *et al.*, 1984), although this may not be true for oceanic systems (Jackson and Williams, 1985). Usually, labile components of the dissolved nitrogen pool represent only 5–20% of DON, and the turnover times of these components are often as short as a few hours (Keller *et al.*, 1982; Wright, 1984; Wheeler and Kirchman, 1986). Isotope tracer models for ^{15}N recycling in microplankton communities also suggest some involvement of the DON pool in nitrogen cycling (Laws, 1984). Our results were inconclusive. Recently, LaRoche and Harrison (1987) developed several models using empirical data to support the possible involvement of the DON pool in which particulate nitrogen and DON pools can exchange nitrogen through the intermediate NH_4^+ pool. We can evaluate the significance of the DON pool in

southeastern waters if we assume that DON is the sole source of NH_4^+, and the labile components of the DON pool are recycled as rapidly as NH_4^+. We can also estimate the labile DON fraction and determine whether this fraction meets the nitrogen demand for the phytoplankton and the microheterotrophic community.

From our calculations, only 5.5% ± 0.5% of the DON pool could be recycled on the same time scale of NH_4^+, or about 10% of the DON is recycled daily to meet the daily nitrogen demand of coastal phytoplankton and microheterotrophs. If we assume a balanced daily C:N assimilation ratio of 6.6:1 for phytoplankton, 12 to 29% of the phytoplankton N demand can be met by labile DON. However, if A/Pt >2, which indicates a net heterotrophic N demand, then this agrees with empirical data that show an insignificant fraction of the DON is transferred to southeastern coastal phytoplankton (Bishop *et al.*, 1984). Although Jackson and Williams (1985) suggest that labile DON is an important source of nitrogen for oceanic phytoplankton, this does not seem to be the case in southeastern coastal waters. Thus, microheterotrophs in coastal Georgia waters not only dominate metabolic processes but apparently act as a nutrient sink (Pomeroy and Wiebe, 1988; Griffith *et al.*, 1990) until materials are recycled by bacteria and grazing protozoans (Sherr and Sherr, 1987; Sherr *et al.*, 1988; Verity *et al.*, 1988).

f. Ecological significance. The results presented here add to our understanding of nitrogen flux and recycling in southeastern U.S. coastal waters. Summer-time nitrogen recycling was controlled by microheterotrophs, which effectively competed with phytoplankton for low concentrations of inorganic nitrogen. We believe that bacteria are likely to be important and that they may account for 50% (surface waters) to 90% (bottom waters) of the ammonia uptake in our study (see Harrison *et al.*, 1983). Some results have shown that bacteria prefer to assimilate ammonia even when concentrations of dissolved organic nitrogen are sufficient to meet the nitrogen demand of bacteria in the southeastern estuarine waters (Wheeler and Kirchman, 1986). Thus, bacteria are usually strong competitors of phytoplankton for available ammonia nitrogen under most nutrient conditions. However, depending on the nitrogen content of dissolved organic matter, which is often nitrogen deficient and refractory (see below), bacteria may either retain the essential nitrogen from labile organic compounds when C:N ratios of organic compounds are high or regenerate nitrogen as possibly ammonia when C:N ratios are low (Goldman *et al.*, 1987). In terms of carbon, however, the conversion of detrital carbon to biomass is usually low (see Pomeroy *et al.*, 1984; Ducklow *et al.*, 1986; Pomeroy and Wiebe, 1988). These latter conclusions agree with the high rates of oxygen consumption by microbes in these waters (Hopkinson *et al.*, 1989; Griffith *et al.*, 1990).

The circulation of shelf waters near the southeastern U.S. coastline is generally alongshore toward Cape Hatteras in the spring or Cape Canaveral in the summer-autumn (Blanton *et al.*, 1984). Due to highly seasonal wind regimes (Atkinson *et al.*,

1983; Blanton *et al.*, 1984; Blanton *et al.*, 1989), the rate of alongshore advection of coastal waters is variable, averaging <1 km/day in the summer to 5 km/day in the spring and autumn (Blanton, pers. comm.). It is suspected that southeastern spring blooms are transported off the North Carolina shelf. However, during this summer study, coastal microbial communities had the potential to consume and recycle organic matter and detritus up to 100 times during its southerly transit to the Florida shelf.

Acknowledgments. We wish to express our appreciation to the U.S. Department of Energy, which supported this work through Grants DE-FG09-85ER60311 and DE-AS09-76EV00936. We thank Dr. Jack O. Blanton for comments on residence times of coastal waters. Kris Schindler performed the nutrient chemistry and microbial biomass analyses. Suzanne McIntosh drafted the illustrations and Linda Land typed the manuscript.

REFERENCES

Atkinson, L. P., T. N. Lee, J. O. Blanton and W. S. Chandler. 1983. Climatology of the southeastern United States continental shelf waters. J. Geophys. Res., *88,* 4705–4718.

Bishop, S. S., K. A. Emmanuele and J. A. Yoder. 1984. Nutrient limitation of phytoplankton growth in Georgia nearshore waters. Estuaries, *7,* 506–512.

Bishop, S. S., J. A. Yoder and G. -A. Paffenhofer. 1980. Phytoplankton and nutrient variability along a cross-shelf transect off Savannah, Georgia, U.S.A. Est. Coastal Shelf Sci, *11,* 359–368.

Blanton, J. O., L. -Y. Oey, J. Amft and T. N. Lee. 1989. Advection of momentum and buoyancy in a coastal frontal zone. J. Phys. Oceanogr., *19,* 98–115.

Blanton, J. O., J. A. Yoder, L. P. Atkinson, T. N. Lee, C. R. McClain, D. W. Menzel, G. -A. Paffenhofer, L. J. Pietrafesa, L. R. Pomeroy and H. L. Windom. 1984. A multidisciplinary oceanography program on the southeastern U.S. continental shelf. EOS, *65,* 1202–1203.

Caperon, J., D. Schell, J. Hirota and E. Laws. 1979. Ammonium excretion rates in Kaneohe Bay, Hawaii measured by a N-15 isotope dilution technique. Mar. Biol., *54,* 33–40.

Carpenter, E. J. and S. Dunham. 1985. Nitrogenous nutrient uptake, primary production, and species composition of phytoplankton in the Carmans River estuary, Long Island, New York. Limnol. Oceanogr., *30,* 513–526.

Cuhel, R. L., P. B. Ortner and D. R. S. Leon. 1984. Night synthesis of protein by algae. Limnol. Oceanogr. *29,* 731–744.

Dame, R., T. Chrzanowski, K. Bildstein, B. Kjerfve, H. McKellar, D. Nelson, J. Spurrier, S. Stancyk, H. Stevenson, J. Vernberg and R. Zingmark. 1986. The outwelling hypothesis and North Inlet, South Carolina. Mar. Ecol. Prog. Ser. *33,* 217–229.

DiTullio, G. R. and E. A. Laws. 1983. Estimates of phytoplankton N uptake based on $^{14}CO_2$ incorporation into protein. Limnol. Oceanogr, *28,* 177–185.

—— 1986. Diel periodicity of nitrogen and carbon assimilation in five species of marine phytoplankton: accuracy of methodology for predicting N- assimilation rates and N/C composition ratios. Mar. Ecol. Prog. Ser., *32,* 123–132.

Ducklow, H. W., D. A. Purdie, P. J. leB. Williams and J. M. Davies. 1986. Bacteroplankton: a sink for carbon in a coastal marine plankton community. Science, *232,* 865–867.

Dugdale, R. C. and F. P. Wilkerson. 1986. The use of ^{15}N to measure nitrogen uptake in eutrophic oceans; experimental considerations. Limnol. Oceanogr., *31,* 673–689.

Dunstan, W. M. and L. P. Atkinson. 1976. Sources of new nitrogen for the South Atlantic Bight, *in* Estuarine Processes, M. Wiley, ed. Vol. 1. Academic Press, NY, 69–78.

Eppley, R. W. 1981. Relations between nutrient assimilation and growth in phytoplankton with a brief review of estimates of growth rate in the ocean. Can. Bull. Fish. Aquat. Sci., *210,* 251–263.

Eppley, R. W., E. H. Renger and P. R. Betzer. 1983. The residence time of particulate organic carbon in the surface layer of the ocean. Deep-Sea Res., *30,* 311–323.

Fiedler, R. and G. Proksch. 1975. The determination of nitrogen-15 by emission and mass spectrometry in biochemical analysis: A review. Anal. Chim. Acta, *78,* 1–62.

Fisher, T. R., P. R. Carlson and R. T. Barber. 1982. Carbon and nitrogen primary productivity in three North Carolina estuaries. Est. Coast. Shelf Sci., *15,* 621–644.

Gardner, W. S. and J. A. Stephens. 1978. Stability and composition of terrestrially derived dissolved organic nitrogen in continental shelf waters. Mar. Chem., *6,* 335–342.

Glibert, P. M., F. Lipschultz, J. J. McCarthy and M. A. Altabet. 1982. Isotopic dilution models of uptake and remineralization of ammonium by marine plankton. Limnol. Oceanogr., *27,* 639–650.

Goldman, J. C., D. A. Caron and M. R. Dennett. 1987. Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C:N ratio. Limnol. Oceanogr., *32,* 1239–1252.

Goldman, J. C., J. J. McCarthy and D. G. Peavey. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature, *279,* 210–215.

Griffith, P. C., L. R. Pomeroy, S. C. Wainwright and P. Verity. 1990. Community respiration and the fate of organic matter in the waters of the South Atlantic Bight, Limnol. Oceanogr., (submitted).

Haines, E. B. 1979. Nitrogen pools in Georgia coastal waters. Estuaries, *2,* 34–39.

Hanson, R. B. and C. Y. Robertson; 1988. Spring recycling of ammonium in turbid continental shelf waters off southeastern United States. Cont. Shelf Res. *8,* 49–68.

Harrison, W. G. 1978. Experimental measurements of nitrogen remineralization in coastal waters. Limnol. Oceanogr., *23,* 658–694.

Harrison, W. G., D. Douglas, P. Falkowski, G. Rowe and J. Vidal. 1983. Summer nutrient dynamics of the Middle Atlantic Bight: nitrogen uptake and regeneration. J. Plankton Res, *5,* 539–556.

Hecky, R. E., and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limnol. Oceanogr., *33,* 796–822.

Hobbie, J. E., R. J. Daley and S. Jasper. 1977. A method for counting bacteria on Nuclepore filters. Appl. Environ. Microbial., *33,* 1225–1228.

Hollibaugh, J. T. and F. Azam. 1983. Microbial degradation of dissolved proteins in seawater. Limnol. Oceanogr., *28* 1104–1116.

Hopkinson, C. S., Jr. 1985. Shallow-water benthic and pelagic metabolism: evidence of heterotrophy in the nearshore Georgia Bight. Mar. Biol., *87,* 19–32.

Hopkinson, C. S., Jr., B. F. Sherr, and W. J. Wiebe. 1989. Size fractionated metabolism of coastal microbial plankton. Mar. Ecol. Prog. Ser., *51,* 155–166.

Imberger, J., T. Berman, R. R. Christian, E. B. Sherr, D. E. Whitney, L. R. Pomeroy, R. G. Wiegert and W. J. Wiebe, 1983. The influence of water motion on the distribution and transport of materials in a salt marsh estuary. Limnol. Oceanogr., *28,* 201–214.

Jackson, G. A. and P. M. Williams. 1985. Importance of dissolved organic nitrogen and phosphorus to biological nutrient cycling. Deep-Sea Res., *32,* 223–235.

Keller, M. D., R. M. Mague, M. Badenhausen and H. E. Glover. 1982. Seasonal variations in the production and consumption of amino acids by coastal microplankton. Est. Coast. Mar. Sci., *15*, 301–315.

Kirchman, D. and R. E. Hodson. 1984. Inhibition by peptides of amino acid uptake by bacterial populations in natural waters: Implications for the regulation of amino acid transport and incorporation. Appl. Environ. Microbiol., *47*, 624–631.

Kjerfve, B. and H. N. McKellar, Jr. 1980. Times series measurements of estuarine material fluxes, *in* Estuarine Perspectives, V. S. Kennedy, ed. Academic Press, 341–358.

Kokkinakis, S. A. and P. A. Wheeler. 1987. Nitrogen uptake and phytoplankton growth in coastal upwelling regions. Limnol. Oceanogr., *32*, 1112–1123.

LaRoche, J. and W. G. Harrison. 1987. Compartmental models of nitrogen cycling in tropical and temperate marine environments. Mar. Ecol. Prog. Ser., *38*, 137–149.

Laws, E. A. 1984. Isotope dilution models and the mystery of the vanishing ^{15}N. Limnol. Oceanogr., *29*, 379–386.

—— 1985. Analytic models of NH_4^+ uptake and regeneration experiments. Limnol. Oceanogr., *30*, 1340–1350.

Laws, E. A., W. G. Harrison and G. R. DiTullio. 1985. A comparison of nitrogen assimilation rates based on ^{15}N uptake and autotrophic protein synthesis. Deep-Sea Res., *32*, 85–95.

Lipshultz, F., S. C. Wofsy and L. E. Fox. 1986. Nitrogen metabolism of the eutrophic Delaware River ecosystem. Limnol. Oceanogr., *31*, 701–716.

Malone, T. C., L. H. Crocker, S. E. Pike and B. W. Wendler. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. Mar. Ecol. Prog. Ser., *48*, 235–249.

Malone, T. C., T. S. Hopkins, P. G. Falkowski and T. E. Whitledge. 1983. Production and transport of phytoplankton biomass over the continental shelf of the New York Bight. Cont. Shelf Res., *1*, 305–337.

Paasche, E. 1988. Pelagic primary production in nearshore waters, *in* Nitrogen Cycling in Coastal Marine Environments, T. H. Blackburn and J. Sorensen, eds., SCOPE. John Wiley and Sons, Ltd., 33–57.

Pomeroy, L. R. and D. Deibel. 1980. Aggregation of organic matter by pelagic tunicates. Limnol. Oceanogr., *25*, 643–652.

Pomeroy, L. R., R. B. Hanson, P. A. McGillivary, B. F. Sherr, D. Kirchman and D. Deibel. 1984. Microbiology and chemistry of fecal products of pelagic tunicates: rates and fates. Bull. Mar. Sci., *35*, 426–439.

Pomeroy L. R. and W. J. Wiebe. 1988. Energetics of microbial food webs. Hydrobiologia, *159*, 7–18.

Redfield, A. C., B. H. Ketchum and F. A. Richards. 1963. The influence of organisms on the composition of seawater, *in* The Sea, Vol. 2. M.N. Hill, ed., Wiley-Interscience, NY, 26–77.

Remsen, C. C., E. J. Carpenter and B. W. Schroeder. 1972. Competition for urea among estuarine microorganisms. Ecology, *53*, 921–926.

Sherr, E. B. and B. F. Sherr. 1987. High rates of consumption of bacteria by pelagic ciliates. Nature, *325*, 710–711.

Sherr, B. F., E. B. Sherr and C. S. Hopkinson. 1988. Trophic interactions within pelagic microbial communities: Indications of feedback regulation of carbon flow. Hydrobiologia, *159*, 19–26.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenol hypochlorite method. Limnol. Oceanogr., *14*, 799–801.

Solorzano, L. and J. H. Sharp. 1980. Determination of total dissolved nitrogen in natural waters. Limnol. and Oceanogr., *25,* 751–754.

Strickland, J. D. and T. R. Parsons. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Bd. Can. Bulletin 167 (2nd Edition).

Sutcliffe, Jr., W. H., E. A. Orr, and O. Holm-Hansen. 1976. Difficulties with ATP measurements in inshore waters. Limnol. Oceanogr., *21,* 145–149.

Thomas, W. H., E. H. Renger and A. N. Dodson. 1971. Near-surface organic nitrogen in the eastern Tropical Pacific Ocean. Deep-Sea Res., *18,* 65–71.

Turner, R. E. 1981. Plankton productivity and the distribution of fishes on the southeastern U.S. continental shelf. Science, *214,* 351–354.

Verity, P. G., D. B. Craven and S. S. Bishop. 1988. Seasonal studies of production and mortality of planktonic protists in the coastal waters of Georgia. EOS, *69,* 1086.

Wessels, C. and E. Birnbaum. 1979. An improved apparatus for use with the ^{14}C acid-bubbling method of measuring primary production. Limnol. Oceanogr., *24,* 187–188.

Wheeler, P. A., and D. L. Kirchman. 1986. Utilization of inorganic and organic nitrogen by bacteria in marine systems. Limnol. Oceanogr., *31,* 998–1009.

Wheeler, P. A., R. J. Olsen and S. W. Chisolm. 1983. Effects of photocycles and periodic ammonium supply on three marine phytoplankton species. II. Ammonium uptake and assimilation. J. Phycol., *19,* 528–533.

Whiting, G. J., H. N. McKellar, Jr., B. Kjerfve and J. D. Spurrier. 1987. Nitrogen exchange between a southeastern USA salt marsh ecosystem and the coastal ocean. Mar. Biol., *95,* 173–182.

Wright, R. T. 1984. Dynamics of pools of dissolved organic carbon, *in* Heterotrophic activity in the sea. J Hobbie and P. L. Williams, eds., Proc. of NATO ARI, Casais, Portugal, 1981. Plenum Publ. Co.

Yentsch, C. S. and D. Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res., *10,* 221–231.

Yoder, J. A. 1985. Environmental control of phytoplankton production on the southeastern U.S. continental shelf, *in* Oceanography of the Southeastern Continental Shelf, L. P. Atkinson, D. W. Menzel, and K. A. Bush, eds., AGU Press, Washington, 93–103.

Yoder, J. A., L. P. Atkinson, J. O. Blanton, D. R. Deibel, D. W. Menzel, G. -A. Paffenhofer. 1981. Plankton productivity and the distribution of fishes on the southeastern U.S. continental shelf. Science, *214,* 352–353.

Received: *13 April, 1989;* revised: *25 April, 1990.*