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Available Nitrogen and Phosphorus and the Biochemical Cycle in the Atlantic Off New England[1]

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ABSTRACT

The importance of ammonia as a source of available nitrogen for phytoplanktonic populations off New England has been evaluated for August and January 1962. During August, when only trace amounts of nitrate persist in the photic layer, ammonia appears to be the major source of available nitrogen. Therefore, meaningful estimates of the relative amounts of nitrogen and phosphorus being assimilated at such times require consideration of the nitrogen occurring as ammonia. Total available nitrogen:phosphorus ratios of *change* have been derived from the sum of the nitrogen occurring as ammonia, nitrite, and nitrate and from the concentration of phosphate. These ratios have been compared with other data (for August and April) based on the organic nitrogen and phosphorus content of particulate fractions separated from suspension by Millipore filtration and by net tows. The results indicate that the ratios of change for August are somewhat lower than those for January and that the former are accompanied by a comparable depression in the N:P ratios for particulate material separated by Millipore filtration. It is speculated that during late summer, when nitrate and nitrite concentrations are minimal, ammonia forestalls the extreme degree of nitrogen deficiency known for laboratory cultures of nitrogen-starved algal cells.

Introduction. The amount of ammonia-nitrogen within the euphotic layer of the sea is often an important part of the total nitrogen available for protein synthesis by marine phytoplankton. However, estimates of the nitrogen reserve for the reproduction and growth of these organisms have often included only measurements of the nitrogen present as nitrite and nitrate. A previous study of the nitrogen and phosphorus cycles in New England coastal waters (Ketchum *et al.*, 1958) was also based on insufficient ammonia data, although amino-nitrogen was cited as a possible additional source of this element. At the same time, the need for simultaneous observations on the organic nitrogen and phosphorus content of coastal planktonic communities, especially during periods of nitrate depletion, was stressed. This paper elab-

orates further on this subject by including more complete information than in the study just cited, especially on the distribution of ammonia-nitrogen, and by considering the organic nitrogen and phosphorus content of the planktonic material collected simultaneously with water samples.

In November, the upper 50 m of water off New England becomes progressively enriched with nitrate and phosphate as the depth of the mixed layer increases, and at typical oceanic locations beyond the continental shelf a similar process extends mixing to even greater depths. Consequently, by January, shelf water becomes vertically homogeneous with respect to both density and available plant nutrients, and the latter attain their maximum annual concentration. In May, following the spring flowering and the recommencement of temperature stratification, the concentrations of nitrate and phosphate have already been reduced to about 1.0 and 0.5 $\mu g A/l$, respectively. These marginal nutrient conditions undergo further depletion as the summer progresses, with the actual residual concentrations depending upon the selective nutritional requirements of the resident phytoplankton.

Previous measurements for these waters have revealed how surface N:P atomic ratios, based solely on nitrogen as nitrite plus nitrate, approached zero as summer progressed due to a quantitative removal by September of nitrite and nitrate. On this basis the native phytoplankton would necessarily appear to assimilate these elements at a higher ratio than that presented to them in their native habitat. However, ammonia-nitrogen is also a suitable source of nitrogen for these organisms and must also be seasonally evaluated, especially for the summer months, before a realistic opinion of the degree of plant adaptation to the summer quantities of available nitrogen and phosphorus is possible.

The depletion of nitrate during late summer from the waters of Long Island Sound has been described by Riley and Conover (1956). Ketchum *et al.* (1958) have shown that low, summer nitrate concentrations comparable to those of Long Island Sound are widespread and extend seaward to the more oceanic surface waters off the New England coast. At such times the assimilation of nitrogen and phosphorus by the native phytoplankton as indicated by atomic ratios, N:P, for these elements in solution appeared anomalous from the 15:1 ratio commonly proposed by Redfield (1934), Fleming (1940), and others. For the remainder of the year, however, the data provided ratios (ammonia neglected) corresponding to $(NO_2^- - N + NO_3^- - N):PO_4^- - P = 15:1$, which compared favorably (within statistical limits) with similar ratios noted and generally accepted for living marine organisms (Redfield, 1958).

During 1962 the distribution of nitrite, nitrate, ammonia, and phosphate over an increased area of these waters was observed. Elementary analyses for the corresponding amounts of organic nitrogen and phosphorus separated from suspension by Millipore filtration or by net tows were also included to provide a basis for comparison with previously recorded seasonal variations.
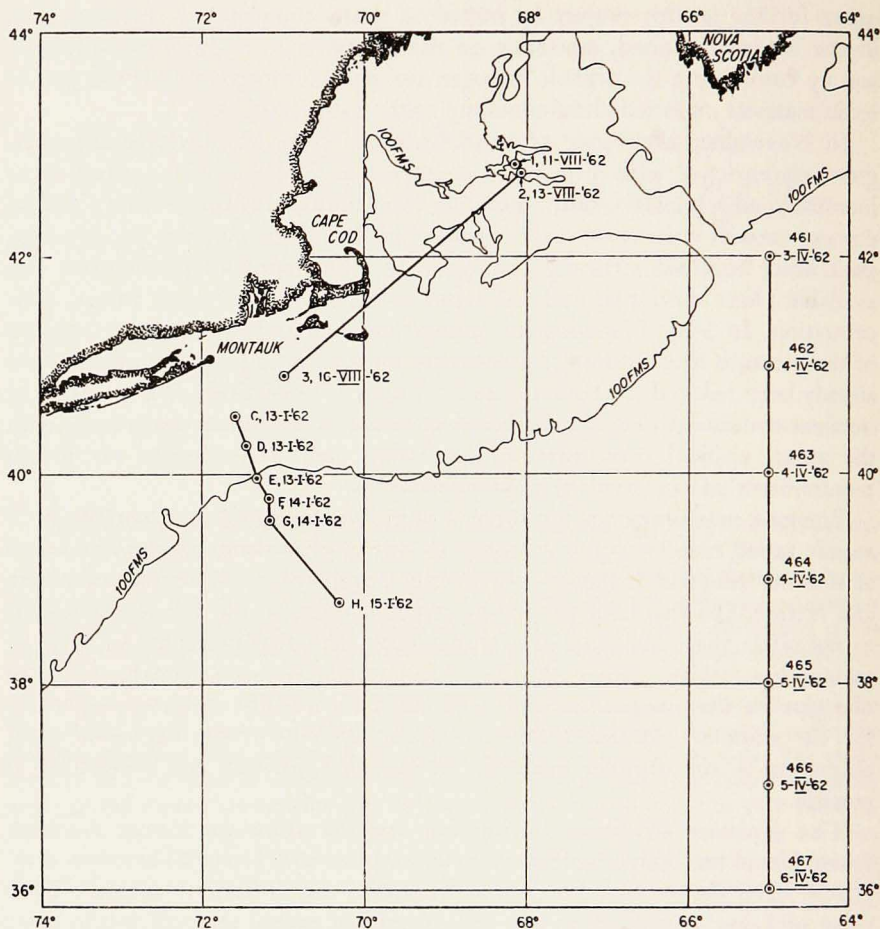
Figure 1. Station locations, identification, and dates of sampling.

Sample Collections and Methods. Pertinent observations were made at widely separated locations off New England during January, April, and August 1962 (Fig. 1). Besides the observations discussed below, hydrographic observations of temperature and salinity were completed for each sampling depth.

(1) January; R.V. CHAIN Cruise 22, Sts. C–G; across the continental shelf of New England (see Appendix for exact locations); bottom depth range 70–2800 m; dissolved plant nutrients including nitrogen and phosphorus were measured at all five locations.

(2) April; R.V. CHAIN Cruise 25, Sts. 461–467, one degree apart; south of Nova Scotia (see Appendix for exact locations); bottom depth at St. 467 more than 4700 m; dissolved nutrients and the nitrogen and phos-

phorus content of suspended parparticulate matter were observed for depths above 200 m.

(3) August; R.V. CRAWFORD Cruise 83, Sts. 1–3: Sts. 1 and 2 in the Gulf of Maine and St. 3 south of Cape Cod (see Appendix for exact locations); bottom depth range 50–225 m at Sts. 1 and 2; small suspended particulate matter was separated by Millipore filtration; larger suspended particles and plankton were obtained by net tows; dissolved plant nutrients, including nitrogen and phosphorus, were measured at all three locations.

SOLUBLE NITROGEN AND PHOSPHORUS ANALYSES. Water samples collected for analysis of inorganic nitrogen (ammonia, nitrite, and nitrate) and phosphate were immediately frozen on shipboard at about $-15°C$ pending analysis at Woods Hole within ten days, except for the April collections, which were analyzed aboard CHAIN. Nitrate-nitrogen was determined colorimetrically as nitrite following reduction with hydrazine according to Mullin and Riley (1955). Although independent nitrite measurements were always included, the initial nitrite concentration was usually less than 10°/o of the nitrate-nitrogen, hence the nitrate method provided a satisfactory estimate of the combined amount of nitrite and nitrate-nitrogen to ± 10°/o (Vaccaro et al., 1962). Ammonia, also determined colorimetrically, following the method proposed by Kruse and Mellon (1953), was complexed with chloramine-T and pyrazolone in the presence of pyridine and extracted with carbon tetrachloride prior to measurement of the optical density. The limit of detection by this method, according to Strickland and Parsons (1960), is about 0.20 $\mu g A/l$, with a precision of $\pm 0.45/n^{1/2} \mu g A/l$ at the 5 $\mu g A/l$ level. To estimate the total quantity of readily *available* plant nitrogen, hereafter designated as EN, the amounts of soluble inorganic nitrogen present as nitrite, nitrate, and ammonia, were summed. Inorganic phosphorus was estimated according to the method of Wattenberg (1929, 1937), Robinson and Thompson (1948), and Wooster and Rakestraw (1951) to about ± 8°/o, as discussed by Ketchum et al. (1955).

PARTICULATE NITROGEN, PHOSPHORUS, AND CHLOROPHYLL ANALYSES. Particles with diameters ranging from 0.5 to 360 μ were obtained for elementary nitrogen and phosphorus analyses by using both vacuum microfiltration and net tows. The smallest particles, down to about 0.5 μ, were retained on 25-mm glass fiber Reeve Angel filters after passage of measured seawater volumes. Aggregates of larger particles measuring 360, 160, and 75 μ were separated by towing a triple exclusion net at three knots for about 20 minutes through the surface waters. The nets were so arranged that water was consecutively filtered through nets of mesh numbers 2, 10, and 20, respectively, to provide the particle distribution described above. Aliquots from each net were obtained for dry weight and for organic nitrogen and phos-

phorus analyses with the plankton-splitting device described by McEwen *et al.* (1954). Each aliquot was immediately transferred to a tared microfilter under vacuum, stored in the refrigerator with silica gel, and ultimately brought to constant weight. The particulate organic nitrogen content was measured by the micro-Dumas method, using the nitrogen analyzer of the P. H. Coleman Company. Particulate organic phosphorus was determined by the method described by Harvey (1948) and modified by Ketchum *et al.* (1955). Chlorophyll was estimated as recommended by Richards with Thompson (1952) and modified by Creitz and Richards (1955) for use with a Millipore filter.

Results.

AMMONIA-NITROGEN AND THE ESTIMATION OF AVAILABLE NITROGEN. Fig. 2 shows the vertical distribution of ammonia, nitrite plus nitrate, and phosphate during August and January at the indicated locations. For comparison, the ratios of concentration for nitrogen:phosphorus are given with and without the ammonia-nitrogen included. The resulting relations are believed to be typical of conditions northeast and south of Cape Cod in winter compared with summer.

In August, the 50-m water column south of the Cape at St. 3 (Fig. 2a) contained less than 1 μgA/l of ammonia-nitrogen at the surface and about 4 μgA/l at 50 m. The concentration of nitrate-nitrogen was about .10 μgA/l at the surface and increased to only .50 μgA/l at 50 m. At comparable depths, phosphate-phosphorus was .25 and 1.25 μgA/l, respectively.

August observations in the Gulf of Maine at St. 2 for the upper 100 m (Fig. 2b) showed a maximum ammonia concentration of about 2 μgA/l at 25 m. The upper 25 m contained only trace quantities of nitrate, but at greater depths nitrate increased rapidly and attained a concentration of 14 μgA/l at 100 m. The comparable phosphate changes were .50 in the upper 25 m and 1.43 μgA/l at 100 m.

In August, the depth of the nutrient mixed surface layer northeast and south of Cape Cod measured 20 to 30 m; however, the surface temperature south of the Cape was about 4°C warmer and the salinity about .40 °/oo higher than for the Gulf of Maine. Table 1 indicates that, throughout the entire water column south of Cape Cod, the relative stability, based on density (σ_t) across the thermocline, was approximately twice that observed in the Gulf of Maine. The single negative stability value, shown for the 30-to-40-m calculation south of Cape Cod, is questionable, but this may be caused by an aberrant salinity measurement, since the recorded temperatures agree with the bathythermograph observations. If this value is real, however, the phenomenon would presumably be of short duration and would be accompanied by vigorous vertical turbulence.

For additional information on the stability difference between the two locations in August, the pertinent data for past years filed at the Woods Hole

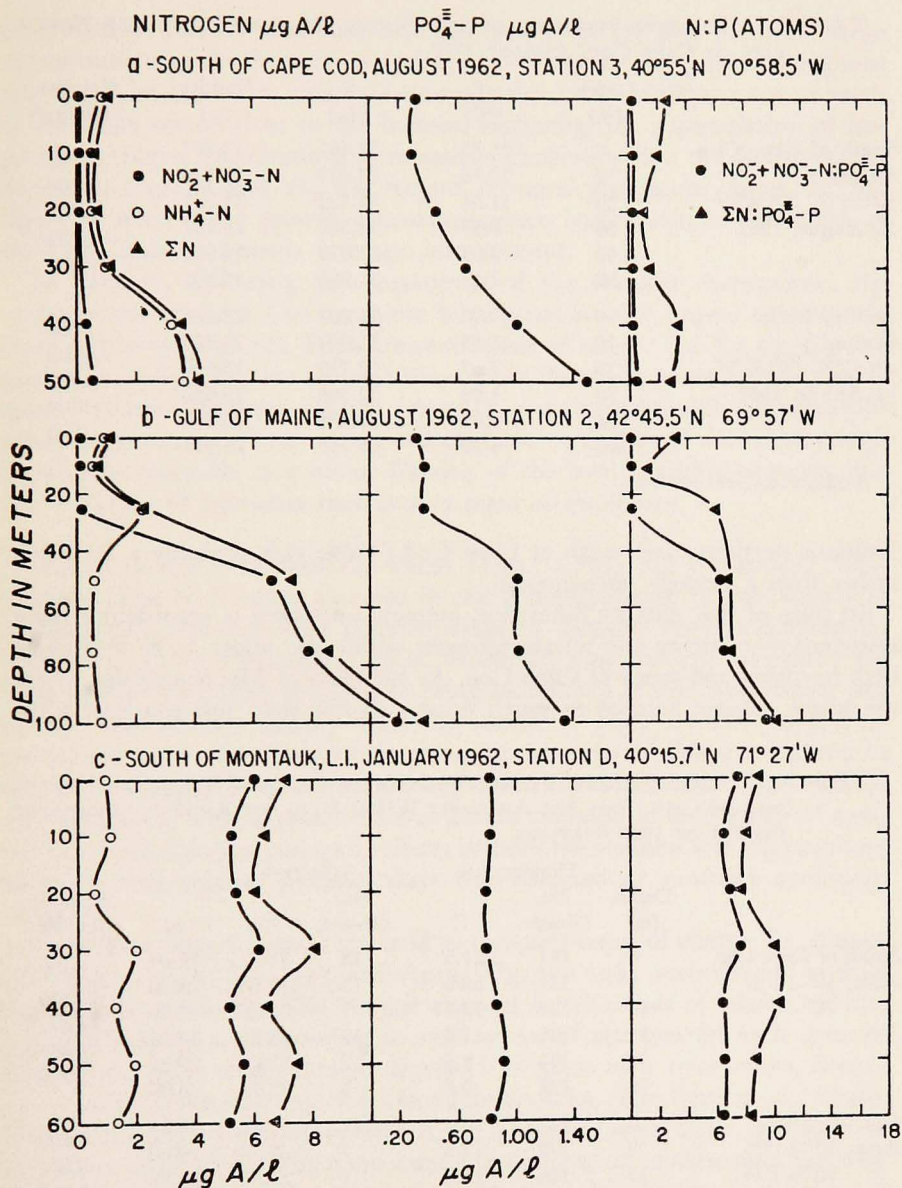Figure 2. Vertical changes in available nitrogen fractions during August and January 1962 as compared with phosphate-phosphorus by ratios of concentration, $\Delta N: \Delta P$ (atoms).

Oceanographic Institution have been examined. All of the data employed (Table II) refer to locations within 30 miles of the August stations. They strengthen the evidence that the difference in stability in August between the

TABLE I. Relative Stability of the Water Columns South and North-east of Cape Cod, August 1962.

	Depth (m)	T (°C)	S (°/oo)	Density (σ_t)	Relative Stability*
South of Cape Cod	0	21.35	32.467	22.497	2,600
Station 3	10	20.75	32.429	22.626	20,600
34°55'N, 70°58'W	20	11.01	32.422	24.791	3,700
15 August 1962	30	8.47	32.360	25.157	−2,300
	40	8.03	31.979	24.923	7,500
	50	7.12	31.965	25.036	
Gulf of Maine	0	17.31	31.987	23.156	650
Station 2	10	15.95	32.004	23.480	11,300
42°45'N, 69°57'W	25	7.07	32.119	25.166	1,900
13 August 1962	50	4.64	32.368	25.652	800
	75	4.81	32.594	25.845	600
	100	4.22	32.745	25.996	

* $(\Delta\sigma_t \times 10^5)/(\Delta D \text{ [meters]})$.

locations northeast and south of Cape Cod (Table 1) is probably a recurring rather than a cursory phenomenon.

In spite of this stability difference, ammonia-nitrogen is consistently more abundant than nitrite and nitrate-nitrogen within the upper 30 m in August both northeast and south of Cape Cod. At the Gulf of Maine stations, where the water column extends to much greater depths than just south of Cape

TABLE II. Mean Relative Stability of Water Columns South and North-east of Cape Cod; All Available WHOI Data for August, within One Degree of 1963 Stations.

	Depth (m)	Temperature No. Observ.	°C	Salinity No. Observ.	°/oo	σ_t	Relative Stability
South of Cape Cod	0	141	21.5	18	31.92	22.04	1,800
Area, 40° ± 1°N	9	137	20.9	13	31.86	22.18	10,300
70° ± 1°W	15	124	18.7	1	31.96	22.80	13,400
	31	136	11.8	13	32.81	24.94	1,600
	46	131	9.6	2	32.63	25.18	2,900
	76	122	9.8	3	33.78	26.06	
Gulf of Maine	0	227	18.3	11	31.86	22.81	3,000
Area, 42° ± 1°N	9	173	17.3	7	31.88	23.08	5,000
70° ± 1°W	15	166	14.8	1	31.56	23.38	7,740
	30	172	8.3	5	31.56	24.55	5,800
	46	151	6.1	1	32.37	25.37	2,700
	76	137	4.9	4	32.98	26.10	710
	100	135	4.6	8	33.15	26.27	600
	150	74	5.1	5	33.57	26.57	180
	200	56	5.8	7	33.82	26.66	
	250	17	6.2	−	−	−	

Cod, nitrate exceeds ammonia-nitrogen below 30 m, and relatively large concentrations of the former (10 μg A/l at 90 m) apparently persist throughout the year. The maximum ammonia concentration in the shallower waters south of the Cape occurs close to the bottom, suggesting the accumulation of important nitrogen contributions from ammonification within the sediments. As shown in Figs. 2a and 2b, the August nitrogen:phosphorus ratios for the layers of active plant growth approximate zero both northeast and south of the Cape unless ammonia is taken into account.

In January, following the breakdown of the summer thermocline, the waters south of Cape Cod are quite homogeneous with respect to inorganic plant nutrients (Fig. 2c). High concentrations of nitrate (ca. 8.0 μg A/l) and phosphate (0.8 μg A/l) are the rule throughout the entire water column, while ammonia concentrations, though irregular, remain comparable to those observed in summer. These winter nitrate concentrations are sufficiently high to relegate ammonia to a minor fraction of the total available nitrogen, and the influence of ammonia then is at a seasonal minimum.

RATIOS OF CHANGE DERIVED FROM TOTAL AVAILABLE NITROGEN:PHOSPHORUS. The N:P ratios discussed in the previous section pertain strictly to ratios of concentration that describe dissolved nutrient reserves temporarily outside the living biochemical cycle. However, they are not necessarily related to the elementary proportions being assimilated in situ, since either one or the other element usually occurs in excess. A more realistic estimate of the in-situ ratio of assimilation is given by the ratio of *change* calculated as the rate of change, $\Delta N:\Delta P$, from the regression of total available nitrogen, ΣN, on phosphorus. This approach derives a ratio common to each group of data; the ratio describes the biological effects of both assimilation and regeneration, assuming that mixing processes have not obscured or modified conditions in situ.

Data from three locations are used to compute ratios of change for August (Fig. 3a), January (Fig. 3b), and April (Fig. 3c) 1962 according to visually drawn lines of best fit. The August analyses for the Gulf of Maine indicate a ratio of change corresponding to 10.8 atoms of nitrogen for each atom of phosphorus. This value, though depressed in terms of a 15:1 norm, is consistent with previously reported low summer ratios (Ketchum *et al.*, 1958). Ratios of change for January and April, however, were 21:1 and 15:1 at the indicated locations. The point scatter common to all of these plots probably reflects the advection and mixing of neighboring water masses at the time of observation. In any case, the slopes for January and April are both significantly greater in magnitude than the slope for August.

PARTICULATE ANALYSES FOR ORGANIC NITROGEN AND PHOSPHORUS BY MILLIPORE FILTRATION. Besides the analyses of dissolved nitrogen and phos-
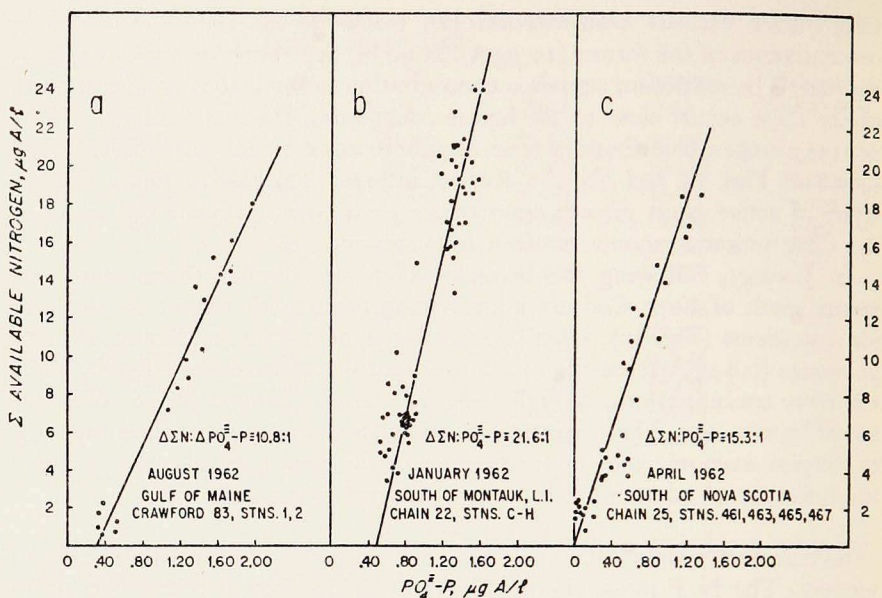
Figure 3. Ratios of change during August and January 1962 for total available nitrogen:phosphorus (atoms), for Atlantic waters off New England from regression of ΣN on phosphate-phosphorus.

phorus discussed above, additional information on the particulate organic matter removed by Millipore filtration has been compiled. These results are summarized in Table III for material that is believed to be largely represent-ative of surface phytoplankton, with larger admixtures of partially decomposed animal and plant cells included in the samples from greater depths. While independent estimates of detritus are not available, the observed differences in chlorophyll are believed to reflect the relative importance of green plants at the depths indicated.

The August observations in the Gulf of Maine locate the largest con-centrations of particulate nitrogen and phosphorus as well as chlorophyll within the upper 50 m. For these depths the range of particulate N:P ratios (11.2:1 to 13.2:1) is in good agreement with the dissolved ratio of change (10.8:1) cited in the previous section for the same water column. In con-trast, the ratio of concentration of N:P for the same depths was less than 6.0:1 (Fig. 2b). Below 50 m the particulate N:P ratio increased to 17.3:1 (Table III), probably because of a more rapid loss of phosphorus than of nitrogen from nonliving detritus (Menzel and Ryther, 1963, in preparation).

In April the chlorophyll concentration south of Nova Scotia was almost 10 times greater than that during August in the Gulf of Maine (Table III). While the particulate nitrogen and phosphorus concentrations at Sts. 461–467

TABLE III. Relation between Nitrogen, Phosphorus, N:P, and Chlorophyll a in Millipore-filtered Particulate Matter, and the Available N and P in the Surrounding Sea Water During August and April 1962 off New England.

| | No. of Analyses | | | Mean Concentration | | | |
	N	P	Chl.a	N (μg A/l)	P (μg A/l)	Chl.a (mg/m3)	N:P (atoms)
August 1962, Gulf of Maine							
Particulate samples							
0– 10 m.................	13	15	4	0.98	.087	.238	11.2
10– 50 m.................	1	4	6	1.08	.082	.306	13.2
50–250 m.................	5	11	13	0.76	.044	.075	17.3
Dissolved ΣN:P, all depths							
Ratio of change	27	27	—	—	—	—	10.8
Ratio of concentration	38	26	—	—	—	—	6.0
April 1962, S. of Nova Scotia							
Particulate samples							
0– 10 m.................	6	6	6	2.64	0.16	2.36	16.5
10– 50 m.................	12	12	12	3.09	0.13	2.65	23.8
50–100 m.................	17	17	15	2.83	0.12	2.97	23.6
110–300 m.................	6	6	6	1.69	0.05	0.85	33.8
Dissolved ΣN:P, all depths							
Ratio of change	35	35	—	—	—	—	15.3
Ratio of concentration	41	41	—	—	—	—	13.2

were also greater in April, the change was not proportional, since the nitrogen increase was greater than that of phosphorus. The occurrence of maximum chlorophyll concentrations between 50 and 100 m is more typical of deeper oceanic conditions in the Atlantic than of the more shallow coastal waters. For Sts. 461–467 the particulate N:P ratios for the upper 50 m were 16.5:1–23.8:1 and increased to 23.6:1–33.8:1 for depths between 50 and 300 m. The accompanying data show that the corresponding ratios of change and of concentration were, respectively, 15:1 and 13:1. Here also the higher N:P particulate ratios at greater depths appear to reflect more rapid release of phosphate relative to deamination.

PARTICULATE ANALYSES FOR ORGANIC NITROGEN AND PHOSPHORUS BY NET TOWS. Table IV summarizes results from analyses of particulate matter obtained from net tows in the Gulf of Maine during August. No obvious systematic changes in nitrogen or phosphorus content for the various mesh numbers were detected. Very likely the occasional discrepancies shown between neighboring or replicate analyses are suggestive of rather large sampling errors or of a patchy distribution of the plant and animal components. Nitrogen, taken as per cent composition of the dry weight of these plant-animal mixtures, ranged from 4.3 to 8.5, while phosphorus, on a similar basis, varied from

TABLE IV. AVAILABLE NITROGEN AND PHOSPHORUS IN UPPER 5 M VS. THE PER CENT (DRY WEIGHT) OF NITROGEN AND PHOSPHORUS AND THE RATIO OF N:P (ATOMS) FOR VARIOUS NET HAULS TAKEN IN THE GULF OF MAINE, AUGUST 1962.

	Mesh	Sample Comp.	Surface Water ΣN ($\mu gA/l$)	P ($\mu gA/l$)	$\Sigma N:P$ (atoms)	Tow Analyses, dry wgt. N (%)	P (%)	N:P (atoms)
42°47′N	# 20	20% copepods;						
69°54′W		80% *Ceratium*						
13 August		and diatoms	0.75	0.34	2.20	(a) 6.48	0.76	18.8
Time: 2100						(b*) 6.17	0.69	19.8
	# 10	95% copepods	0.75	0.34	2.20	8.08	1.03	17.4
	# 2	95% copepods	0.75	0.34	2.20	7.50	—	—
42°50′N	# 20	95% *Ceratium*						
69°50′W		and diatoms	0.51	0.37	1.38	(a) 4.35	0.53	18.1
14 August						(b*) 4.26	0.55	17.1
Time: 0900	# 10	60% copepods;						
		40% dino-						
		flagellates	0.51	0.37	1.38	(a) 7.00	0.82	19.0
						(b*) —	0.74	—
						(c*) —	0.74	—
	# 2	95% copepods	0.51	0.37	1.38	6.82	0.75	20.1
42°49′N	# 20	30% copepods						
69°48′W		and nauplii;						
14 August		70% *Ceratium*						
Time: 1600		and diatom sp.	0.54	0.30	1.80	(a) 7.56	1.04	16.1
						(b*) 7.17	1.06	15.0
	# 10	97% copepods	0.54	0.30	1.80	(a) 8.50	1.08	17.4
						(b*) 8.06	0.92	19.4
	# 2	97% copepods	0.54	0.30	1.80	(a) 8.40	1.07	17.3
						(b*) 8.50	1.19	15.8

* Repeated analyses.

0.5 to 1.2 %. The atomic ratios of N:P for these samples were appreciably higher (15:1 to 20:1) than for the surface Millipore-filtered counterparts described above. The simultaneous ratios of concentration for dissolved N:P at the surface were extremely low (1.38 to 2.20) as compared with the over-all 10.9:1 ratio of change previously noted for the entire water column.

Discussion. By late summer, nitrogen assimilation by marine phytoplankton in the surface waters off New England has reduced nitrate to trace amounts close to the limit of sensitivity of the analytical method employed. Over-all, the winter-to-summer decrease in nitrate exceeds twentyfold. Ammonia persists, however, throughout the summer at about half of its winter concentration, and by August it has become the more abundant source of plant nitrogen. Conversely during winter, although higher concentrations of each type of nitrogen are present, nitrate-nitrogen is five or six times more abundant

than ammonia. Unlike nitrate, phosphate appears to be present in excess amounts throughout the year.[2]

It appears that the relative abundance of ammonia as opposed to nitrate during summer in the euphotic waters off New England coincides with maximum stratification of the water column due to increased surface temperatures. High nitrate concentrations, which persist throughout the year at subeuphotic depths, become progressively more isolated from the surface as the seasonal decline in solar radiation approaches. With high stability, nitrate enrichment of the surface waters is ultimately minimized because of reduced vertical mixing across a strong thermocline. Until the occurrence of active nitrification within the upper layer is more conclusively demonstrated, it must be assumed that, at such times, the major impetus to the nitrogen cycle is provided by ammonia because of its more rapid exchange between organisms and environment and because of its direct addition from the atmosphere in association with rain (Menzel and Spaeth, 1962).

The annual variation in available phosphorus within these waters, unlike that of nitrogen, is much less pronounced, and excess amounts are the rule throughout the year. In part, this feature supports the low N:P ratios of concentration observed during summer. Even during winter, however, the maximum observed N:P ratio for the euphotic layer in terms of concentration is only about 10:1, hence the ratio of *change* is a more realistic basis for determining the relative amounts of nitrogen and phosphorus being assimilated. Ratios calculated in this manner for January and April substantiate the hypothesis that nitrogen and phosphorus assimilation and regeneration are proceeding quite typically at a ratio approximating 15:1. In August, however, even the indicated ratios of change are reduced to about 11:1, suggesting a degree of environmental adaptation by the summer planktonic communities to lesser available nitrogen concentrations.

The analyses of particulate nitrogen and phosphorus provide a quantitative basis for assessing the extent of this seasonal adaptation to the summer supply of available nitrogen and phosphorus. When nitrate was virtually absent from the upper 50 m during August, the phytoplankton contained nitrogen and phosphorus (dry weight basis) at a ratio corresponding to 12:1. This condition was accompanied by generally higher ratios (up to 20:1) in the coarser net material. Comparable ratios measured by Harris and Riley (1956) for Long Island Sound are given as 12.6:1 for August phytoplankton and 20.6:1 for July zooplankton. For March of the same year, when large amounts of available nitrogen were present, the same authors reported a ratio of 17.2:1 for Long Island Sound phytoplankton.

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[2] Kuenzler (unpublished data) has compared two chemical methods: that cited here and a bioassay technique for estimating dissolved phosphate. His results suggest that the method employed here gives results approximately 0.10 ug A/l too high for our lowest phosphate concentrations. A correction of this magnitude would increase Σ N:P ratios of concentration, especially in nutrient-poor summer surface waters, but in terms of phytoplankton requirements, a phosphorus excess would still remain.

Evidence from laboratory studies with cultures of marine and freshwater phytoplankton clearly indicates that the amount of available nitrogen accompanying cell division and growth determines the ultimate amount of cellular nitrogen assimilated. Thus, Ketchum and Redfield (1949) induced variations in the cellular nitrogen content of *Chlorella pyrenoidosa* ranging from about 2.5 to 9.0% of the ash-free dry weight. Even greater nitrogen extremes have been noted within the same organisms by Spoehr and Milner (1949). Actually, the present summer particulate ratios for phytoplankton would fall within the upper quartile of these ranges for cultures, even under conditions of extreme nitrate depletion. Logically, the presence of ammonia at such times appears to stabilize and measurably enhance the amount of nitrogen cycled biochemically through the food chain by supporting, at the primary production stage, a higher protein level than would otherwise be possible if nitrate were the sole nitrogen source available.

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APPENDIX

Vertical Distribution of Available Plant Nitrogen and Phosphorus, $\mu gA/l$, in Atlantic Waters off New England during August, January, and April 1962.

	Depth (m)	NH_4^+-N	NO_2^--N	NO_2^-+ NO_3^--N	ΣN	$PO_4^{=}-P$
GULF OF MAINE						
CRAWFORD	1	1.31	.021	0.42	1.72	0.33
Cruise 83	10	0.62	.021	0.09	0.71	0.50
Station 1	25	1.06	.044	0.19	1.25	0.56
42°48.8′N	50	0.54	.062	9.26	9.80	1.25
69°51.2′W	75	0.50	.012	8.44	8.94	1.28
11/VIII/62	100	1.09	.074	9.26	10.4	1.43
Fig. 3a	125	0.85	.024	12.2	13.0	1.44
	150	1.48	.018	12.8	14.3	1.62
	175	0.57	.018	13.9	14.5	1.72
	225	0.57	.032	13.2	13.8	1.71
CRAWFORD	1	0.96	.044	0.03	0.99	0.32
Cruise 83	10	0.50	.021	0.01	0.51	0.37
Station 2	25	2.06	.030	0.11	2.17	0.37
42°45.5′N	50	0.50	.024	6.66	7.16	1.06
69°57′W	75	0.50	.015	7.85	8.35	1.17
13/VIII/62	100	0.79	.009	12.9	13.7	1.34
Figs. 2b, 3a	125	—	—	—	—	—
	150	0.57	.029	14.6	15.2	1.54
	175	1.23	.027	14.9	16.1	1.75
	185	0.50	.047	17.5	18.0	1.96
SOUTH OF CAPE COD						
CRAWFORD	1	0.79	0.02	0.04	0.83	0.32
Cruise 83	10	0.50	0.01	0.10	0.60	0.30
Station 3	20	0.50	0.01	0.01	0.51	0.45
40°55′N	30	0.89	0.04	0.05	0.94	0.66
70°58′W	40	3.16	0.39	0.27	3.43	1.05
16/VIII/62	50	3.58	0.47	0.45	4.03	1.49
Fig. 2a						
SOUTH OF MONTAUK, L.I.						
CHAIN	1	1.52	0.18	5.12	6.64	0.88
Cruise 22	10	2.02	0.17	6.36	8.38	0.77
Station C	20	1.33	0.15	5.66	6.99	0.90
40°31.4′N	30	0.85	0.16	5.00	5.85	0.82
71°34.9′W	40	1.12	0.16	5.83	6.95	0.73
13/I/62	50	1.28	0.18	5.47	6.75	0.78
Fig. 3b	60	1.67	0.21	5.00	6.67	0.76

	Depth (m)	NH_4^+-N	NO_2^--N	NO_2^-+ NO_3^--N	ΣN	$PO_4^\equiv$-P
SOUTH OF MONTAUK, L.I.						
CHAIN	1	0.94	0.15	6.10	7.04	0.81
Cruise 22	10	1.12	0.19	5.24	6.36	0.81
Station D	20	0.55	0.12	5.42	5.97	0.79
40° 15.7'N	30	1.97	0.16	6.01	7.98	0.79
71°27.0'W	40	1.23	0.22	5.12	6.35	0.85
13/I/62	50	1.95	0.18	5.65	7.60	0.91
Figs. 2c, 3b	60	1.30	0.13	5.12	6.42	0.82
CHAIN	1	0.99	0.12	5.71	6.70	0.82
Cruise 22	10	1.17	0.10	5.77	6.94	0.80
Station E	24	1.17	0.16	5.29	6.46	0.77
39°58.5'N	48	0.62	0.11	4.82	5.44	0.83
71°19'W	72	1.04	0.04	7.50	8.54	0.60
13/I/62	97	1.14	0.06	9.10	10.2	0.69
Fig. 3b	145	0.69	0.10	19.9	20.6	1.13
	193	0.98	0.22	19.6	20.6	1.42
CHAIN	1	1.52	0.12	5.41	6.93	0.82
Cruise 22	10	2.10	0.13	—	—	0.82
Station F	25	0.78	0.13	5.90	6.68	0.84
39°46.5'N	50	0.98	0.08	5.90	6.88	0.60
71°11.5'W	75	0.85	0.06	7.27	8.12	0.67
14/I/62	100	0.98	0.06	13.9	14.9	0.90
Fig. 3b	200	0.86	0.05	18.4	19.3	1.36
	300	1.14	0.09	22.9	24.0	1.66
	400	1.11	0.03	22.9	24.0	1.52
	500	0.75	0.06	18.1	18.9	1.39
	600	0.91	0.07	15.1	16.0	1.32
	700	0.77	0.06	18.3	19.1	1.28
	800	1.60	0.07	19.5	21.0	1.30
	900	0.88	0.08	19.1	20.0	1.31
	1000	2.06	0.12	14.5	16.6	1.27
	1200	2.43	0.05	17.6	20.0	1.32
CHAIN	1	1.62	0.20	4.23	5.85	0.67
Cruise 22	10	0.54	0.23	3.28	3.82	0.72
Station G	25	0.61	0.22	4.34	4.95	0.53
39°35.4'N	50	0.61	0.23	4.12	4.73	0.58
71°09'W	75	0.72	0.16	6.13	6.85	0.56
14/I/62	99	0.78	0.11	8.15	8.93	0.88
Fig. 3b	199	0.88	0.10	16.1	17.0	1.42
	298	3.02	0.08	19.6	22.6	1.62
	398	0.67	0.04	17.9	18.6	1.50
	497	1.12	0.04	18.0	19.1	1.49
	596	1.32	0.04	20.2	21.5	1.40

	Depth (m)	NH_4^+-N	NO_2^--N	NO_2^-+ NO_3^--N	ΣN	$PO_4^{\equiv}-P$
SOUTH OF MONTAUK, L.I.						
	696	1.12	0.04	19.9	21.0	1.30
	795	0.91	0.04	16.2	17.1	1.26
	895	1.14	0.06	14.1	15.2	1.30
	994	3.44	0.04	19.5	22.9	1.30
	1292	0.96	0.04	14.7	15.7	1.24
CHAIN	1	0.67	0.20	2.81	3.48	0.60
Cruise 22	10	0.69	0.17	3.41	4.10	0.67
Station H	25	1.07	0.16	4.88	5.95	—
38°46.2′N	50	0.53	0.14	4.94	5.47	0.53
70°18.1′W	75	1.01	0.15	—	—	0.48
15/I/62	100	0.88	0.21	4.17	5.05	0.62
Fig. 3b	200	0.98	0.06	17.6	18.6	1.42
	300	0.72	0.14	18.6	19.3	1.56
	400	1.07	0.08	19.1	20.2	1.49
	499	0.50	0.10	15.1	—	1.37
	599	0.53	0.03	19.8	20.3	1.26
	698	0.92	0.05	16.1	17.0	1.36
	796	0.75	0.04	17.4	18.2	1.28
	893	0.66	0.06	12.6	13.3	1.32
	990	1.04	0.08	14.7	15.7	1.26
	1277	0.88	0.04	18.7	19.6	1.17
SOUTH OF NOVA SCOTIA						
CHAIN	1	1.82	0.14	1.84	3.66	0.56
Cruise 25	10	1.89	0.12	1.92	3.81	—
Station 461	25	2.45	0.08	2.81	4.26	0.53
42°00′N	50	2.47	0.14	2.28	4.75	0.46
65°00′W	75	1.67	0.16	4.15	5.82	0.50
3/IV/62	100	0.78	0.30	3.84	4.62	0.54
Fig. 3c	125	0.86	0.26	10.1	11.0	0.89
	150	1.12	0.19	15.2	16.3	1.16
	200	1.03	0.10	17.5	18.5	1.33
CHAIN	1	1.61	0.18	1.89	3.50	0.30
Cruise 25	10	1.38	0.15	2.24	3.62	0.30
Station 463	25	1.20	0.16	2.50	3.70	0.33
40°00′N	50	0.77	0.24	3.38	4.15	0.38
65°00′W	75	0.41	0.34	7.30	7.71	0.61
4/IV/62	100	2.02	0.33	7.37	9.39	0.58
Fig. 3c	125	1.72	0.29	9.05	10.8	0.60
	150	1.85	0.24	12.1	13.9	0.88
	200	1.22	0.06	15.7	16.9	1.20

	Depth (m)	NH_4^+-N	NO_2^--N	$NO_2^- + NO_3^--N$	ΣN	$PO_4^{\equiv}-P$
SOUTH OF NOVA SCOTIA						
CHAIN	1	0.69	0.10	0.84	1.53	0.21
Cruise 25	10	1.42	0.10	0.96	2.38	0.21
Station 465	25	0.60	0.27	4.02	4.62	0.32
38°00′N	51	0.54	0.14	4.53	5.07	0.29
65°00′W	76	0.60	0.19	9.05	9.65	0.53
5/IV/62	102	2.10	0.12	10.4	12.5	0.61
Fig. 3c	128	1.01	0.05	11.2	12.2	0.71
	153	0.96	0.04	13.8	14.8	0.87
	204	0.96	0.03	17.4	18.4	1.13
CHAIN	1	0.09	0.17	0.74	0.83	0.12
Cruise 25	10	1.20	0.17	1.21	2.41	0.06
Station 467	25	0.50	0.20	1.18	1.68	0.10
36°00′N	50	1.14	0.18	0.92	2.06	0.12
65°00′W	75	1.18	0.18	0.85	2.03	0.06
6/IV/62	100	0.66	0.17	0.88	1.54	0.01
Fig. 3c	125	0.77	0.19	0.99	1.76	0.02
	150	0.97	0.20	1.34	2.31	0.02
	200	0.73	0.17	1.03	1.76	0.06