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Nitrogen uptake and phytoplankton growth in coastal upwelling regions[1]

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Abstract

Uptake of nitrogenous nutrients by microplankton off the Washington and Oregon coasts was measured during the 1985 upwelling period. Nitrogen uptake rates in low-NO_3^- waters (<5 μM) were 0.020–0.258 μmol N liter^{-1} h^{-1} and were primarily supported by regenerated nitrogen (71% of total uptake). Nitrogen uptake rates in high-NO_3 waters (≥20 μM) were 0.281–1.480 μmol N liter^{-1} h^{-1} and new (NO_3^-) nitrogen supported 83% of total uptake. Phytoplankton N was estimated by assuming a constant Chl *a*:PN for phytoplankton and was used to calculate phytoplankton-specific uptake rates.

Despite differences in nutrient concentrations, PN and Chl *a* at three upwelling sites (Oregon, Benguela, and Peru), NO_3^- uptake normalized to Chl *a*, and estimates of NO_3^--supported phytoplankton growth rates are remarkably similar. Nitrate uptake supports growth rates on the order of 1–2 d^{-1}. Estimates of phytoplankton growth from rates of NH_4^+ + NO_3^- uptake range from 1.36 to 4.79 d^{-1} and are negatively correlated with concentrations of NO_3^- and phytoplankton N. The apparent increase in phytoplankton growth rates for waters with lower nitrogen availability may result from heterotrophic bacterial utilization of NH_4^+ nitrogen.

The coastal regions of Oregon and Washington provide an opportunity for studying nitrogen utilization over a wide range of NO_3^- concentrations during the spring and summer upwelling period. Cold, nutrient-rich surface waters are found adjacent to the coast after periods of moderate to strong northern winds. Nearshore, cold waters form irregular north-to-south bands of high productivity and biomass. Surface NO_3^- concentrations decrease rapidly as nearshore waters move offshore, due to nutrient utilization by phytoplankton (Small and Menzies 1981). Frequent fluctuations in wind patterns cause large changes in upwelling intensity and hence surface water density within 15 km of shore. These changes in turn lead to NO_3^- distributions which are highly variable in space and time.

Upwelling areas are generally characterized by high concentrations of nutrients in surface waters, high productivity and biomass, and a high proportion of "new production" (sensu Dugdale and Goering 1967). Like the northeast Pacific coastal region, however, most areas of coastal upwelling are subject to significant spatial and temporal variability in these characteristics. In contrast, stratified oceanic regions exhibit strong seasonal variations but are more homogeneous, at least on short temporal scales. Interest in nutrient utilization by phytoplankton recently has been focused on the low-nutrient regions, in order to investigate potential nutrient limitation of phytoplankton growth. Detailed analysis of nutrient utilization in nutrient-rich regions is complicated by the heterogeneity of these systems, but is subject to fewer analytical problems with ^{15}N-tracer techniques than similar analyses in nutrient-impoverished areas (Dugdale and Wilkerson 1986).

A clearer understanding of the dynamics of nutrient availability and primary production in upwelling regions may aid in the interpretation and design of nitrogen utilization experiments in more nutrient-impoverished areas.

The major goal of this study was to examine the uptake of inorganic and organic nitrogen in coastal waters off Oregon and Washington during the upwelling season. This is the first reported study using ^{15}N tracers to measure uptake and regeneration of nitrogen in these waters. The relationships among nutrient concentrations, plant biomass, and NO_3^- utilization are examined in detail and compared to results derived from studies in other coastal upwelling regions.

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Methods

Sampling—Nitrogen uptake experiments were performed during July 1985, 8–115 km off the coast of Oregon and Washington (Fig. 1). Seawater samples from 15 m were collected aboard RV *Wecoma* with 30-liter Niskin bottles at 15 stations. Morning collection times were between 0530 and 0830 and midday collection times were between 1015 and 1445. A Wilden (model MP-2) air-driven pump with a double Teflon diaphragm was used aboard RV *Sacajawea* at station 0 to collect water from 10 m. The sample water was screened through 200-μm nylon Nitex mesh and pooled into 50-liter Nalgene carboys. The prescreened water from the 50-liter carboys was then transferred to 2.7-liter polycarbonate bottles for experimental incubations. Samples from each station were preserved in 5% glutaraldehyde for determination of relative abundance of phytoplankton genera. Subsamples of 1 or 10 ml were settled and examined with an inverted microscope.

Analyses—Nutrient analyses were performed on seawater after filtration through precombusted, glass-fiber filters (Whatman GF/F). Samples for dissolved NO_3^-, NO_2^-, and PO_4^{3-} were frozen (−20°C) in acid-washed polyethylene bottles and then measured onshore with a Technicon AutoAnalyzer. Dissolved NH_4^+ was measured manually aboard ship with the phenolhypochlorite reaction as described in Strickland and Parsons (1972), but scaled down to 10-ml volume. Ammonium concentrations were measured for each NH_4^+ incubation bottle for initial concentration and again at each sampling point. The mean precision (SD) of triplicate NH_4^+ analyses was 0.025 μM. Samples for dissolved urea were stored frozen in polyethylene containers for analysis onshore with the urease method (McCarthy 1970). A Sigma urease (type 4) preparation was used for the analyses instead of the Worthington urease preparation of McCarthy (1970). The Sigma enzyme preparation had lower NH_4^+ contamination and maintained higher activity over a longer storage period than did the Worthington. Standards for the urea determinations were assayed with 2,000-m filtered seawater which contained undetectable levels of both NH_4^+ and urea. The mean precision (SD) of duplicate urea analyses was 0.021 μM urea-N.

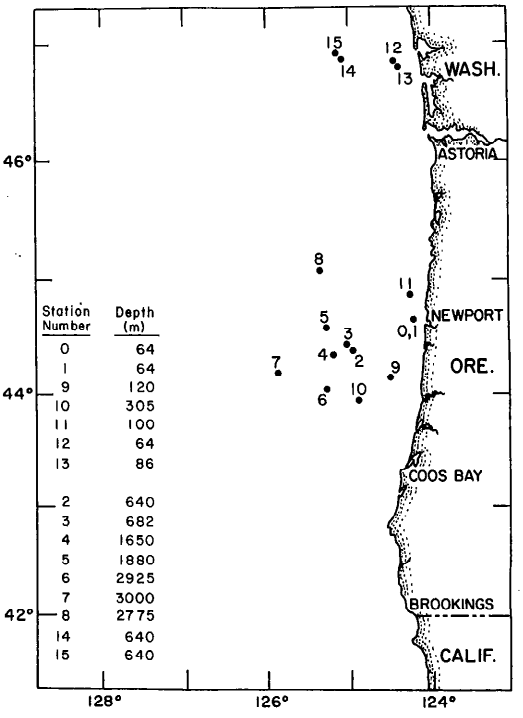

Fig. 1. Locations for low-NO_3^- stations (2–8, 14, and 15) and high-NO_3 stations (0, 1, and 9–13) off the coasts of Oregon and Washington.

Particulate material for Chl *a* and particulate nitrogen (PN) analyses was collected on 25-mm, precombusted, glass-fiber filters (Whatman GF/F) under vacuum (<180 mm of Hg). Chl *a* samples were stored frozen under vacuum for 1–2 weeks until analyses could be performed with a fluorometer (Turner Designs) following procedures described by Strickland and Parsons (1972) (mean C.V. for duplicates, 10.4%). Particulate nitrogen samples were stored frozen and then dried for 24 h at 60°C. Particulate nitrogen and carbon concentrations were determined with a Perkin-Elmer CHN ana-

lyzer (mean C.V. for duplicates, 3.6%). Subsurface light intensity was measured with a LiCor quantum/radiometer/photometer (model Li-185a). Light intensities at 0.5 m, at the time of water collection, ranged from 80 to 600 μEinst m^{-2} s^{-1}. Thus, light limitation of phytoplankton activity in the mixed layer was unlikely during our sampling.

Nitrogen uptake—Rates of nitrogen uptake were measured with simulated in situ conditions for bottle incubations with ^{15}N tracers for NO_3^-, NH_4^+, and urea (Dugdale and Goering 1967). Nitrate uptake was measured at 10 stations and urea and ammonium uptake were measured at all 16 stations. Uptake rates are presented in units of μmol N $liter^{-1}$ h^{-1}. The ^{15}N-uptake experiments commenced within 1–2.5 h of water collection, after larger zooplankton were removed by screening through 200-μm Nitex filters. Additions of 0.1 μM NH_4^+-N [$(^{15}NH_4)_2SO_4$, 99.7 atom%], 0.2 μM urea-N [$CO(^{15}NH_2)_2$, 95.1 atom%], and 2.9 μM NO_3^- ($Na^{15}NO_3$, 99.2 atom%) were made to separate incubation bottles.

Incubation bottles were covered with one layer of neutral-density screening to reduce the sunlight intensity by 50% and placed in Plexiglas deck boxes cooled by circulating surface seawater. Station 0 bottles were maintained near ambient temperature in a walk-in cold room and exposed to "cool white" fluorescent light screened to approximate in situ light intensity. Frequent sampling was used to assess and avoid potential underestimates of uptake rates caused by substrate depletion or isotope dilution. Ammonium uptake was measured at 0, 30, 60, and 120 min; urea uptake at 60, 120, and 180 min; and nitrate uptake at 120 and 240 min. Uptake experiments were ended by filtration (<180 mm of Hg) of 1.2–2.7 liters of seawater for collection of particulate matter onto 47-mm, precombusted, glass-fiber filters (Whatman GF/F). The filters were immediately frozen and then dried at 60°C for 24 h after return to the shore-based laboratory. Subsamples of the filtrates from the NH_4^+ incubation bottles were analyzed immediately for NH_4^+, and the rest of the sample was saved for determination of atom% ^{15}N of dissolved NH_4^+. Concentration and recovery of NH_4^+ for isotopic analysis was by steam distillation and subsequent evaporation (Glibert et al. 1982).

Samples were prepared for isotopic analysis by first converting organic and inorganic nitrogen to nitrogen gas with a dry micro-Dumas combustion (Fiedler and Proksch 1975). The atom% ^{15}N for samples was then determined by emission spectrometry (Fiedler and Proksch 1975; Harrison 1983) with a Jasco ^{15}N analyzer (model N-150 NIA-1). Details of sample preparation were adapted from LaRoche (1983) and are described by Wheeler and Kirchman (1986). When significant NH_4^+ regeneration occurred, NH_4^+ uptake measurements were corrected for isotope dilution as described below. Analogous procedures for the determination of urea isotope dilution are not yet available. Therefore rates of urea uptake may be underestimated for the "trace" addition experiments.

Ammonium uptake rates were calculated by dividing the rate of increases of ^{15}N in the particulate material (atom% ^{15}N) by the atom% enrichment of NH_4^+ in the dissolved pool (Glibert et al. 1982):

$$\text{Uptake} = \{[\text{d(atom\% } ^{15}\text{N of PN})/\text{d}t]/R\} \times \text{PN}$$

where R is the atom% enrichment of dissolved NH_4^+ during the incubation period, and PN is the amount of nitrogen in the particulate material (μmol N $liter^{-1}$). Three to four time points were used for each linear regression. The value of PN used for calculations was the mean for the incubation period and was determined from the initial measured value plus the increase resulting from measured nitrogen assimilation.

Daily (24 h) uptake rates were calculated from the short-term uptake rates with a 15-h uptake period for NO_3^- (photoperiod was 15 h) and a 24-h period for NH_4^+. Phytoplankton specific growth rates (μ) were calculated from the equation:

$$\mu = 3.32 \log_{10}[(\text{PP-N}_0 + \Delta\text{PP-N})/\text{PP-N}_0]$$

where PP-N_0 is the initial phytoplankton nitrogen, and ΔPP-N is the daily increase in phytoplankton nitrogen calculated from the measured uptake rates.

Ammonium concentration and atom%

Table 1. Physical parameters, nutrient concentrations, and biomass in the northeast Pacific. (Nondetectable—nd; no data available — dash.)

	Sta.	Location	Temp. (°C)	NO_3^-	NO_2^-	PO_4^{3-}	NH_4^+	Urea	PN	Chl *a* (μg liter^{-1})
				(μM)						
22 Jul	2	44°22.35′N, 124°57.55′W	16.5	1.2	nd	0.58	0.16	0.34	2.71	1.58
22 Jul	3	44°22.60′N, 124°58.30′W	—	0.8	nd	0.32	0.11	0.18	4.35	2.54
23 Jul	4	44°18.75′N, 125°11.51′W	17.2	0.7	nd	0.42	0.18	0.27	0.80	0.16
23 Jul	5	44°29.39′N, 125°15.47′W	18.0	0.6	nd	0.44	0.26	0.10	0.80	0.23
24 Jul	6	43°59.10′N, 125°16.47′W	13.0	3.3	0.11	1.06	0.51	nd	4.45	4.14
24 Jul	7	44°09.54′N, 125°52.54′W	16.0	0.8	nd	0.50	0.16	0.34	1.31	0.32
25 Jul	8	45°02.21′N, 125°15.60′W	16.5	1.1	nd	0.38	0.06	nd	1.08	0.22
29 Jul	14	46°50.13′N, 125°05.88′W	14.0	4.6	0.44	1.28	1.23	0.03	1.74	1.17
29 Jul	15	46°50.17′N, 125°07.02′W	14.3	2.3	0.23	1.16	0.84	0.04	2.76	1.86
3 Jul	0	44°40.00′N, 124°12.00′W	11.5	21.5	0.26	1.81	0.18	0.02	18.46	23.10
21 Jul	1	44°40.00′N, 124°12.00′W	11.8	49.1	0.39	4.26	0.27	0.03	3.25	5.17
25 Jul	9	44°06.47′N, 124°30.88′W	10.2	22.3	0.34	1.79	0.06	0.23	8.49	11.29
26 Jul	10	43°52.47′N, 124°54.83′W	10.2	20.1	0.36	2.06	0.62	0.10	6.51	11.12
27 Jul	11	44°50.98′N, 124°13.70′W	10.0	31.2	0.34	2.61	0.44	0.13	6.35	9.29
28 Jul	12	46°49.60′N, 124°26.30′W	11.7	36.9	0.69	3.12	0.16	0.35	3.72	5.31
28 Jul	13	46°49.24′N, 124°24.51′W	12.2	48.3	0.48	3.89	nd	0.34	1.70	1.95

enrichment were measured at each time point for the NH_4^+ incubations. When isotope dilution was significant (stations 1, 2, 4, 8, 11, and 14), the rate of decrease was determined by linear regression of ln R against time. The exponential mean value for atom% enrichment during the incubation period was then used to calculate uptake rate. When the change was not significant, the initial value for atom% enrichment of NH_4^+ ([tracer addition × 99.7]/[ambient + tracer]) was used.

Data for comparison with other upwelling areas are from the Peru and Benguela upwelling systems. The Peru data are from 6-h incubations of water collected from the 50% light depth and exposed to 50% of surface light intensities (Dugdale and Wilkerson 1986). The Benguela results are from unshaded, 4–6-h simulated in situ incubations for surface water samples (Probyn 1985). These two regions were selected on the basis of similar nutrient levels, temperatures, and incubation conditions. Isotope dilution of labeled NH_4^+ was not measured in either of these studies, however, and NH_4^+ uptake rates are likely to be underestimated. The use of 24-h incubations in many earlier studies precludes a more extensive regional comparison, since the effects of substrate depletion and isotope dilution may compromise rate estimates for NH_4^+ uptake.

Results

Physical and chemical parameters—Table 1 summarizes nutrient concentrations, biomass, and physical parameters for the 16 stations sampled in the northeast Pacific. Nitrate concentrations at 15 m were high (>20 μM) for shallow stations (<0.4 km) and low (<5 μM) for deeper stations (Fig. 2A). For stations deeper than 0.1 km, NO_3^- concentration and temperature were negatively correlated at temperatures <15°C (Fig. 2B). The range of NO_3^- concentrations observed during this study was extremely broad, i.e. 0.6–49 μM, and well distributed over that range.

For presentation of results, stations have been separated into two groups according to ambient concentration of NO_3^-. Shallow, nearshore stations with NO_3^- concentrations >20 μM (0, 1, and 9–13) are designated high-NO_3^- stations; deeper, offshore stations with NO_3^- concentrations <5 μM (2–8, 14, and 15) are designated low-NO_3^- stations. Water temperatures ranged from 10° to 12.2°C in nearshore, high-NO_3^- waters and from 13° to 18°C in offshore, low-NO_3^- waters.

Concentrations of regenerated forms of nitrogen (NH_4^+ + urea) ranged from 0.06 to 1.26 μM and were generally much lower than those of NO_3^- (Table 1). Urea concentrations were usually high (>0.15 μM)

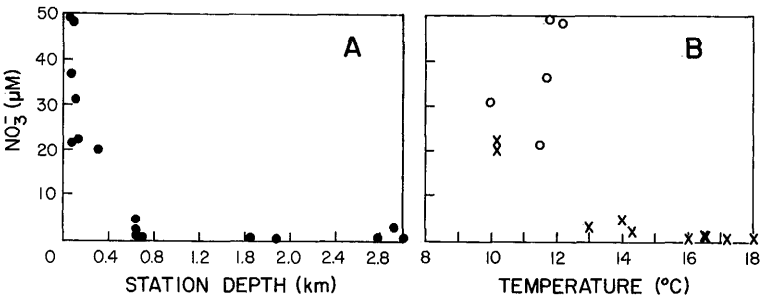

Fig. 2. Nitrate concentrations plotted vs. station depth (A) and temperature (B). Stations <0.1 km deep—O; stations >0.1 km deep—×.

when NH_4^+ was low (<0.2 μM); conversely, they were low (<0.15 μM) when NH_4^+ was high (>0.2 μM).

Biomass distribution—Both PN and Chl *a* concentrations were low in waters with lowest and highest NO_3^- concentrations, while biomass concentrations were highest in waters with intermediate levels of NO_3^- (Fig. 3). The data for the ratio of Chl *a* : PN arrange into two groups: high Chl *a* relative to PN in high-NO_3^- waters and low Chl *a* relative to PN in low-NO_3^- waters. A hyperbolic curve fits the data well, though it should be noted that no data are available for NO_3^- concentrations between about 7 and 20 μM (Fig. 3C). Differences were pronounced between the genera present in low- vs. high-NO_3^- waters. The unicellular diatoms *Rhizosolenia* and *Nitzschia,* and an unidentified naked dinoflagellate were abundant in low-NO_3^- waters, while the diatoms *Asterionella, Nitzschia,* and *Thalassiosira* were most abundant in high-NO_3^- waters. Most of the diatom genera present in high-NO_3^- waters were chain-formers. *Nitzschia* was abundant at both low- and high-NO_3^- stations; dominance at low-NO_3^- stations, however, occurred only at the higher NO_3^- concentrations within that group. The diatom *Chaetoceros* was common in both low- and high-NO_3^- waters.

Nitrogen uptake rates—The time-course of assimilation of $^{15}NH_4^+$ into PN was frequently nonlinear over the 2-h incubation period. The rate of accumulation of ^{15}N often decreased by the 1- and 2-h time points. Consequently, only the initial "linear" portion of the time-course data was used for calculating uptake rates. Isotope dilution was not significant during NH_4^+ uptake experiments at stations 0, 6, 10, and 12. For the remaining experiments, isotope dilution was significant, and the exponential mean atom% ^{15}N of dissolved NH_4^+ was used to calculate uptake rates. Details are reported elsewhere (Kokkinakis 1987; Kokkinakis and Wheeler in prep.). When isotope dilution is taken into consideration, the ratio of corrected : uncorrected uptake rates ranged from 1.10 to 2.39, averaging 1.65 (Kokkinakis 1987).

Nitrate uptake rates were positively correlated with ambient NO_3^- concentrations, ranging from 0.004 to 0.151 μmol N liter^{-1} h^{-1} in low-NO_3^- waters and from 0.245 to 1.248 in high-NO_3^- waters (Table 2). Ammonium and urea uptake rates were comparable to NO_3^- uptake in low-NO_3^- waters (0.002–0.095 μmol N liter^{-1} h^{-1}) but were much lower than NO_3^- uptake in high-NO_3^- waters (0.009–0.232 μmol N liter^{-1} h^{-1}: Table 2). Ammonium uptake was high in low-NO_3^- waters, ranging from 36 to 65% of total uptake with an average of 51%. Urea uptake was also important, ranging from 7 to 37% of total uptake with an average of 20%, while NO_3^- uptake ranged from 12 to 57% with an average of 28%. In high-NO_3^- waters, however, NO_3^- uptake was dominant, accounting for an average of 83% of the total nitrogen assimilated by the plankton. Ammonium uptake averaged 13% of the total, while urea uptake averaged only 4% of total. Thus, uptake of regenerated nitrogen (NH_4^+ and urea) was dominant (71%) in low-NO_3^- waters, and uptake of new nitrogen (NO_3^-) was dominant (83%) in high-NO_3^- waters.

We used an average Chl *a* : cell N of 2.25 (μg Chl *a* : μmol cell N) for phytoplankton

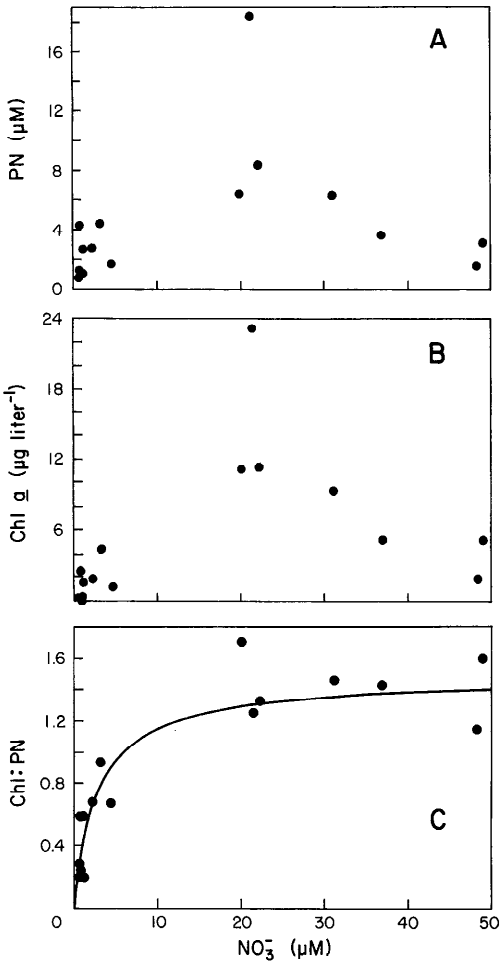

Fig. 3. Biomass plotted vs. NO_3 concentration. A. Particulate nitrogen (PN). B. Chl *a*. C. Chl *a*:PN. Parameters for the hyperbolic curve shown were determined from the Eadie-Hofstee linear transformation.

(Darley 1980) to estimate the portion of PN present as phytoplankton N. Phytoplankton N ranges from 9 to 76% of total PN (Fig. 4A). Knowing the portion of PN that is present as phytoplankton N, we can also calculate the rate of phytoplankton-specific NO_3^- uptake, which should be equivalent to the rate of NO_3^--supported phytoplankton growth. These rates of NO_3^--supported growth range from 0.21 to 1.88 d^{-1} (Fig. 4B).

Discussion

Physical and chemical parameters—Nitrate concentrations and water temperatures off the Oregon coast during this study were similar to surface measurements reported by Small and Menzies (1981). Highest NO_3^- concentrations and coldest waters occurred in the nearshore region. Conversely, lowest NO_3^- levels and warmest waters were found farther offshore (Table 1, Fig. 1). Small and Menzies (1981) recorded a surface temperature as low as 8°C, with a corresponding NO_3^- concentration of 30 μM during a strong upwelling period nearshore. Nearshore temperatures reported in this study were never <10°C, although NO_3^- concentrations were sometimes as high as 49 μM. These high concentrations may result from upwelling of elevated NO_3^- levels found at the bottom of the water column in waters <100 m deep during late summer (Small and Menzies 1981).

Table 2. Nitrogen uptake rates for the northeast Pacific. Rates are reported for only ten stations since NO_3^- uptake was not measured at six of the stations shown in Fig. 1.

Sta. No.	NO_3^- (μM)	Uptake (μmol N liter^{-1} h^{-1}) NO_3^-	NH_4^+	Urea	% new production
		Low NO_3			
4	0.7	0.004	0.018	0.011	12.1
8	1.1	0.013	0.032	0.008	25.0
2	1.2	0.044	0.074	0.069	23.6
6	3.3	0.151	0.095	0.020	57.0
14	4.6	0.005	0.013	0.002	25.0
		High NO_3			
10	20.1	0.438	0.084	0.019	81.0
0	21.5	1.248	0.232	0.059	81.1
11	31.2	0.694	0.125	0.019	82.7
12	36.9	0.245	0.026	0.021	84.0
1	49.1	0.383	0.050	0.009	86.7

The relationship of total PN (particles <200 μm) and Chl *a* to NO_3^- concentration followed the normal pattern for upwelled waters (Small and Menzies 1981; MacIsaac et al. 1985). Highest NO_3^- waters had relatively low PN and Chl *a* concentrations (sta. 1, 12, and 13), and stations with intermediate concentrations of NO_3^- (sta. 0, 10, and 11) had highest levels of PN and Chl *a*. Nitrate was utilized rapidly at high-biomass stations. For example, NO_3^- uptake at station 0 was 1.2 μmol N liter^{-1} h^{-1}. At this uptake rate, phytoplankton would deplete the 21 μM NO_3^- to <5 μM in 1 d, assuming no new inputs of NO_3^- and no

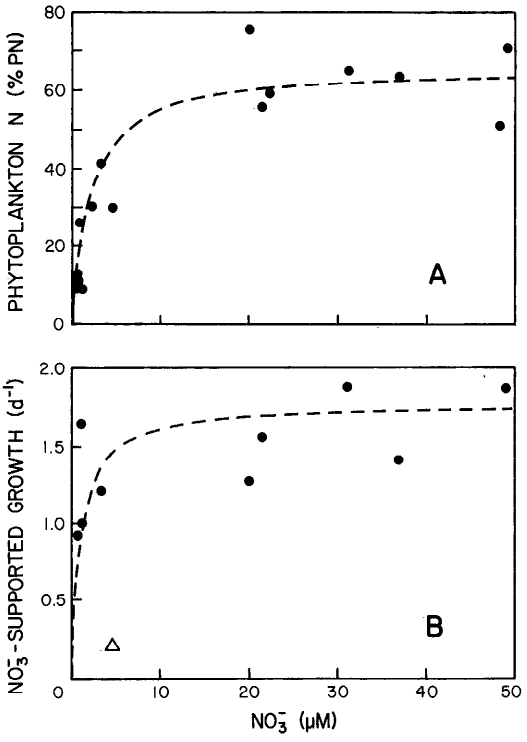

Fig. 4. A. Phytoplankton N plotted vs. NO_3^- concentration. B. NO_3^--supported phytoplankton growth rate plotted vs. surface NO_3^- concentration. Stations where NH_4^+ was <1 μM—●; station 14 where NH_4^+ was 1.23 μM and may have inhibited NO_3^- uptake—△. Parameters for the hyperbolic curves shown were determined from the Eadie-Hofstec linear transformation.

decrease in NO_3^- uptake rates in response to lowered concentrations of NO_3^-.

Mass balance for tracer incubations—Mass balance calculations indicate that more $^{15}NH_4^+$ left the dissolved pool than was recovered in the particulate fraction. The ratio of $^{15}NH_4^+$ removed from the dissolved pool: ^{15}N assimilated into PN ranged from 1.5 to 20.0, averaging 6.8 (Kokkinakis 1987; Kokkinakis and Wheeler in prep.). Laws (1984) reported a similar ratio of $^{15}NH_4^+$ removed to ^{15}N assimilated in PN (1.5–5.6, averaging 3.1) for rates reported by Glibert et al. (1982). Dugdale and Wilkerson (1986) also noted an imbalance between the removal of dissolved inorganic nitrogen (DIN), as $^{14}NH_4^+$ and $^{15}NH_4^+$ or NO_3^-, and the uptake of DIN into the PN fraction. They reported a ratio of net NH_4^+ removed from the dissolved pool: ^{15}N-estimated NH_4^+ uptake averaging 1.51. Similarly, the ratio of (NO_3^- removed: ^{15}N-estimated NO_3^- uptake) averaged 1.32. In an earlier study, Chan and Campbell (1978) found that only 40% of the $^{15}NO_3^-$ removed from the dissolved pool was accounted for in the particulate fraction (a ratio of 2.5). Together, these results imply that rates of ^{15}N-estimated uptake are likely to underestimate nitrogen utilization by plankton. Furthermore, the discrepancy appears to be larger for NH_4^+ than NO_3^-, especially in low-nutrient water.

Details of the mass balance calculations were presented by Kokkinakis (1987) and will be the subject of a later publication. The relatively constant concentration of NH_4^+ in most waters suggests that NH_4^+ uptake and regeneration are usually tightly coupled (Glibert 1982). The failure to recover all of the ^{15}N as dissolved NH_4^+ and nitrogen assimilated into the particulate fraction suggests that either NH_4^+ uptake rates are underestimated by current procedures or that NH_4^+ regeneration is overestimated. Uptake rates may be underestimated if excretion of labeled dissolved organic nitrogen occurs or if some of the nitrogen is taken up by microorganisms that pass through the glass-fiber filters used for these analyses. We have chosen to use the measured NH_4^+ uptake rates (assimilation) rather than the higher regeneration rates in an effort to draw conclusions on the conservative side. Implications of the alternate choice will be discussed below.

Regional comparison of uptake rates and estimated growth rates—Combined nitrogen uptake rates for NO_3^-, NH_4^+, and urea were on average 6.4 times greater in high-NO_3^- than in low-NO_3^- waters. Nitrate was quantitatively the most important nitrogen source at the high-NO_3^- stations (83% on avg). The average for total nitrogen assimilated in high-NO_3^- stations, 0.70 μmol N liter^{-1} h^{-1}, is close to averages reported by MacIsaac et al. (1985) (NO_3^- assimilation only) and Probyn (1985) in other upwelling regions (0.45 and 0.35 μmol N liter^{-1} h^{-1}, respectively).

In this study, PN, Chl *a*, and NO_3^- concentrations decreased in the offshore direction, but Chl *a*: PN was hyperbolically re-

Table 3. Biomass, nutrients, and nitrogen uptake in the Peru (Dugdale and Wilkerson 1986) and Benguela (Probyn 1985) coastal upwelling regions.

PN (μM)	Chl *a* (μg liter^{-1})	NO_3^- (μM)	NH_4^+ (μM)	Uptake rate (nmol liter^{-1} h^{-1})			Phytoplankton growth (d^{-1})			Phyto-plankton N (% total PN)
				NO_3^-	NH_4^+	Sum	NO_3^-	NH_4^+	Sum	
Northeast Pacific										
1.08	0.22	1.10	0.06	13	32	45	1.644	3.145	4.789	9.1
2.71	1.58	1.20	0.16	44	74	118	1.001	1.818	2.819	25.9
4.45	4.14	3.30	0.51	151	95	246	1.209	1.162	2.371	41.3
6.51	11.12	20.10	0.62	438	84	522	1.273	0.493	1.766	75.9
18.46	23.10	21.50	0.18	1,248	232	1,480	1.557	0.625	2.182	55.6
6.35	9.29	31.20	0.44	694	125	819	1.882	0.787	2.670	65.0
3.72	5.31	36.90	0.16	245	26	271	1.411	0.338	1.749	63.4
3.25	5.17	49.10	0.27	383	50	433	1.873	0.606	2.479	70.7
Peru upwelling										
9.39	18.30	9.42	0.37	462	225	687	0.932	0.735	1.667	86.6
9.10	5.65	11.05	0.48	178	282	461	1.095	1.885	2.980	27.6
3.33	1.48	13.55	0.72	50	97	147	1.148	2.174	3.322	19.8
2.58	1.88	17.20	0.24	86	59	145	1.401	1.434	2.835	32.4
3.90	2.61	18.62	0.24	121	94	214	1.415	1.555	2.970	29.7
3.16	1.87	18.76	0.28	5	107	112	0.120	2.035	2.156	26.3
2.30	1.12	24.00	0.17	0	78	78	0.000	2.255	2.255	21.6
2.45	0.94	24.50	0.27	70	91	161	1.881	2.629	4.510	17.1
Benguela upwelling										
6.79	5.56	1.05	0.22	229	31	260	1.311	0.379	1.690	36.4
8.93	7.88	1.45	0.24	186	57	243	0.887	0.476	1.363	39.2
4.36	2.14	1.90	0.11	443	21	464	3.078	0.613	3.692	21.8
8.00	7.08	6.84	0.92	254	114	368	1.196	0.903	2.099	39.3

lated to NO_3^- concentrations. In order to evaluate the generality of the relations observed among NO_3^- concentrations, biomass, and NO_3^- uptake in coastal upwelling areas, we compare our results with data sets from the Peru and Benguela upwelling regions in Table 3. The unimodal distribution of particulate nitrogen as a function of NO_3^- concentration observed in the northeast Pacific upwelling was not evident in the Benguela upwelling due to a much narrower range of NO_3^- concentrations there (Fig. 5A). Chl *a* (not shown), PN (Fig. 5A), and Chl *a* : PN (Fig. 5B) are positively correlated with NO_3^- at low NO_3^- concentrations, however, as was observed in the northeast Pacific.

In the Peru upwelling system (Fig. 5A, B) both PN and Chl *a* : PN were much lower at high concentrations of NO_3^- than in the northeast Pacific. Most of the available PN and NO_3^- uptake data for the Peru upwelling system are from sampling during 1976 and 1977. Unfortunately, there is evidence that Chl *a* levels and primary production are anomalously low for both of these years (Barber and Smith 1981). Mean integrated primary production for the Peru upwelling region was low (<2 g C m^{-2} d^{-1}) in 1977 and 1978 compared to 6.3 and 4.3 g C m^{-2} d^{-1} in 1966 and 1979 (Barber and Smith 1981). Low production in recently upwelled water has been attributed to either low seed populations in the upwelled water (Barber and Smith 1981) or to the need for conditioning of recently upwelled water before phytoplankton growth (Barber et al. 1971). High specific primary productivity but low Chl *a* at 23 m during the 1977 Peru sampling suggests that an abnormally low seed population was present during that year. The generality of the nutrient-biomass relations for the Peru upwelling region needs to be examined during more typical conditions.

Despite questions concerning biomass levels during the 1977 and 1978 Peru upwelling periods, the high specific primary productivity in 1977, 47 mg C(mg Chl *a*)$^{-1}$ h^{-1} (Barber and Smith 1981), suggests that

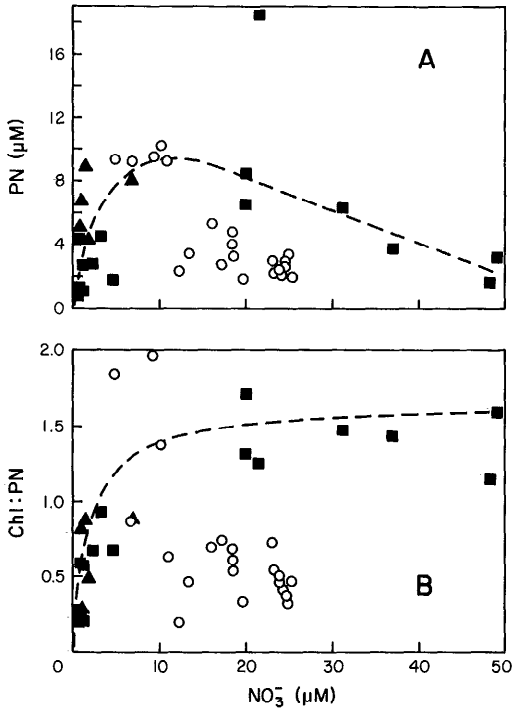

Fig. 5. Biomass plotted vs. NO_3^- concentration for regional comparison. A. Particulate N (PN). Curve was drawn by inspection. B. Chl *a* : PN. Northeast Pacific—■; Benguela upwelling region—▲; Peru upwelling—○. Hyperbolic curve shown is from Fig. 4 (northeast Pacific data).

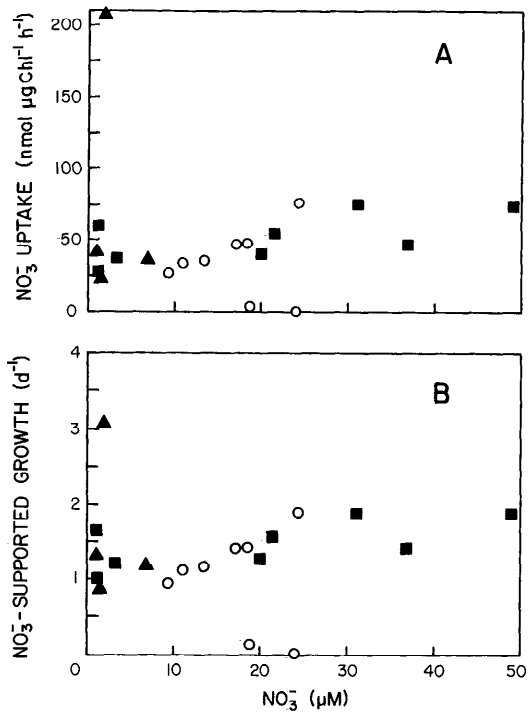

Fig. 6. Nitrate uptake rates (A) and NO_3^--supported phytoplankton growth rates (B) for regional comparison. Criteria used for data selection given in text. Symbols as in Fig. 5.

it is valid to compare uptake rates for all three upwelling areas after normalization to Chl *a* biomass. For comparison of uptake rates, only stations where $[NO_3^-]$ was >1.0 μM and $[NH_4^+]$ was <1.0 μM are included. Reasons for using these criteria were to eliminate the complications of enhanced uptake after nutrient additions and potential suppression of NO_3^- uptake by high ambient concentrations of NH_4^+. Excluding one high and two very low rates, NO_3^- uptake ranges from 25 to 75 nmol N (μg Chl *a*)$^{-1}$ h^{-1} (Fig. 6A). The presence of detrital PN and heterotrophic PN (microzooplankton and bacteria) leads to underestimates of nitrogen-specific uptake rates for natural assemblages of phytoplankton (Dugdale and Goering 1967); if we assume that the mean Chl *a* : PN for diatoms (2.25 μg Chl *a* : μmol cell N) reported by Darley (1980) is representative for phytoplankton in these upwelling regions, NO_3^- uptake supports phytoplankton specific growth rates of 1.0–2.0 d^{-1} (Fig. 6B).

If utilization of NH_4^+ is also included for the estimate of specific phytoplankton growth, then specific growth rates range from 1.4 to 4.8 d^{-1} (Table 3, Fig. 7). Inclusion of urea uptake would result in even higher estimates of growth rates for the northeast Pacific (Kokkinakis and Wheeler in prep.) and the Benguela (Probyn 1985) upwelling regions. Since urea uptake has not been measured for most upwelling systems (including Peru), however, it was not included in our estimates of phytoplankton growth rates for this study. In addition, it should be noted that the NH_4^+ uptake rates for the Peru and Benguela upwelling regions have not been corrected for possible isotope dilution and may be underestimates for that reason. Since maximum growth rates reported for temperatures ≤ 15°C are ~2 doublings per day (Eppley 1972), it is noteworthy that 50% of the data shown in Fig. 7B

indicate growth rates ≥ 2.5 d^{-1}. Either changes in Chl *a* : phytoplankton N or heterotrophic utilization of NH_4^+ nitrogen could lead to an overestimate of phytoplankton growth. The ratio Chl *a* : cell N for exponentially growing phytoplankton ranges from 1.17 to 3.50 μg Chl *a* (μmol N)$^{-1}$ (with a mean of 2.12) and appears to be similar for marine phytoplankton regardless of size or class (Parsons et al. 1961). Hence, it seems likely that a significant portion of the discrepancy between maximum rates of phytoplankton growth and the calculated rates summarized here must be due to heterotrophic utilization of NH_4^+ nitrogen.

Heterotrophic utilization of NH_4^+ nitrogen has been reported for other regions (Eppley et al. 1977; Laws et al. 1985; Wheeler and Kirchman 1986) and may account for these high estimates of phytoplankton growth in northeast Pacific coastal waters and other upwelling regions (Table 3). Examination of the relationship between estimated phytoplankton growth rates and the portion of total PN present as phytoplankton N further suggests that heterotrophic uptake of NH_4^+ increases as phytoplankton N becomes a smaller fraction of total PN (Fig. 7A). The implication of this result for lower trophic level nutrient dynamics is obvious. In recently upwelled water, phytoplankton biomass and activity are dominant. As the water ages, increased primary production is followed by an increase in secondary production. Secondary production can be attributed to both micro- and macrograzers and is known to be accompanied by an increase in bacterial production. We suggest that a significant portion of this bacterial production is supported by NH_4^+ nitrogen.

The percentage of new production in high-NO_3^- waters reported here for the northeast Pacific exceeds averages reported for similar regions. For example, Yoder et al. (1983) reported 50% new production over the continental shelf of the U.S. and Harrison et al. (1983) reported 67% in the Middle Atlantic Bight. Probyn (1985) found 48% new production in higher NO_3^- (8–25 μM) nearshore waters in the Benguela region, but also reported 71% in lower NO_3^- shelf waters (<7 μM). Ammonium inhibition of NO_3^- uptake may be responsible for the low percentage of new production at two of Probyn's three nearshore stations (NH_4^+ was 0.40 and 0.75 μM). Similar concentrations of NH_4^+ in our study (e.g. sta. 10 and 11) did not appear to inhibit NO_3^- uptake in high-NO_3^- waters.

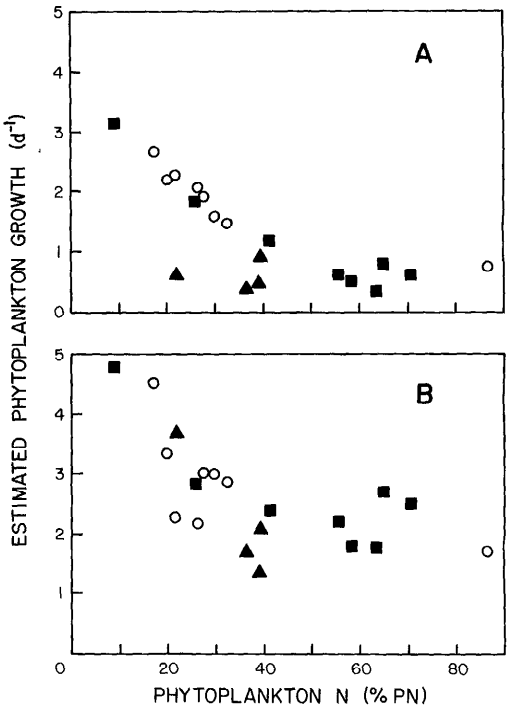

Fig. 7. A. Ammonium-supported growth rates plotted vs. phytoplankton N (as % total PN). B. Ammonium + NO_3^--supported growth rates. Symbols as in Fig. 5.

Minas et al. (1986) used hydrographic and chemical data to analyze productivity in several upwelling areas. They characterize the Peru, SW Africa, and Costa Rica Dome regions as high nutrient, low chlorophyll areas with slowly growing standing stocks. In comparison, the NW Africa upwelling region usually has high chlorophyll, low nutrient conditions (Minas et al. 1986). Further, Minas et al. hypothesized that the high nutrient, low chlorophyll conditions result from heavy grazing pressure and are also distinguished by a relatively low percentage of new production [$f < 0.5$, $f = NO_3^-$ uptake/NO_3^- + NH_4^+ uptake)]. Our results for the northeast Pacific contrast with this characterization in two ways: chlorophyll

biomass was highest when NO_3^- concentrations were still ≥ 20 μM (high nutrient, low chlorophyll conditions), and the percentage of new production was very high (81–87%, $f > 0.8$) in the recently upwelled waters. The high percentage new production in our study indicates that grazing pressure was relativley low in the high-NO_3^- waters and that conditions of high nutrient, high chlorophyll, and high percentage of new production characterize this situation.

Implications of underestimated NH_4^+ uptake rates—Harrison (1983) noted that substrate depletion and isotope dilution may result in a 3-fold to 10-fold underestimate of NH_4^+ uptake rates. More recent evaluation of results from tracer incubations indicate an additional problem. Rates of NH_4^+ regeneration measured by isotope dilution often exceed rates of NH_4^+ assimilation into particulate nitrogen. Harrison (1978) found that regeneration exceeded assimilation by averages of 30 and 54%, respectively, in Pacific coastal water and in the CEPEX mesocosm experiments. The mean ratio of regeneration : uptake for stations where both rate measurements are given was 10.6 in the regional study conducted by Glibert (1982). Harrison et al. (1983) also found that regeneration consistently exceeded uptake in the Middle Atlantic Bight but did not report the magnitude of the difference. For the coastal waters sampled during this study, the ratio of regeneration : uptake rates ranged from 1.1 to 44.1, with a mean value of 11.0 (Kokkinakis 1987). This mean is consistent with the ratio of ($^{15}NH_4^+$ removed from the dissolved pool : ^{15}N assimilated into PN) discussed previously.

The precision of measurements of NH_4^+ regeneration is usually not reported. When sufficient measurements have been made to estimate precision, however, the C.V. is relatively high, e.g. the mean C.V. for 20 experiments reported by Lipschultz et al. (1986) is 66.3%. The C.V. for regeneration rates that were significantly >0 in this study ranged from 5.4 to 51.7% with a mean value of 25.2% (Kokkinakis 1987). Hence one rationale for using assimilation rates, rather than regeneration rates, as a measure of NH_4^+ utilization is the greater precision that is usually obtained for assimilation rates (Glibert et al. 1982). Greater precision does not, however, imply greater accuracy. Inability to recover all ^{15}N as dissolved NH_4^+ and labeled particulate material and elevated regeneration rates relative to uptake rates both indicate that assimilation of ^{15}N into particulate material may actually underestimate rate of utilization.

Results presented in the literature (Glibert 1982; Laws 1984; Lipschultz et al. 1986; this study) indicate that rates of NH_4^+ uptake could be underestimated by a factor of 3–10. If NH_4^+ uptake is systematically underestimated, then current estimates of new production as a fraction of total production, NO_3^- uptake/(NO_3^- + NH_4^+ uptake), are overestimates. Furthermore, the estimates of phytoplankton growth rates reported here may be systematic underestimates. A 3-fold to 10-fold increase in estimates of "phytoplankton growth rates" would obviously result in unrealistically high rates, lending further support to our hypothesis concerning assimilation of inorganic nitrogen (i.e. NH_4^+) by heterotrophic rather than phototrophic organisms.

Conclusions

The results of this study demonstrate a clear relationship between Chl *a* : PN and ambient NO_3^- concentrations in an upwelling region. Assumption of a constant Chl *a* : cell N for phytoplankton was used to estimate the portion of particulate nitrogen present as phytoplankton. It allowed calculation of phytoplankton specific growth rates. Results from such calculations for three upwelling areas provide typical rates of maximal phytoplankton growth (1–2 d^{-1}) on NO_3^-. Inclusion of NH_4^+ as a nitrogen source and the assumption that all NH_4^+ uptake is by phytoplankton, however, indicate an unusually fast growth of phytoplankton. Since these estimated growth rates are inversely correlated with nitrogen availability and the percentage of total PN present as phytoplankton, we suggest that the discrepancy is due to heterotrophic utilization of NH_4^+ nitrogen.

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