
Nitrogen dynamics in lower Narragansett Bay. II. Phytoplankton uptake, depletion rates of nitrogenous nutrient pools, and estimates of ecosystem remineralization

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Abstract. Phytoplankton nitrogen demand in lower Narragansett Bay, Rhode Island, measured during the winter–spring of 1977–78 and summers of 1978 and 1979, is compared with estimates of zooplankton and the benthic nitrogen remineralization drawn from the results of experimental field studies. Measured uptake rates would generally lead to the depletion of available nitrogenous nutrient stocks within hours, and usually exceeded estimates of benthic plus zooplankton remineralization. Additional estimates of nitrogen inputs from sewage and riverine sources appear insufficient to make up the difference. The discrepancy lends support to the paradigm that water column remineralization by microheterotrophs may supply much, if not most, of the nitrogen needs of coastal phytoplankton.

Introduction

The central role of nitrogen in the nutrient dynamics of marine phytoplankton communities is well recognized, if not fully understood. Standing stocks of nitrogenous nutrients in coastal (Ryther and Dunstan, 1971; McCarthy *et al.*, 1977) and oceanic waters (Eppley *et al.*, 1973; Eppley and Peterson, 1979) are usually insufficient to support observed primary production rates for more than brief periods. Particulate organic nitrogen (PON) and dissolved organic nitrogen (DON) must be continually mineralized and recycled to supply the ongoing nitrogen needs of growing phytoplankton communities (Eppley and Peterson, 1979; Jackson and Williams, 1985). Because surface inorganic nitrogenous nutrient concentrations generally remain low in spite of continuous input and remineralization, phytoplankton nitrogen demand must usually exceed nitrogen input and remineralization rate processes. Recognizing this, numerous investigations have been carried out to quantify nitrogen remineralization pathways in marine waters, including macrozooplankton (e.g. Harris, 1959; Martin, 1968; Ikeda, 1974; Szyper *et al.*, 1976; Kremer, 1977; Smith, 1978; Vargo, 1979) bacteria (e.g. Von Brand *et al.*, 1937; Harrison, 1978; Glibert, 1982; McCarthy *et al.*, 1984), microzooplankton (e.g. Caperon *et al.*, 1979; Harrison, 1980; Paasche and Kristiansen, 1982b; Glibert, 1982; Verity, 1985) and the benthos (e.g. Hargrave, 1973; Rowe *et al.*, 1975; Nixon, 1981; Fisher *et al.*, 1982; Officer *et al.*, 1982; Garber, 1984; Kelly and Nixon, 1984).

Smayda (1974) demonstrated that nitrogen is the principle nutrient limiting phytoplankton growth and standing crop in lower Narragansett Bay. Continuous culture bioassays have confirmed this (Goldman, 1976). Nixon and Pilson (1983) prepared an annual nitrogen

budget for Narragansett Bay, pointing out discrepancies between the magnitude of estimated annual phytoplankton nitrogen demand and available nitrogen from remineralization and terrestrial sources to meet this demand. Direct measurement of nitrogen uptake rates (Furnas *et al.*, 1976; Glibert and Goldman, 1981; Goldman *et al.*, 1981; Fisher *et al.*, 1981; Paasche and Kristiansen, 1982a; Glibert *et al.*, 1982b; Furnas, 1983) and indirect estimates of nitrogen depletion times extrapolated from ^{14}C uptake measurements (Durbin *et al.*, 1975) convincingly show that relevant time scales for nitrogen uptake by coastal phytoplankton populations can be hours or less.

Here, we present estimates of dissolved inorganic nitrogen turnover rates in lower Narragansett Bay and compare measured rates of nitrogen uptake by phytoplankton with local estimates of nitrogen remineralization and input. ^{15}N tracer measurements of nitrogen uptake (Furnas, 1983) are used to estimate *in situ* demand for ammonium, nitrate and urea. Functional relationships derived from a body of experimental studies carried out in Narragansett Bay over the last few years can be used to estimate instantaneous or seasonal remineralization by the benthos (Nixon *et al.*, 1976; Nixon, 1981), macrozooplankton (Vargo, 1976), tintinnids (Verity, 1985) and ctenophores (Kremer, 1977). Nixon and Pilson (1983) budgeted annual riverine, sewage and N-fixation inputs of nitrogen to Narragansett Bay. Experimental measurements of remineralization by microflagellates and bacteria have not been reported. Presumably, differences between *in situ* uptake, remineralization and N inputs will give a first-order estimate of the importance of these latter two groups.

Methods

Thirty ^{15}N -uptake experiments were conducted during the winter-spring of 1977-78 ($n=8$), the summer of 1978 ($n=9$) and the summer of 1979 ($n=13$). Ammonium, nitrate and urea uptake were measured in 22 experiments. Uptake of ammonium and either nitrate or urea was determined in the remaining eight. Details of the experimental and analytical procedures have been given previously (Furnas, 1983).

Depletion times for dissolved nitrogen stocks are calculated by dividing measured substrate concentrations ($[\text{N}] \mu\text{g-at l}^{-1}$) by the transport rate ($q_{\text{N}} \mu\text{g-at l}^{-1} \text{h}^{-1}$) for the nitrogen species. Depletion times are not true turnover rates, but the time required to fully take up a particular nitrogen species in the absence of remineralization or other inputs.

An estimate of benthic ammonium remineralization ($\text{ng-at l}^{-1} \text{h}^{-1}$), averaged over the 8-m water column, was calculated by the equation:

$$E_{(\text{benthos})} = 0.125 e^{0.16t_b} + 1.9$$

derived from (Nixon *et al.*, 1976) where t_b ($^{\circ}\text{C}$) is the bottom water temperature. Bottom water temperature was measured at the time of sample collection with a mercury thermometer. Benthic release of dissolved organic nitrogen (DON) is assumed to be 10% of the benthic ammonium release rate (Nixon, 1981).

Mixed community macrozooplankton (excluding ctenophores) ammonium excretion ($\text{ng-at l}^{-1} \text{h}^{-1}$) was calculated as a function of mean water column temperature (t_m) and macrozooplankton dry weight ($\mu\text{g l}^{-1}$) by the equation:

$$E_{(\text{macrozooplankton})} = 2.97 (\text{ZP dry wt}) (0.709t_m - 5.74)$$

(Vargo, 1976). Macrozooplankton samples for biomass determinations were collected by oblique tows with a flow meter equipped 0.25-m net (153- μm mesh). The samples were split once and half dried to constant weight at 60°C. Macrozooplankton release of DON (principally urea) is assumed to be half the ammonium excretion rate (Vargo, 1976).

Ctenophores were sampled by taking duplication bottom-to-surface hauls with a 1-m² net (1-mm mesh). The animals were sorted into size classes and counted in the field (Deason, 1982). Estimates of biomass and ammonium excretion by each size class were made according to Kremer (1977). DON release by ctenophores is assumed to be 53% of the ammonium excretion rate (Kremer, 1977).

Verity (1985) estimated annual nitrogen remineralization by tintinnids in lower Narragansett Bay to be 53 $\mu\text{g-at l}^{-1}$, $\geq 75\%$ of which occurs during the summer. As tintinnid abundances were not recorded during the study periods herein, first-order seasonal estimates of winter–spring and summer tintinnid N remineralization will be taken as 13.2 and 39.8 $\mu\text{g-at l}^{-1}$. These gross seasonal rates give average N input rates of 2.1 and 16.6 $\text{ng-at l}^{-1} \text{h}^{-1}$, respectively.

Nixon and Pilson (1983) estimated that 585×10^6 g-at of nitrogen enters Narragansett Bay each year from N-fixation, runoff, rivers and sewage. A seasonal breakdown was not given. Divided into the volume of the bay (2.56×10^{12} l, Kremer and Nixon, 1978), this yields a first-order estimate of input from these sources of 26.1 $\text{ng-at N l}^{-1} \text{h}^{-1}$.

Results

Figure 1 shows the observed seasonal changes in surface nitrogenous nutrient concentrations. Pre-spring bloom concentrations of nitrate + nitrite, ammonium and urea exceeded 15, 8.5 and 3.5 $\mu\text{g-at N l}^{-1}$, respectively. Dissolved nutrient stocks disappeared rapidly with the onset of the spring bloom. Following termination of the spring bloom, ammonium concentrations generally remaining $< 1 \mu\text{g-at l}^{-1}$. Through both summers, surface ammonium concentrations were generally $< 1 \mu\text{g-at l}^{-1}$. Late-spring nitrate levels were consistently low and usually undetectable. During summer, nitrate concentrations were generally below detection limits, but slight increases (ca. 1 $\mu\text{g-at l}^{-1}$) were observed each summer in early August, just prior to the inception of the late summer diatom bloom. Urea was detectable at low concentrations during the sum-

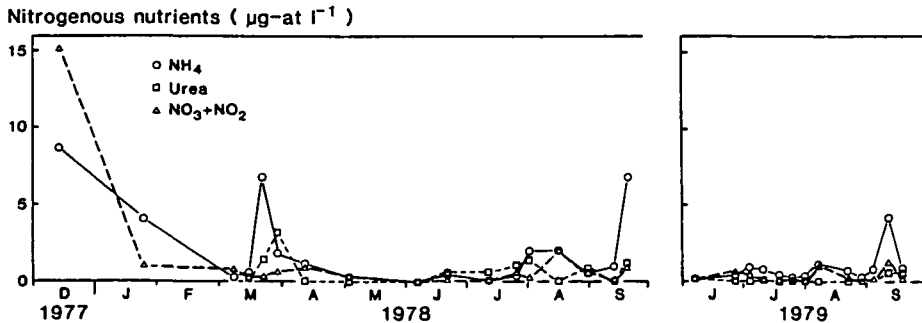


Fig. 1. Surface nitrogenous nutrient concentrations in lower Narragansett Bay.

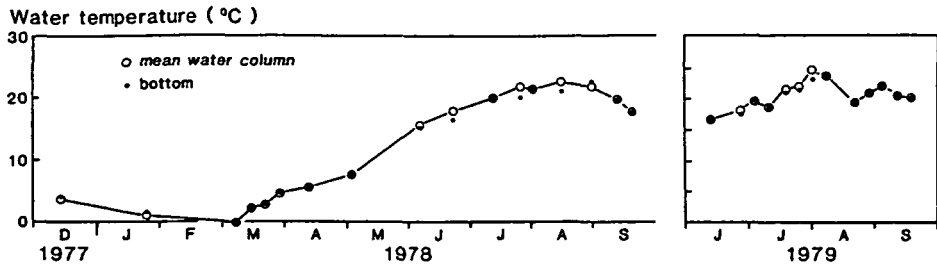


Fig. 2. Mean water column and bottom water temperatures in lower Narragansett Bay.

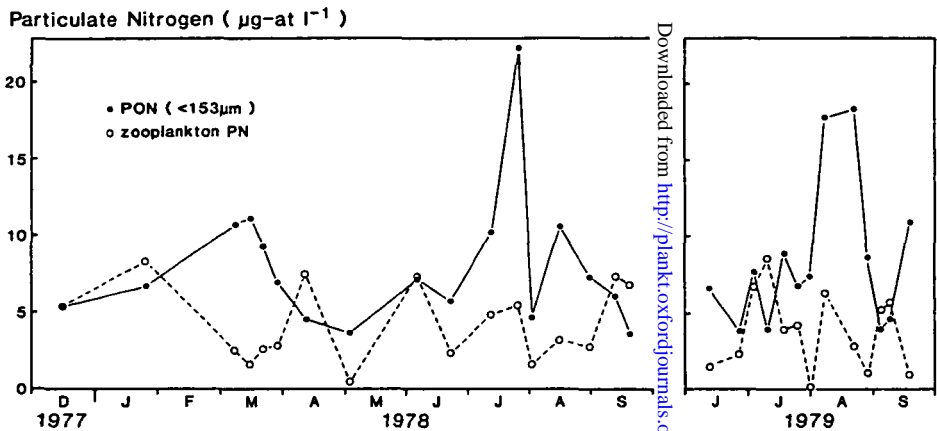


Fig. 3. Surface concentrations of PON (< 153 µm fraction) and zooplankton PN (> 153 µm fraction) in lower Narragansett Bay.

mer of 1978, but not in 1979. Sharp increases in ammonium concentrations were observed following the collapse of diatom blooms in late September.

Water temperatures (Figure 2) ranged between -0.2°C (early March) and 25°C (August). The water column in lower Narragansett Bay is generally well mixed by tidal currents with surface-to-bottom temperature gradients rarely $>0.5^{\circ}\text{C}$.

Surface particulate organic nitrogen (PON) concentrations in the $<153\ \mu\text{m}$ fraction ranged between 3.4 and $22.2\ \mu\text{g-at l}^{-1}$ (Figure 3). PON concentrations generally exceeded summed concentrations of dissolved nitrogenous nutrients. Mean water column macrozooplankton nitrogen concentrations ($>153\ \mu\text{m}$), ranged between 0.1 and $8.5\ \mu\text{g-at N l}^{-1}$; levels similar to or slightly lower than PON concentrations in the $<153\ \mu\text{m}$ fraction.

Nitrogen uptake rates (Figure 4) varied considerably during the study period. The observed transport rates varied little with temperature. Rapid uptake was observed in all seasons, regardless of nutrient concentrations. Peaks in transport rates were associated with phytoplankton biomass peaks in late-March, July and late August. Ammonium was the principle nitrogen species utilized by both winter-spring and summer populations. Urea was the next most important nitrogen source. Nitrate uptake was consistently

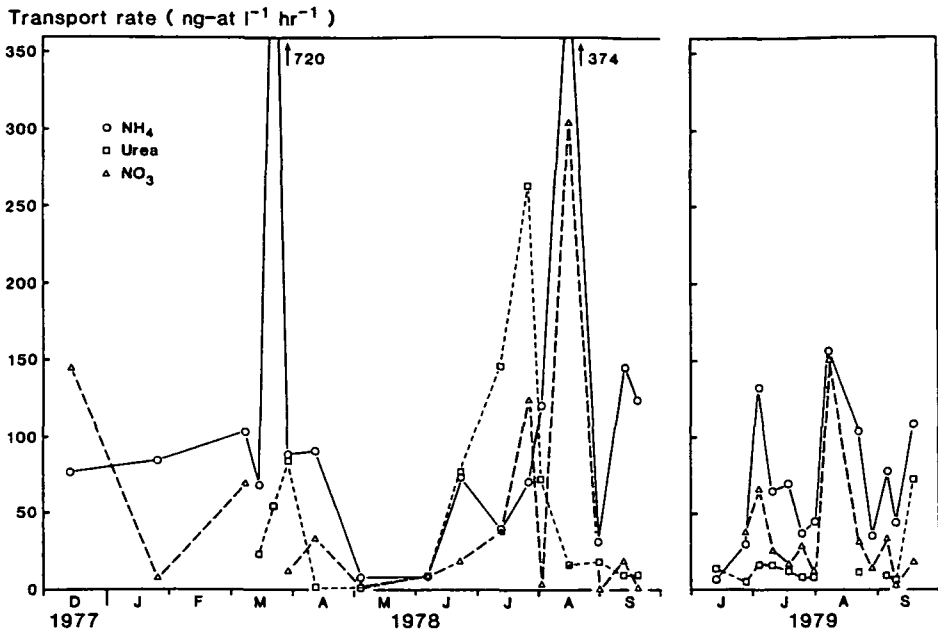


Fig. 4. Measured uptake rates ($\text{ng-at l}^{-1} \text{h}^{-1}$) of ammonium, nitrate + nitrite and urea-N in the near-surface waters of lower Narragansett Bay.

observed in winter–spring and summer experiments at rates inversely proportional to ambient ammonium levels.

Winter–spring nitrogen depletion times (Table I) varied considerably. During the spring bloom (March 7–21), ammonium depletion times ranged between 3 and 9 h. Urea was undetectable prior to three of five spring experiments. Assuming concentrations equal to the detection limit ($0.1 \mu\text{g-at N l}^{-1}$), calculated depletion times are < 1 h. In contrast, all but two spring nitrate depletion times exceeded 2 days, even at the lowest observed nitrate concentrations.

Summer stocks of nitrogenous nutrients were generally very rapidly utilized. Surface populations took up $\geq 80\%$ of all available nitrogen within 6 h in 14 of 22 summer experiments. Complete uptake during an experiment would result in underestimation of the uptake rate during early portions of those experiments. For that reason, calculated summer uptake rates and depletion times should be considered as conservative estimates of actual *in situ* rates and times. For reasons not fully understood, uptake rates in a few experiments were dramatically slower, resulting in considerably longer depletion times. These slower turnover rates usually occurred during the late summer, when diatoms dominated the phytoplankton. Means of summer depletion times calculated without these long depletion times (means in parentheses) indicate that surface nitrogenous nutrient stocks were generally being taken up and recycled between two and nine times daily.

The continual and rapid utilization of all nitrogen species implies active regeneration or input. Estimated benthic and macrozooplankton nitrogen remineralization rates,

Table I. Depletion times of dissolved nitrogenous nutrient stocks during the 1977–78 winter–spring and summers of 1978/1979. Summer mean values in parentheses were computed without the starred (*) values

Date	NH ₄ ⁺	NO ₃ ⁻ hours	Urea-N
Winter–Spring 1977–78			
12–13	113	105	
1–24	48	132	
3–7	3.3	11	
3–14	8.1		<0.1
3–21	9.2		28
3–28	21	53	38
4–11	13	26	<0.1
5–2	40	114	0.1
Mean	32.0	73.5	13.3
Summer 1978			
6–6	<0.1	<0.1	<0.1
6–20	7.2	3.7	6.1
7–11	2.8	3.2	4.0
7–25	5.6	3.8	4.1
8–1	16	62	20
8–15	5.6	6.6	<0.1
8–29	18	> 1000*	44*
9–12	6.6	4.3	<0.1
9–19	55	407*	125*
Mean	13.0 (7.7)	165 (6.0)	22.6 (4.9)
Summer 1979			
6–12	7.5		5.7
6–26	12	18.0	<0.1
7–3	7.9	7.5	2.4
7–10	11.8	6.7	11.0
7–17	6.5	2.9	<0.1
7–24	6.8	5.2	<0.1
7–31	8.0	1.8	<0.1
8–7	7.6	7.5	
8–21	7.3	4.9	<0.1
8–28	8.6	>0.1	
9–4	9.6	6.6	<0.1
9–11	97*	517*	104*
9–18	8.3	10.0	8.2
Mean	15.3 (8.5)	49.0 (6.5)	12.0 (2.8)

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averaged over the water column, ranged between 0.9 and 46.3 ng-at l⁻¹ h⁻¹ (Table II, Figure 5). Estimated remineralization was most rapid during the summer when water temperatures were highest. Winter–spring remineralization rates ranged between 0.9 and 5.4 ng-at l⁻¹ h⁻¹. From very low winter rates, remineralization estimates increased steadily from early May onwards as water temperatures rose to summer levels. This increase is largely due to the benthic component. Between April and August, calculated

Table II. Estimates of nitrogen remineralization by macrozooplankton, ctenophores and the benthos; replacement times for water column ammonium stocks by these sources, measured ammonium + urea uptake rates and estimated remineralization as a percent of measured ammonium + urea uptake. Values in parentheses are percents of the total estimated remineralization by the sources shown.

Date	Macro zooplankton	Estimated remineralization ($\text{ng-l}^{-1} \text{h}^{-1}$)		Total	NH_4 replacement times (h)	NH_4 + urea uptake ($\text{ng-at l}^{-1} \text{h}^{-1}$)	Regeneration as % of NH_4 + urea uptake
		Ctenophores	Benthos				
Winter-Spring 1977-78							
12-13	2.0 (54)	-	1.7 (46)	3.7	3000	77	4.8
1-24	2.3 (66)	-	1.2 (34)	3.5	1580	84	4.2
3-07	1.0 (53)	-	0.9 (47)	0.9	200	104	1.8
3-14	1.4 (52)	-	1.3 (48)	2.7	777	68	3.0
3-21	0.9 (39)	-	1.4 (61)	2.3	3600	773	0.3
3-28	1.2 (39)	-	1.9 (61)	3.1	520	172	1.3
4-11	3.2 (59)	-	2.2 (41)	5.4	293	93	5.8
5-02	0.2 (6)	-	3.0 (94)	3.2	9	9	35.6
Summer 1978							
6-06	5.3 (33)	-	10.6 (67)	15.9	3.8	18	88.3
6-20	2.0 (13)	-	12.9 (87)	14.9	8.2	152	9.8
7-11	4.8 (18)	-	21.8 (82)	26.6	4.3	187	14.2
7-25	5.7 (20)	-	22.9 (80)	28.6	4.3	335	8.5
8-01	1.7 (6)	-	28.7 (94)	30.4	23.5	194	15.7
8-15	4.2 (14)	0.09 (0.3)	26.5 (86)	30.8	78.1	391	7.9
8-29	2.7 (8)	0.64 (1.8)	32.6 (91)	35.9	78.9	51	69.8
9-12	6.7 (23)	0.65 (2.2)	21.5 (75)	28.8	31.0	156	18.3
9-19	5.8 (26)	0.50 (2.3)	15.9 (72)	22.2	32	134	16.4
Summer 1979							
6-12	1.0 (7)	-	12.9 (93)	13.9	28.1	21	66.2
6-26	1.7 (10)	-	15.6 (90)	17.3	26.1	36	48.1
7-03	5.1 (20)	-	20.8 (80)	25.9	34.8	149	17.4
7-10	6.7 (28)	-	17.5 (72)	24.4	39.2	81	29.9
7-17	3.3 (11)	-	26.5 (89)	29.8	39.0	83	35.9
7-24	4.2 (13)	-	28.7 (87)	32.9	10.4	47	70.0
7-31	0.1 (0)	-	37.6 (99)	37.7	11.7	54	60.5
8-07	6.7 (15)	0.14 (0.3)	39.5 (85)	46.3	29.7	156	29.7
8-21	2.4 (11)	0.05 (0.2)	20.2 (89)	22.7	40.0	116	19.5
8-28	0.9 (3)	0.01 (0.04)	25.6 (97)	26.5	12.4	35	75.7
9-04	6.0 (10)	-	28.2 (90)	31.2	27.0	87	35.9
9-11	5.8 (19)	0.02 (0.06)	24.0 (81)	29.8	163	50	59.6
9-18	0.8 (4)	-	21.8 (96)	11.6	44.1	182	12.4

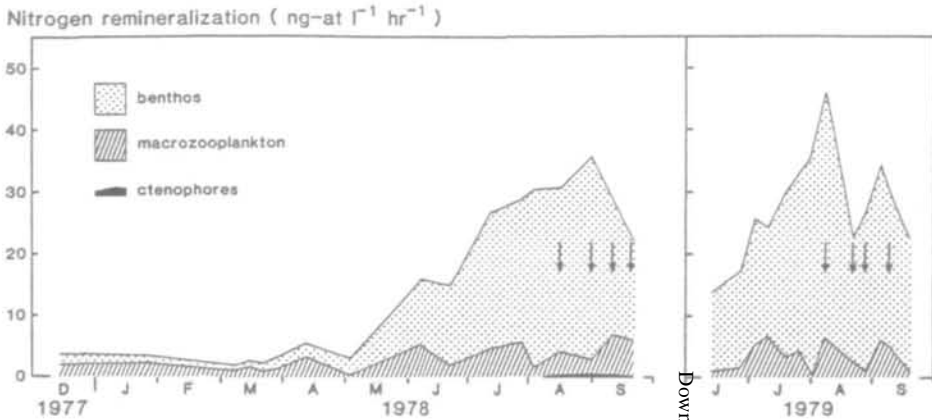


Fig. 5. Top. Cumulative plot of estimated nitrogen remineralization rates (ng-at l⁻¹ h⁻¹), averaged over the water column, by the benthos, macrozooplankton and ctenophores. Arrows identify experimental dates when ctenophores were present in significant numbers.

benthic nitrogen release rates increased nearly 7-fold. In contrast, estimates of macrozooplankton remineralization increased <2-fold. Overall, estimated summer remineralization rates ranged between 14 and 46.3 ng-at l⁻¹ h⁻¹.

Of the three sources for which functional estimations of remineralization were made, the benthos was the most important; its relative share ranging between 34 and 99 + % of the total estimable regeneration (Table II). On a relative basis, macrozooplankton (excluding ctenophores) were most important during the winter-spring, supplying regenerated nitrogen at rates equivalent to the benthos and tintinids. In contrast, average summer benthic nitrogen release rates were approximately equal to macrozooplankton and average microzooplankton N remineralization combined.

Ctenophores were not an important nitrogen source in the lower bay during the summers studied. They were present in significant numbers for only brief periods during the late summer. Estimates of ctenophore nitrogen remineralization never exceeded 2.3% of total benthic plus macrozooplankton remineralization.

Estimated nitrogen remineralization by macrozooplankton and the benthos were consistently lower than measured uptake rates (Table II, Figure 6). Replacement times for dissolved nutrient stocks from these two sources were frequently of the order of days, or longer. Differences between uptake and remineralization were most pronounced during the winter-spring when uptake rates were high, but due to cold water temperatures, estimates of remineralization rates were at their lowest. During the winter-spring, estimated remineralization by the benthos, and macrozooplankton with one exception, was <10% of measured nitrogen uptake. In summer experiments, estimated benthic and macrozooplankton remineralization rates ranged between 4 and 70% of measured nitrogen uptake. Uptake exceeded calculated benthic and macrozooplankton remineralization by 2-fold in 16 of 22 summer experiments, and by 5-fold in 11 experiments. Estimated remineralization was similar to measured uptake only during brief inter-bloom periods (6 of 22 experiments) when uptake declined dramatically, rather than by any dramatic increase in regeneration. Calculated runoff, sewage and riverine inputs generally (Figure 6) fail to make up the difference between

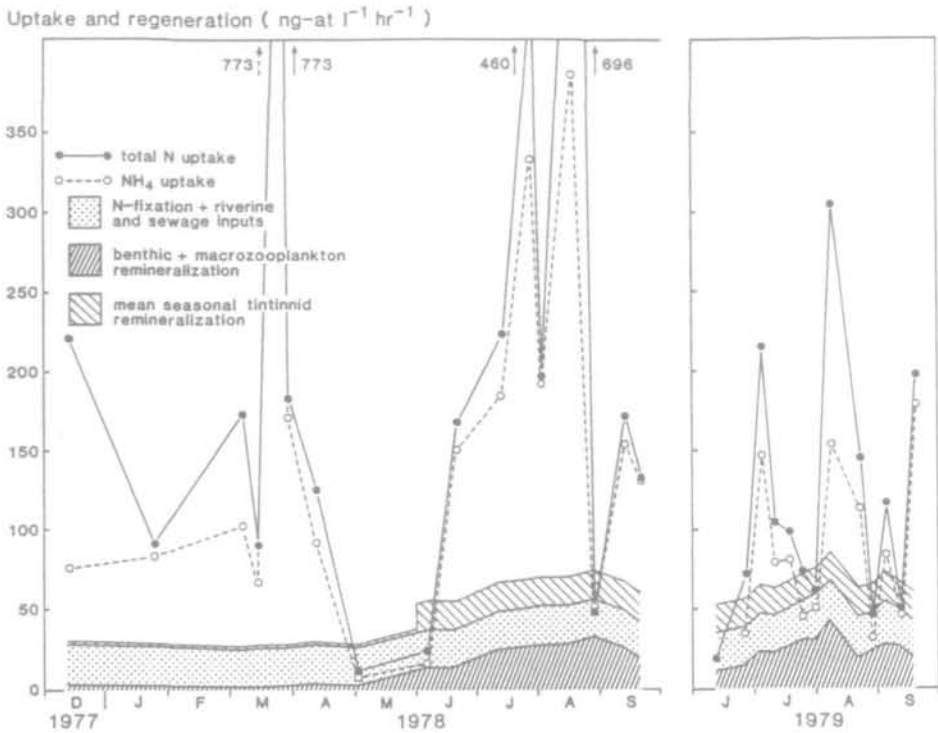


Fig. 6. Seasonal relationships of estimated remineralization and external inputs of nitrogen to measured uptake rates of ammonium and total N in lower Narragansett Bay.

uptake and remineralization. While this input estimate lacks any temporal variation it is clear that external nitrogen inputs are generally insufficient to meet the calculated deficit between nitrogen demand and remineralization.

Discussion

A comparison between the magnitude of dissolved nitrogenous nutrient stocks and measured rates of nitrogen uptake indicates that nitrogen pools in lower Narragansett Bay are rapidly recycled for much of the winter–spring and summer to meet phytoplankton N demand. As observed in Chesapeake Bay (McCarthy *et al.*, 1977), levels of particulate nitrogen were consistently larger than dissolved nitrogenous nutrient pools. Based on the measured uptake rates, estimates of nitrogenous nutrient depletion times (analogous to turnover times) were frequently of the order of hours. These direct measurements confirm and extend earlier indirect estimates of rapid nitrogen turnover inferred from primary production and substrate-saturated nitrate uptake rates (Durbin *et al.*, 1975; Furnas *et al.*, 1976). Depletion times for individual nitrogen species were generally shorter during the summer, largely because dissolved nitrogenous nutrient levels were lower, rather than because of much higher uptake rates.

The functional relations used for estimating benthic, macrozooplankton and ctenophore remineralization were based on local studies. Summed, these estimates fall near the

Table III. Seasonal estimates of integrated phytoplankton nitrogen demand and nitrogen inputs to the water column in lower Narragansett Bay. Values in parentheses give total inputs as a percent of nitrogen demands

	Nitrogen demand		Remineralization ($\mu\text{g-at } 1^{\text{st}}$)				External inputs	Total inputs
	NH_4^+ + urea	Total N ^a	Macro-zooplankton	Tintinnids ^b	Ctenophores	Benthos		
Winter-Spring 1977-78	418 (26.8)	557 (20.1)	6.0	13.2	0	5.2	87.7	112.1
Summer 1978	477 (36.2)	620 (27.9)	10.1	39.8	0.5	56.2	65.8	172.4
Summer 1979	195 (86.3)	285 (59.0)	8.3	39.8	0.1	58.1	61.4	167.7

^a NH_4^+ + NO_3^- + urea-N.

^bFrom Verity (1985): summer remineralization taken as 75% of annual remineralization.

upper end of the range of remineralization rates found in coastal waters (Sharp *et al.*, 1982). Comparison of measured uptake rate with estimates of micro- and macrozooplankton excretion, benthic N regeneration and inputs from streams and sewage, show that these sources were generally insufficient to meet instantaneous or seasonal nitrogen demand by winter–spring and summer phytoplankton populations (Table III, Figure 6).

If anything, the uptake rates used herein are conservative. Accounting for the known effects of incubation length (Goldman *et al.*, 1981; Glibert and Goldman, 1981), substrate exhaustion during incubations (Fisher *et al.*, 1981) and microplankton remineralization in bottles (Glibert *et al.*, 1982a) would increase estimates of phytoplankton uptake rates, decrease the calculated depletion times and accentuate the differences shown between uptake and remineralization. In balance, no uptake measurements were made at night. Both nitrate and ammonium uptake can vary over diel cycles (MacIsaac, 1978), with slower rates at night, but this effect may be less pronounced when cells are nitrogen limited (Syrett, 1962).

Of the nitrogen sources for which predictive relations are available, benthic remineralization was the largest. Recent calculations of nitrogen inputs to Narragansett Bay over an annual cycle (Nixon and Pilson, 1983) suggest the benthos recycles approximately 25% of the net annual N demand estimated from primary production. Comparable estimates of benthic inputs in other coastal systems average 35% of annual demand (Fisher *et al.*, 1982). Higher, 'event scale' episodes of remineralizations appear to follow periods of enhanced deposition (Garber, 1984; Kelly and Nixon, 1984), but the consistent excess of phytoplankton N demand over supply suggests that these events do not make up the difference. The discrepancy between nitrogen uptake and estimates of remineralization may be further exacerbated by benthic denitrification which appears to remove one-third of the nitrogen reaching the bottom in lower Narragansett Bay (Seitzinger *et al.*, 1980).

Macrozooplankton were clearly not a major source of remineralized nitrogen for the phytoplankton. Comparison of measured uptake rates with calculated remineralization estimates corroborates local budgets prepared from primary production data by Vargo (1979) and Oviatt *et al.* (1981) suggesting that macrozooplankton contribute only a minor portion of phytoplankton nitrogen demand. Though seasonally dominating the zooplankton community of lower Narragansett Bay (Deason, 1982), ctenophores were not an important remineralization source. Macrozooplankton appear to influence local phytoplankton dynamics largely by controlling the inception, magnitude and composition of bloom events through grazing and predation (Deason and Smayda, 1982), rather than by directly supplying nutrients.

Annual estimates of nitrogen inputs from fish and nitrogen fixation (Nixon, 1981) convert to mean hourly rates of 0.01 and 0.3 ng-at N l⁻¹ h⁻¹, respectively; clearly not large on a short-term basis. Local effects may, however, be important (Oviatt *et al.*, 1972).

Stream discharge and sewage are the major exogenous sources of combined nitrogen for Narragansett Bay (Nixon and Pilson, 1983), but average input rates per unit volume (25.8 ng-at l⁻¹ h⁻¹) rarely equalled or exceeded measured phytoplankton nitrogen uptake.

When integrated over seasonal intervals, combined river and sewage inputs would

supply 17, 11 and 23% of integrated phytoplankton nitrogen demand for the 1977–78 winter–spring, 1978 summer and 1979 summer periods, respectively. Comparable integrations of benthic plus macrozooplankton remineralization totalled 2, 11 and 23% of integrated N demand for the same time intervals.

The large and continual discrepancy between conservatively measured uptake rates and estimates of ecosystem nitrogen inputs lends further support to the idea that water column remineralization by bacteria and protozoa supplies much of the short-term nitrogen needs of coastal phytoplankton (Harrison, 1978; Glibert, 1982; Paasche and Kristiansen, 1982b; Harrison *et al.*, 1983; Verity, 1985).

Verity (1985) estimated that tintinnids alone can supply between 11 and 18% of the nitrogen needed to support annual primary production in lower Narragansett Bay. Within seasons, levels of tintinnid abundance and remineralization vary considerably and during brief episodes can potentially supply the bulk of phytoplankton nitrogen needs. As no estimates of tintinnid biomass were made during the present study, weekly estimates of tintinnid excretion could not be calculated. Over seasonal intervals, however, tintinnids may supply as much as 40% of integrated nitrogen inputs (Table III) and 2–14% of integrated nitrogen demand.

Estimates of microflagellate and bacterial biomass and activity were not determined during the experiments reported herein. The observed discrepancies between uptake and inputs clearly suggest that these groups may recycle a significant fraction of the nitrogen required by phytoplankton.

Although not addressed in calculated estimates of remineralization, bacterial processing of DON may be an important source of nitrogen. Measured u.v.-oxidizable DON concentrations in lower Narragansett Bay are of the order of $10 \mu\text{g-at l}^{-1}$ (Furnas, in preparation), clearly a major water column pool of fixed nitrogen. Active sub-pools such as amino acids, generally present in nanomolar concentrations (Clark *et al.*, 1982; Keller *et al.*, 1982), appear to turn over on time scales between minutes and days (Keller *et al.*, 1982). Slower mineralization over longer time scales may make much of the remaining DON available to phytoplankton (Jackson and Williams, 1985), but the contribution of bulk DON to dynamic budgets over the short time scales shown to be important is unknown.

Recent appraisals of phytoplankton dynamics in a number of shallow estuaries suggest that benthic grazing may regulate phytoplankton cycles and nutrient dynamics (Cloern, 1982; Officer *et al.*, 1982). The results presented herein would indicate that benthic processes in lower Narragansett Bay do not have a controlling role in the short-term (daily) dynamic balance between phytoplankton and nitrogenous nutrients. Benthic influences appear to be important over longer or seasonal time scales (Furnas, in preparation). The results herein suggest that in estuarine waters of only moderate depth, water column processes can dominate instantaneous nitrogen fluxes and probably those of other nutrients. The depth range in which a switch from benthic to water column regulation of short-term nutrient dynamics occurs is not known, but probably varies between estuarine systems and seasonally within individual estuaries. Elucidation of the variety of nutrient rate processes occurring within estuaries and the dynamics of the groups of organisms reacting to or controlling these processes clearly requires attention to the full range of time and spatial scales over which these processes occur.

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