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Gross and net nitrogen uptake and DON release in the euphotic zone of Monterey Bay, California

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Abstract

^{15}N tracer techniques were used to measure rates of NH_4^+ and NO_3^- uptake, dissolved organic nitrogen (DON) release resulting from both ammonium (NH_4^+) and nitrate (NO_3^-) uptake, and NH_4^+ regeneration at discrete depths throughout the euphotic zone in Monterey Bay, California, at a site, H3, outside the plume of direct upwelling influence. In March 1993, 94% of the inorganic nitrogen taken up was NH_4^+, and the primary fate of nitrogen uptake was particle production. In September 1993, NH_4^+ and NO_3^- uptake were more in balance, and the primary fate of nitrogen uptake was DON. We suggest that grazing was an important mechanism resulting in DON release in March and that a combination of grazing and a more physiologically stressed phytoplankton population produced the higher observed rates of DON release in September. During both cruises, the percentage of nitrogen released as DON increased with depth, suggesting that deeper in the water column, a smaller percentage of the nitrogen taken up is incorporated into sinking particles. Based on these data, we suggest that the DON pool acts as an intermediate between DIN assimilation and the net formation of particles for export and will thus affect carbon flow in Monterey Bay.

Primary production in marine systems can be characterized as new or regenerated depending on the nitrogen substrate used; NO_3^- is generally considered to fuel new production (in the absence of significant dinitrogen fixation), while NH_4^+ fuels regenerated production (Dugdale and Goering 1967; Eppley and Peterson 1979). Oceanographers have used ^{15}N-labeled NO_3^- and NH_4^+ to measure nitrogen uptake rates and thus estimate rates of new and regenerated production assuming that uptake of ^{15}N label into the cell results in the production of biomass. This assumption, however, is not completely valid. The disappearance of ^{15}N label from the NH_4^+ or NO_3^- substrate pool is often not balanced by an equal appearance of ^{15}N in particulate nitrogen (PN; Glibert et al. 1982; Price et al. 1985; Ward et al. 1989; Slawyk et al. 1990). This observation led some researchers to hypothesize that DON was an alternate fate for the missing ^{15}N (Laws 1984; Ward et al. 1989)

Researchers have now directly measured the passage of ^{15}N label from the NH_4^+ or NO_3^- substrate pool into the DON pool (Bronk and Glibert 1991, 1993*a*,*b*, 1994; Bronk et al. 1994; Slawyk and Raimbault 1995). If ^{15}N is present in the DON pool at the end of an incubation, then accounting for the accumulation of ^{15}N exclusively within the PN fraction results in an underestimate of the amount of nitrogen taken up by the cell during the incubation. To obtain a better estimate of the total amount of nitrogen taken up, the amount of ^{15}N that accumulates in both the PN and DON pools over time must be quantified. Bronk et al. (1994) used the term ''net uptake rate'' to denote the rate of accumulation of nitrogen in the PN pool and ''gross uptake rate'' to denote the total rate of nitrogen uptake, which includes both PN and DON production. They found that an average of 32 ± 17% of the nitrogen taken up as NH_4^+ or NO_3^- was released as DON in environments ranging from relatively eutrophic estuaries to the oligotrophic ocean (Bronk et al. 1994). Hu and Smith (1998) found that 15 ± 12% of the NO_3^- taken up was released as DON in the Ross Sea, Antarctica. Thus, DON release appears to be a significant flux of both organic nitrogen and associated carbon.

The work described above shows that release of ^{15}N to the DON pool should be considered, either via direct measurements or theoretically, when interpreting nitrogen uptake data. The next question is the significance and magnitude of this phenomenon from an ecological standpoint. The debate over whether dissolved organic matter (DOM, including dissolved organic carbon [DOC] and DON) release is an ecologically relevant process or merely an experimental artifact has persisted for decades. Significant rates of DON release (regardless of the mechanism of release—e.g., passive exudation or cell breakage during grazing) are consistent with the idea that microbial food webs are quantitatively important to elemental flux in aquatic systems. Substantial rates of DON release are also suggested by a number of experimental and large-scale oceanographic observations.

Experimentally, DON release has been indicated or quantified with a wide array of analytical techniques. First, as noted above, the importance of DON release has been hypothesized based on deficits in ^{15}N mass balances (Glibert et al. 1982; Laws 1984; Ward et al. 1989). Second, Collos

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et al. (1992), using wet chemical analyses, demonstrated high rates of release and reincorporation of DON as a result of NO_3^- and NH_4^+ uptake in batch cultures. Third, in the equatorial Pacific, Eppley and Renger (1992) found that more NO_3^- was removed from solution than was indicated by ^{15}N-based NO_3^- uptake rates, which suggests that there is another unmeasured nitrogen flux that needs to be considered. Fourth, off the coast of Oregon, Dickson and Wheeler (1995) found that NH_4^+ concentrations decreased in 80% of their experiments, although regeneration rates, measured with ^{15}N, were usually greater than uptake rates. They note, but do not supply actual data, that when uptake rates were corrected for loss of ^{15}N label to the DON pool, NH_4^+ uptake and regeneration were in balance. Finally, release of ^{15}N to the DON pool has been measured in a wide range of environments, suggesting the ubiquitous nature of DON release (Bronk at al. 1994; Slawyk and Raimbault 1995; Hu and Smith 1998).

Significant rates of DON release are also suggested by larger scale field measurements. First, in a number of field studies, inverse relationships between NO_3^- and DON concentrations have been observed, which suggest a transfer and accumulation of nitrogen from a dissolved inorganic to a dissolved organic form. Such a trend was documented in the English Channel (Butler et al. 1979), the subarctic Pacific (Maita and Yanada 1990), and Chesapeake Bay (Bronk et al. 1998). Second, imbalances between estimates of new production, measured as NO_3^- uptake, and loss of nitrogen via sinking particles suggest a possible role for DOM in balancing nitrogen budgets (Toggweiler and Carson 1995). In the equatorial Pacific, NO_3^--based new production was 10–20 mmol N m^{-2} d^{-1} (McCarthy et al. 1996); loss of nitrogen in the form of sinking particles, however, was only 0.3–0.6 mmol N m^{-2} d^{-1} (Buesseler et al. 1995). Buesseler et al. noted that ''the general conclusion is that a significant fraction of total production leaves the equator as a horizontal advective DOM flux, rather than a vertical particulate organic carbon (POC) flux.'' These new production and particle flux data suggest that, on the time scale of the measurements, a large fraction of the NO_3^- taken up and assumed to be the new production (which, in theory, should be returned to the deep ocean as PN) did not find its way into sinking PN but was released as DON instead. Finally, Libby and Wheeler (1997) measured PN and DON concentrations in longitudinal transects across the equator in the Pacific. Their data suggest that 37 $\pm$ 14% and 81 $\pm$ 54% (mean $\pm$ SD) of net NO_3^- depletion accumulates as DON to the north and south of the equator, respectively, again suggesting substantial DON release as a result of inorganic nitrogen assimilation.

Despite the large amount of evidence that suggests the importance of DON release, there are few direct measurements of this process in the field (Bronk et al. 1994) and no systematic information on regional, seasonal, or depth patterns. In the present study, we investigated the quantitative relationship between net and gross nitrogen uptake and DON release in Monterey Bay during May and September 1993 to measure rates of DON release directly and thus provide a more detailed understanding of nitrogen flux in that system. These data are the first vertical profiles of DON release directly measured in the ocean. The specific objectives of this study were (1) to quantify the flux of NH_4^+ and NO_3^- into the PN fraction and subsequently into the DON pool using ^{15}N tracer techniques; (2) to use these data to estimate rates of gross and net NH_4^+ and NO_3^- uptake and DON release, resulting from both NH_4^+ and NO_3^- uptake; and (3) to reexamine the balance between new and regenerated production.

Our study site, Monterey Bay, is the largest open bay on the west coast of the U.S. The Bay is situated in an eastern boundary region and generally experiences seasonal upwelling between March and October (Rosenfeld et al. 1994). The site where our experiments were performed, H3, was located in the center of the Bay and was outside the plume of direct upwelling influence. The hydrography at H3 is controlled more by the California Current system than by active upwelling centers directly. During both cruises, we sampled a water mass that was likely composed of aged upwelled water that was transported via the California Current. Previous work by Chavez and Smith (1995) and Pilskaln et al. (1996) in Monterey Bay suggests a possible role for DON in balancing nitrogen budgets in this system. For example, in the spring upwelling period in 1991, POC export accounted for only 52% of NO_3^--based new production. Did the remaining 48% of new production produce DON and not sinking particles? Here, we present evidence that DON production is a quantitatively important process in Monterey Bay and that it is a feasible explanation to balance the discrepancy between new production and particle flux estimates.

Methods

Field sampling—Water was collected, using 10- or 30-liter Niskin or Go-Flo bottles, from within the euphotic zone at Sta. H3 (36°46.7′N, 122°01.0′W; *see* map in Pilskaln et al. 1996). Uptake experiments were performed with water from six depths in March 1993; night incubations were performed on 13 March 1993, and day incubations were performed the following morning. In September, five depths were sampled; both day and then night incubations were performed on 26 September 1993. Depths were chosen to span the range of nitrogen and light environments within the euphotic zone. During each cast, temperature, salinity, and fluorescence were measured with a SeaBird CTD.

Ambient nitrogen and pigment concentrations—Water from each depth of the vertical profile was filtered through precombusted (450°C for 2 h) Whatman GF/F filters. The filter was retained and used to measure the concentration of chlorophyll *a* (Chl *a*), and the filtrate was frozen for later determination of nutrient concentrations in the laboratory. Concentrations of NO_3^- and NO_2^- were measured with a Technicon AutoAnalyzer, and concentrations of NH_4^+ were measured manually with the phenol/hypochlorite technique (Grasshoff et al. 1983). We defined DON as organic nitrogen < 0.2 μm as measured with ultraviolet (UV) oxidation. The concentration of DON was measured by the UV oxidation technique (Armstrong and Tibbits 1968); H_2O_2 was added (50 μl per 20-ml sample), and samples were irradiated for 18 h with a 1,200-W Hg vapor lamp. We routinely made

NH_4^+ additions to artificial seawater and measured an oxidation efficiency of ≥94%. Concentrations of Chl *a* were measured according to the fluorometric technique in Parsons et al. (1984) after grinding the filter in acetone and allowing the ground filter to extract in acetone overnight. Concentrations of PN and particulate carbon (PC) were measured on precombusted GF/F filters collected at the end of the incubation; PN and PC filters were analyzed with a Control Equipment carbon–hydrogen–nitrogen (CHN) analyzer.

Uptake and regeneration of inorganic nitrogen—Rates of NH_4^+ and NO_3^- uptake were measured with ^{15}N tracer techniques using 0.1 μg-at N l-1iter additions for both NH_4^+ and NO_3^- incubations. All ^{15}N, ^{14}C, and ^3H tracer incubations were done in on-deck flow-through incubators constructed of clear Plexiglas under simulated in situ light and temperature conditions; light was attenuated with blue Plexiglas shields and neutral density screens. Experiments were done in 4-liter polycarbonate bottles, and samples were incubated for between 4 and 6 h. At the end of each incubation, samples were filtered through precombusted GF/F filters. Filters were subsequently dried at 50°C and ampoulated using the micro-Dumas method (Barsdate and Dugdale 1965). PN atom percent enrichment samples were analyzed either on a Jasco emission spectrometer (model N-150; Fiedler and Proksch 1975) or on a Europa 20/20 mass spectrometer. The filtrate from the NH_4^+ incubation was collected and frozen for later determination of ^{15}N atom percent enrichment of the NH_4^+ pool; these data were used to calculate the rate of NH_4^+ regeneration and to correct the NH_4^+ uptake rates for isotope dilution (Glibert et al. 1982; Glibert and Capone 1993).

Size fraction concentration experiments—In September, we incubated additional water at 20 and 40 m that was concentrated twofold with respect to the >10-μm fraction, which likely consisted of grazers and larger phytoplankton prey. We concentrated the sample by filling a 1-liter beaker with water and then gently depressing a piece of polyvinyl chloride tubing, with 10-μm Nitex mesh attached to the bottom, into the sample. We drew off 500 ml of the <10-μm filtrate. $^{15}NH_4^+$ additions were made to the remaining water, which now had a concentration of the >10-μm fraction approximately twice that of the original water, and rates of NH_4^+ uptake, DON release, and NH_4^+ regeneration were measured.

Isolation of the DON pool—We developed a new technique for isolating the DON pool for use in these studies. At the end of the incubations, an aliquot from each of the NH_4^+ and NO_3^- incubations was passed through a 0.2-μm Supor filter, to remove small organisms (Bronk and Glibert 1994), and frozen. In the lab, DON was isolated with a series of chemical manipulations designed to remove the ^{15}N-labeled inorganic NH_4^+ and NO_3^- present in the sample. To isolate the DON pool from NH_4^+ incubations, the pH of the samples was elevated slightly (to pH 8.9), and the NH_4^+ was removed with vacuum distillation (Glibert et al. 1982). The pH was increased by adding 0.125 M sodium borate buffer (1 ml added to a 200-ml seawater sample); borate buffer was used rather than the commonly used MgO out of concern for loss of $DO^{15}N$ to the NH_4^+ pool due to base hydrolysis. The NH_3 evolved was captured by bubbling through 0.0024 N HCl, which was subsequently boiled down and spotted onto a precombusted GF/F filter and analyzed on an emission spectrometer.

In the case of NO_3^- incubations, 200 ml of seawater was brought just to the boiling point after the addition of 5 ml of a saturated MgO solution (MgO was precombusted overnight at 500°C) and 2.0 g of DeVarda's Alloy. The addition of DeVarda's Alloy reduces NO_3^- and NO_2^- to NH_3, which is lost during boiling. We found that the DeVarda's Alloy was contaminated with nitrogen when purchased. To wash the alloy, it was stirred on a hot plate set on low in 0.01 N NaOH for ~1 h. After heating, the alloy was rinsed with 10% HCl and then with copious amounts of Milli-Q water and placed in a muffle oven (100°C) for several hours until dry. We also found that grinding the alloy with an electric mortar and pestle, thereby increasing its surface area, increased the alloy's efficiency.

In the case of NH_4^+ incubations, the concentrate remaining after the steam distillation contained $DO^{15}N$ and any unlabeled NO_3^- and NO_2^- present in the sample; we did not physically remove the unlabeled NO_3^- and NO_2^- but corrected the final DON atom percent enrichment mathematically. In the case of NO_3^- incubations, the concentrate remaining after boiling with DeVarda's contained only $DO^{15}N$. Both types of concentrates were transferred to a 100-ml quartz tube, H_2O_2 was added (50 μl per 20 ml seawater), and the concentrates were UV oxidized for 18 h (Armstrong and Tibbits 1968). After the oxidation, all the DON in the sample was then in the form of NO_3^-. The resulting NO_3^- was reduced to NO_2^- by shaking the sample with spongy cadmium for 1.5 h (Jones 1984); spongy cadmium was used because it allowed a large number of samples to be reduced simultaneously.

The NO_2^- produced was isolated by successive treatments with an aniline solution, then a β-naphthol solution, and finally an extraction with trichloroethylene (TCE; Olson 1981). The isolated DON, now in the form of an azo dye dissolved in the TCE, was evaporated down in a fume hood, spotted onto a precombusted GF/F filter, and the nitrogen atom percent enrichment measured with an emission spectrometer. The concentration of DON, now in the form of NO_2^-, present in the final NO_2^- extract was calculated. We note that for every 1 μg-at N present as NO_2^-, there was 1 μg-at N present as aniline that was introduced in the extraction process; we corrected for the presence of this aniline when calculating the final DON atom percent enrichment. We spotted only enough of the extract onto the precombusted GF/F filter to provide the 5 μg of nitrogen needed for analysis on the emission spectrometer. This procedure allowed us to duplicate, and often triplicate or better, the final DON atom percent determination.

We recovered 91.5 ± 19.4% of the DON initially present from NH_4^+ incubations and 78.4 ± 17.5% of the DON from NO_3^- incubations with these protocols. The loss of DON associated with these isolation procedures occurs primarily during the initial distillation step for samples from NH_4^+ incubations and during the boiling with DeVarda's Alloy for

samples from NO_3^- incubations. We have used this method on samples from a number of different environments, and occasionally, the DON recovery efficiency for filtrates from NO_3^- incubations is quite low (<50%). This is likely due to differences in DON pools and the harsh conditions generated by the DeVarda's Alloy. Isolation efficiencies must be checked on every sample.

We removed 100% of the NH_4^+ in samples from NH_4^+ incubations and 100% of both the NH_4^+ and NO_3^- in samples from NO_3^- incubations. We note, however, that removal of NH_4^+ and NO_3^- was monitored via wet chemical analysis of the concentrations of NH_4^+ and NO_3^- in the sample just prior to UV oxidation; the detection limit of these analyses is $\pm$ 0.03 μg-at N liter^{-1}. Though individual ^{15}N incubations were not routinely duplicated, all chemical analyses of the various nitrogen concentrations and ^{15}N atom percent enrichments were done in duplicate or better.

Nitrogen rate calculations—Net uptake rates of NH_4^+ and NO_3^- were calculated according to the commonly used equations introduced by Dugdale and Goering (1967). In the case of NH_4^+ incubations, the atom percent of the NH_4^+ pool was corrected for isotopic dilution (Glibert et al. 1982). Rates of NH_4^+ regeneration were calculated according to Glibert et al. To calculate gross NH_4^+ and NO_3^- uptake rates, we first calculated the gross atom percent enrichment of the PN, which included ^{15}N measured in both the PN and the extracellular DON pools (Bronk et al. 1998). To calculate the final gross uptake rate, we substituted the gross PN atom percent enrichment for the net PN atom percent enrichment in the traditional uptake equation (Bronk et al. 1998); the mean coefficient of variation (C.V.) of all gross uptake rates presented is 11.6. The rate of DON release was determined as the difference between the gross and net uptake rates of NH_4^+ or NO_3^- (Bronk et al. 1998); the mean C.V. of all DON release rates presented is 40.0. To calculate daily rates, we multiplied the day rate by 14 h and the night rate by 10 h and then summed the two.

Primary and bacterial production—We measured primary and bacterial production to assess water-column conditions during our experiments. Water availability and time constraints required that primary production and bacterial production measurements be made when nitrogen uptake experiments were not underway.

Primary production was measured with standard ^{14}C techniques. Incubations were done in triplicate 250-ml acid-washed polycarbonate bottles. Each bottle received 75 μCi of $H^{14}CO_3^-$ and was incubated for 6 h under simulated in situ light conditions (*see above*). Incubations were ended by filtration onto 0.2-μm 47-mm Supor filters. One set of triplicates was incubated in light-tight bottles, and the dark uptake was subtracted from the light values to report photosynthetic carbon incorporation. Primary production experiments were started at dawn or midday.

Bacterial production was measured using standard dual-label, ^3H-thymidine (thy) and ^{14}C-leucine (leu), incorporation methods. Aliquots (20 ml) were measured into duplicate 50-ml Corning polycarbonate tubes directly from the Niskin or Go-Flo bottles and uniformly labeled with thy to a final concentration of 10 nM and leu to a final concentration of 20 nM. Tubes were incubated for 1 h in the on-deck incubators, filtered onto 0.2-μm 25-mm Poretics polycarbonate filters, and extracted as described in Chin-Leo and Kirchman (1988). We report production rates in units of nmol $\cdot$ 10^{-3} thy or leu liter^{-1} h^{-1} to avoid the use of uncertain conversion factors.

Results

We present data on ambient conditions, day/night differences in uptake and release rates, results from the grazer experiments, calculations of daily nitrogen flux rates, and estimates of turnover times of the various nitrogen pools. We highlight data in March that illustrate the dominance of NH_4^+ flux, the evidence for advection during the cruise, and the importance of grazing. The September data presentation focuses on the high rates of DON release and potential mechanisms to account for them.

Ambient nitrogen and Chl a *concentrations*—During both cruises, the depth of the mixed layer was deeper than the 1% light depth (Fig. 1). Although the surface temperature was similar during both cruises, salinity and fluorescence profiles indicate the water column was more stratified in March (Fig. 1). Concentrations of NO_3^- were low at the surface (Fig. 2); the nitracline began between 30 and 40 m, and NO_3^- concentrations increased to a maximum of ~45 μM at 500 m and remained high to the bottom at ~900 m (data not shown). Concentrations of DON were slightly higher at the surface and decreased to an approximately constant 4 μM below the euphotic zone (data not shown).

Day/night differences in nutrient and Chl *a* profiles were more pronounced in March than in September (Figs. 2, 3). In March, DON concentrations increased by >4 μM in the 12 h between the night measurement and the day measurement the following morning, while NH_4^+ concentrations decreased over the same period (Fig. 2). In March, Chl *a* concentrations were three to five times higher at night in the upper 10 m (Fig. 3); large day/night differences were not observed in September.

Nitrogen uptake and release rates—Specific NH_4^+ uptake rates were higher than specific NO_3^- uptake rates on both cruises; NH_4^+ uptake rates were up to 34 times higher in March and about five times higher in September (Fig. 4; specific uptake rates are plotted as averages of the day and night rates). In March, specific NH_4^+ uptake rates were also much higher at the surface and decreased with depth; no pronounced depth gradient within the euphotic zone was observed in September (Fig. 4). We observed no significant day/night differences in specific NH_4^+ uptake rates. Specific NO_3^- uptake rates, however, were an average of three and eight times higher during the day than at night in March and September, respectively (data not shown).

In March, both gross and net NH_4^+ uptake rates increased at night (Fig. 5); no such pattern was observed in September (Fig. 6). Net and gross NO_3^- uptake rates, however, were higher during the day during both cruises (Figs. 5, 6). Rates of DON release, resulting from NH_4^+ uptake, were higher at

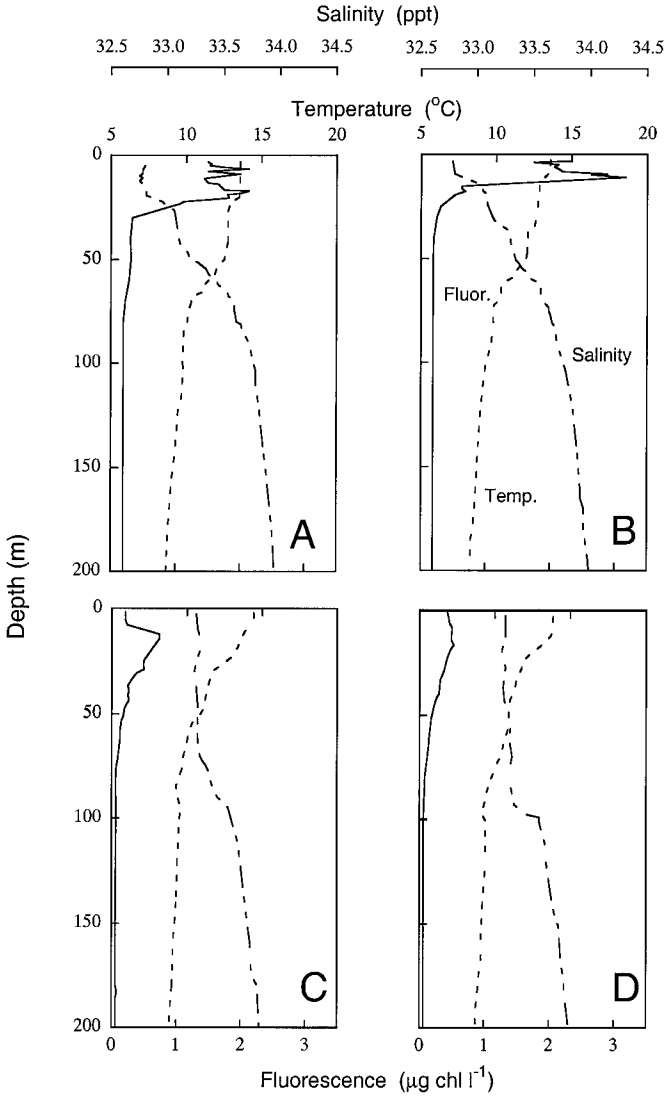

Fig. 1. Hydrographic profiles of fluorescence (solid line), temperature (dashed line), and salinity (dash–solid–dash) in March (A, day; B, night) and September (C, day; D, night) in Monterey Bay.

night in March (Fig. 5) but similar during the day and night in September (Fig. 6). Much more DON was released as a result of NH_4^+ utilization in March, while DON release rates as a result of NH_4^+ and NO_3^- uptakes were more similar in September. In September, an inverse relationship existed between rates of DON release resulting from NH_4^+ uptake and rates of primary production during the day ($r^2 = 0.86$; $n = 5$) and at night ($r^2 = 0.97$; $n = 5$), apparently due to the decrease in primary production with depth.

During both cruises, rates of NH_4^+ regeneration were higher at night than during the day (Fig. 7). Rates of NH_4^+ regeneration were also approximately three times higher in March than in September. When depth-integrated net and gross NH_4^+ uptakes were compared to depth-integrated NH_4^+ regeneration, uptake was over twice as high as regeneration in March, but regeneration was greater than uptake in September (Table 1). These trends were consistent regardless of whether day, night, or daily rates were used in the comparison. In general, the ratio of NH_4^+ uptake to regeneration was higher near the surface and decreased with depth on both cruises (Table 1).

Size fraction concentration experiments—In September during the day, 67% (65 and 70% for 20 and 40 m, respectively) of the Chl *a* was in the <10-μm fraction. In the night experiment, this fraction was smaller, 23 and 50%, respectively. The percentage of PN in the <10-μm fraction was 47–67% with no clear day/night differences. In September, doubling the >10-μm fraction in NH_4^+ incubations increased the rate of DON release by up to a factor of two during the day and up to a factor of three at night, suggesting that the larger size fraction was largely responsible for the release (Fig. 6). Rates of NH_4^+ regeneration were up to 73% higher in the treatment with the added >10-μm fraction (Fig. 7).

Daily rates—In March, the daily rate of total gross DIN uptake (NH_4^+ and NO_3^- combined) was 11 times greater than that measured in September (Fig. 8). Uptake of NH_4^+ accounted for 94% of the depth-integrated DIN uptake measured in March and 67% of the depth-integrated DIN uptake measured in September. Despite the large differences in NH_4^+ uptake rates, DON release resulting from NH_4^+ utilization was similar during both cruises (Fig. 8; note the large change in the x-axis). Accordingly, the ratio of DON release to gross uptake was much higher in September; the ratio of total DON release (from NH_4^+ and NO_3^- uptake) to total gross DIN uptake was 0.20 ± 0.20 in March and 0.68 ± 0.19 in September. DON release, as a percentage of gross DIN uptake, tended to increase with depth (Fig. 9) and was also higher at night during both cruises (data not shown). During both cruises, >90% of the NO_3^- taken up at the base of the euphotic zone was released as DON (Fig. 9).

Turnover times—The turnover times for NH_4^+ were shorter than for NO_3^- on both cruises (Table 2). In March, turnover times of NH_4^+ increased by over a factor of 20 between 1 and 19 m (Table 2). In September, NO_3^- turnover times increased by a factor of five between 1 and 40 m (Table 2). Turnover times for PN, estimated by dividing the ambient PN concentration by the total gross DIN uptake rate, averaged 0.33 d in March and 1.7 d in September (Table 2). The longest turnover times were for DON, with mean times of 5.0 d in March and 8.2 d in September (Table 2).

f-ratios—We recognize the severe limitations of the use of the *f*-ratio to estimate export production (Bronk et al. 1994). We present data on *f*-ratios here, however, to illustrate the effect of DON release on this historically important parameter. In March, *f*-ratios calculated with net or gross uptake rates were approximately the same in the upper 10 m and were ≤0.10 (Table 3). At the base of the euphotic zone, however, the *f*-ratio increased by a factor of five when gross uptake rates were used in the calculation (Table 3). The *f*-ratios calculated from daily rates integrated throughout the euphotic zone were 0.06 in March, regardless of whether net or gross rates were used in the calculation (because the high *f*-ratio at the deepest depth did not contribute greatly to the depth-integrated ratio). In September, *f*-ratios were higher

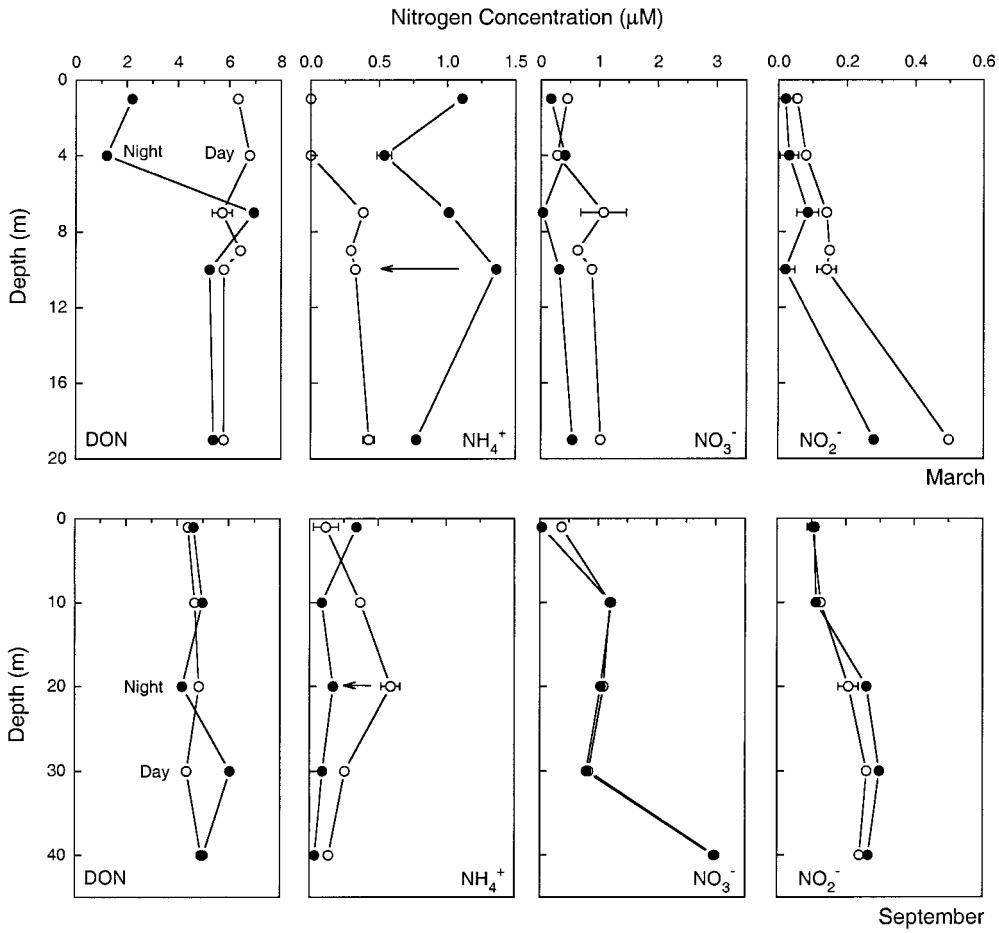

Fig. 2. Vertical profiles of ambient DON, NO_3^-, NO_2^-, and NH_4^+ during the day (○) and night (●) in Monterey Bay during March (upper panels) and September (lower panels). Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

than in March, and the difference between *f*-ratios calculated with gross vs. net uptake rates was greater throughout the euphotic zone; *f*-ratios calculated with daily depth-integrated rates were 0.21 vs. 0.33 when gross uptake rates were used in the calculation (Table 3).

Primary and bacterial production—In general, primary production was highest at the surface and decreased with depth during both cruises (Fig. 10). The C : N ratios of depth-integrated daily carbon and nitrogen uptake were 1.0 and 1.2 in March when gross and net nitrogen uptake rates were used, respectively. These low ratios may be due, in whole or in part, to our use of net carbon uptake rates rather than the more preferable gross uptake rates. They could also indicate significant heterotrophic inorganic nitrogen uptake by bacteria. In September, C : N uptake ratios were 6.4 and 21.3 when gross and net nitrogen uptake rates were used, respectively. Bacterial production was about three times higher at the surface in September, relative to March, and had the same sharp depth gradient observed in primary production (Fig. 10).

Discussion

The two studies presented here provide snapshots of a system in March dominated by NH_4^+ flux, where the primary fate of nitrogen uptake was particle production, vs. a system in September, where NH_4^+ and NO_3^- use was more in balance, and the primary fate of nitrogen uptake was DON. Below, we provide a summary of nitrogen flux rates measured during these two cruises, suggest possible mechanisms responsible for our observations, and discuss the balance between PN and DON production.

Summary of nitrogen flux—In March, nitrogen flux was dominated by NH_4^+ (Fig. 5), which represented 94% of the total DIN uptake (Table 3). The dominance of NH_4^+ as a nitrogen source was also evident in specific uptake rates for NH_4^+, which were 14–34 times greater than those for NO_3^- (Fig. 4). Quantitatively, NH_4^+ was also a more important source of DON release; 12 times more DON was released as a result of NH_4^+ uptake, relative to NO_3^- uptake, even though PN was the main fate of both NH_4^+ and NO_3^- in

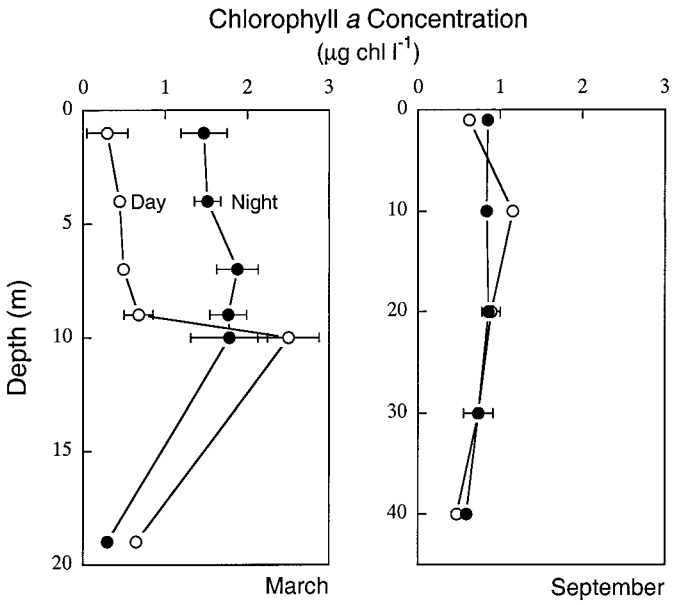

Fig. 3. Vertical profiles of Chl *a* concentrations in uptake experiments during the day (○) and night (●) in Monterey Bay during March (left panel) and September (right panel). Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

March. Rates of NH_4^+ regeneration were also three times higher in March than in September (Fig. 7). The low *f*-ratios we measured in March reflect the importance of regenerated NH_4^+ to the phytoplankton community at this time. Despite the significant rates of DON release observed during March, the use of gross uptake rates did not appear to affect the calculated *f*-ratios, because both gross and net uptake rates were dominated by NH_4^+.

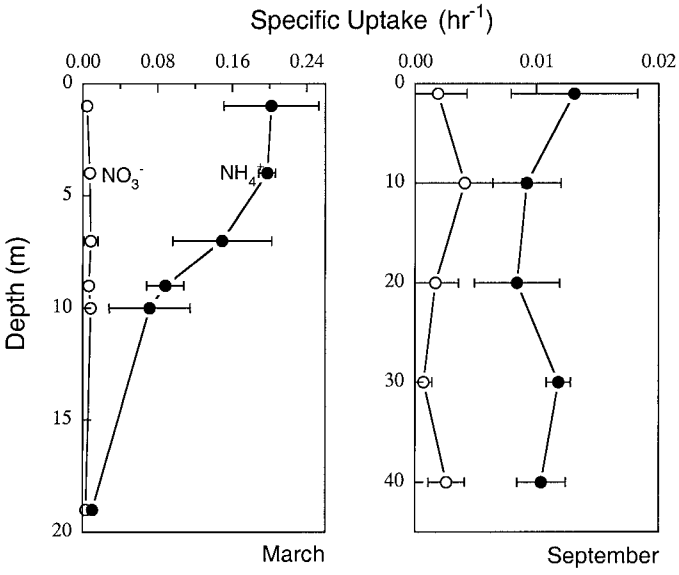

Fig. 4. Rates of NH_4^+ (●) and NO_3^- (○) specific uptake in Monterey Bay during March and September. Rates are the mean of the day and night specific uptake rates. Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

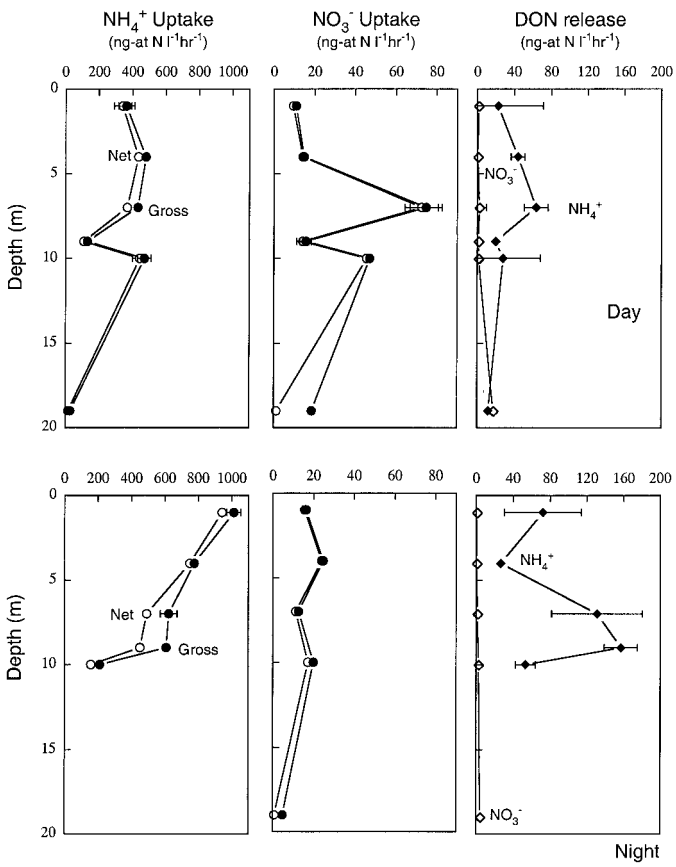

Fig. 5. Vertical profiles of rates of net (○) and gross (●) uptake and DON release from uptake of NH_4^+ (♦) and NO_3^- (◊) during March in Monterey Bay. Upper panels are data from day incubations; lower panels are data from night incubations. Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

Laboratory and field studies have shown that generally phytoplankton and bacteria have a strong preference for NH_4^+ (Wheeler and Kirchman 1986; Dortch 1990; Kirchman and Wheeler 1998). In a range of environments, concentrations of >0.3 μM have been shown to inhibit phytoplankton NO_3^- uptake (Probyn 1988; Wheeler and Kokkinakis 1990). NH_4^+ inhibition of NO_3^- uptake is a likely explanation for the dominance of NH_4^+ utilization and the relatively low NO_3^- uptake rates that we measured in March. This is especially true at night, when NH_4^+ concentrations averaged 0.96 ± 0.31 μM.

In March, there were significant day/night differences in nutrient and pigment concentrations and nitrogen flux rates even though the experiments were performed within 12 h of each other. We also observed evidence of advection of a different water mass into our study site between the two experiments. First, there were significant differences in the hydrographic profiles between the night and day sampling (Fig. 1). At night (Fig. 1B), there was an upper mixed layer approximately 10–12 m thick with a pronounced Chl *a* maximum. The following morning (Fig. 1A), the uppermost lay-

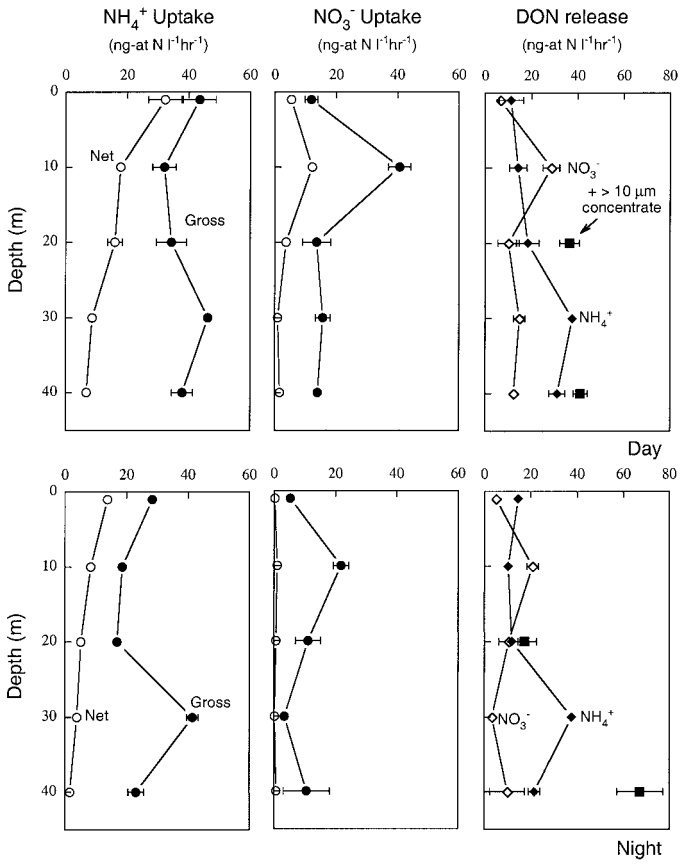

Fig. 6. Vertical profiles of rates of net (○) and gross (●) uptake and DON release from uptake of NH_4^+ (♦) and NO_3^- (◊) during September in Monterey Bay. Upper panels are data from day incubations; lower panels are data from night incubations. Additional experiments were done with sample in which the >10-µm size fraction (presumably grazers and larger phytoplankton prey) had been concentrated (■). Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

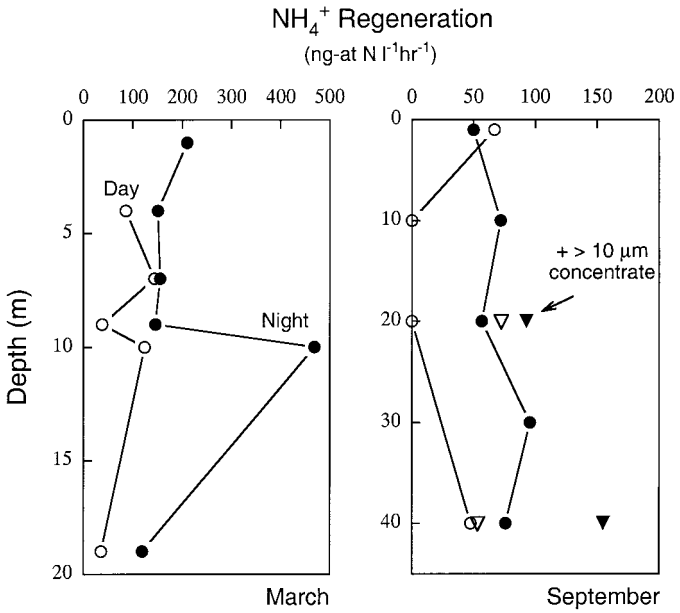

Fig. 7. Rates of NH_4^+ regenerations measured during the day (○) and at night (●) in Monterey Bay during March and September; note the change in scale between panels. In September, additional experiments were done with sample in which the >10-µm size fraction (presumably grazers and larger phytoplankton prey) had been concentrated during the day (▽) and at night (▼). Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

er was 22 m thick and slightly more saline. We infer that a thicker layer of slightly saltier water, containing low Chl *a* concentrations, advected into the area during the night. Second, ambient concentrations of NH_4^+ were near 1 µM at night but had decreased by half or were completely depleted by the following morning (Fig. 2) despite the high rates of NH_4^+ regeneration (Fig. 7). During this same period, the concentration of Chl *a* decreased by a factor of three to five (Fig. 3). Third, approximately 4 µM DON accumulated in the surface waters from the night sampling to the following morning (Fig. 2). Although the accumulation of DON is consistent with the high DON release rates we measured at night, our measured DON release rates were not high enough to account for all the DON accumulation we observed. Finally, depth-integrated NH_4^+ uptake was 2.5 times greater than depth-integrated NH_4^+ regeneration, suggesting that an additional source of NH_4^+ would have been necessary to balance NH_4^+ supply and demand in March (Table 1). The result of the advection of the water mass, which had significantly higher NH_4^+ uptake and regeneration and DON release rates, into the study area was to increase the relative importance of regenerated nitrogen to nitrogen flux in the area.

In September, the euphotic zone was twice as deep as in March, extending to 40 m, and the water column was more well mixed (Fig. 1). As a result, most profiles of nitrogen

Table 1. Ratio of net or gross NH_4^+ uptake (ng-at N $liter^{-1}$ d^{-1}) to NH_4^+ regeneration (ng-at N $liter^{-1}$ d^{-1}) during two cruises in Monterey Bay. Depth-integrated rates were calculated with daily rates.

Cruise	Depth (m)	Net NH_4^+ uptake: NH_4^+ regeneration	Gross NH_4^+ uptake: NH_4^+ regeneration
March	1	4.48*	4.82*
	4	5.01	5.34
	7	2.83	3.4
	9	3.03	3.96
	10	1.21	1.35
	19	0.45†	0.78†
	Depth integrated	2.22	2.51
September	1	0.41	0.62
	10	0.46	0.88
	20	0.48	1.14
	30	0.04*	0.43*
	40	0.08	0.53
	Depth integrated	0.30	0.86

* Data from night experiments only.
† Data from day experiments only.

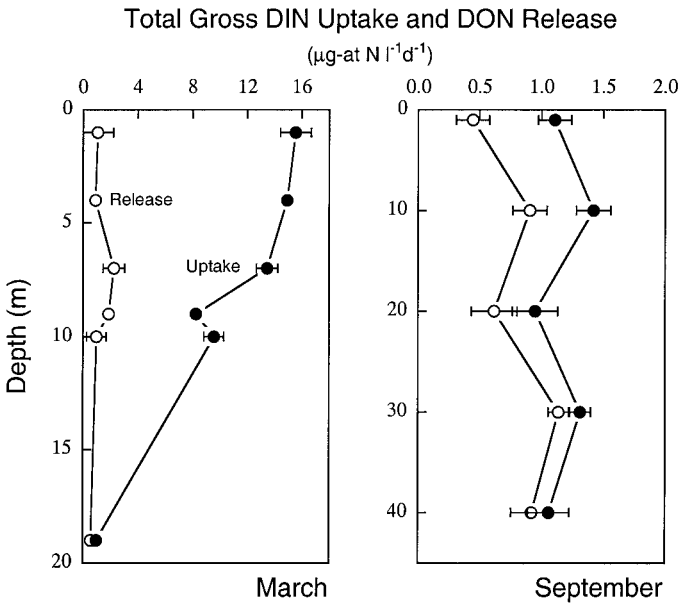

Fig. 8. Ratios of total gross DIN uptake (●, sum of daily NH_4^+ and NO_3^- uptake rates) to total DON release (○, sum of daily DON release rates measured in both the NH_4^+ and NO_3^- incubations) during March and September in Monterey Bay. Daily rates were calculated by multiplying the day rates by 14 h and the night rates by 10 h and then taking the sum of the two. Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

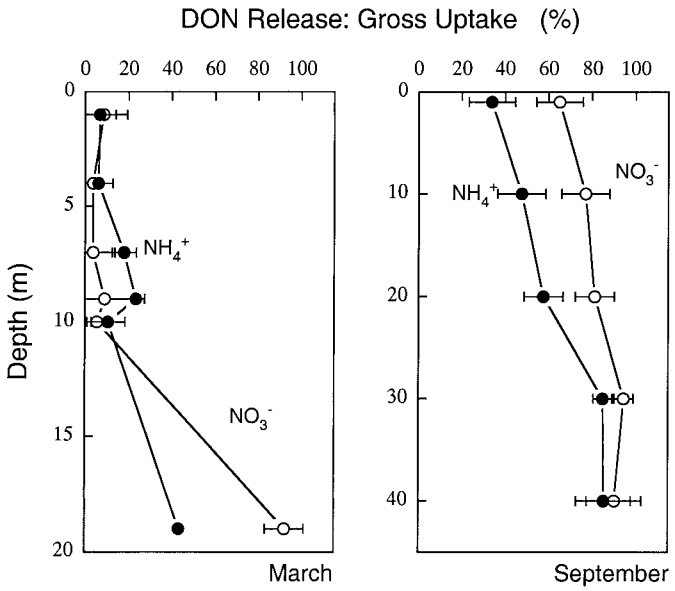

Fig. 9. The ratio of DON release to inorganic nitrogen uptake, expressed as a percentage, as determined in incubations with NH_4^+ (●) and NO_3^- (○) during March and September in Monterey Bay.

concentration and flux rates showed less vertical structure, and uptake rates were much lower (Fig. 8). While NH_4^+ was still taken up at higher rates than NO_3^-, utilization of NH_4^+ and NO_3^- was more equitable. Accordingly, *f*-ratios were about five times higher than in March (Table 3) but reflected more of a decrease in dependence of the plankton on regenerated NH_4^+ than an increase in the use of NO_3^-. Quantitatively, DON release resulting from NH_4^+ and NO_3^- uptake were approximately equal, although a larger percentage of the NO_3^- taken up was released as DON, relative to nitrogen taken up as NH_4^+. There were pronounced gradients in primary and bacterial production and depth, both being highest at the surface (Fig. 10). The depth distribution of bacterial production rates appeared to be more related to primary production ($H^{14}CO_3^-$ uptake) than to DON release or ammonium regeneration, as indicated by the vertical profiles.

In contrast to March, the rate of NH_4^+ regeneration was greater than the NH_4^+ demand in September. In an upwelling zone farther north off the coast of Oregon, Dickson and

Table 2. Turnover times of NH_4^+, NO_3^-, and DON estimated during two cruises in Monterey Bay. Turnover times of NH_4^+ and NO_3^- were estimated using gross uptake rates. DON turnover times were estimated by combining rates of DON release estimated in incubations with NH_4^+ and NO_3^-. Turnover times for PN were calculated using ambient PN concentrations and the combined gross NH_4^- and NO_3^- daily uptake rates.

		Turnover times (days)			
Cruise	Depth (m)	NO_3^-	NH_4^+	DON	PN
March	1	0.97	0.04	4.0	0.13
	4	0.76	0.02	4.4	0.13
	7	0.47	0.06	2.8	0.14
	9	1.68*	0.04	3.5†	0.62*
	10	0.69	0.10	5.6	0.20
	19	2.53	0.89*	9.6*†	0.75*
	Mean ± SD	1.18 ± 0.78	0.19 ± 0.34	5.0 ± 2.4	0.33 ± 0.28
September	1	1.90	0.18	10.7	1.76
	10	1.60	0.24	6.2	1.37
	20	3.71	0.32	9.2	2.05
	30	3.45	0.20	6.1	1.48
	40	10.05	0.20	8.7	1.84
	Mean ± SD	4.14 ± 3.43	0.23 ± 0.06	8.2 ± 2.0	1.7 ± 0.3

* Data from day experiments only.
† Data from NH_4^+ experiments only.

Table 3. *f*-ratios calculated with net and gross uptake rates in March and September in Monterey Bay. The *f*-ratio is the rate of NO_3^- uptake divided by the sum of NO_3^- and NH_4^+ uptakes.

Cruise	Depth (m)	Net *f*-ratio	Gross *f*-ratio
March	1	0.02	0.02
	4	0.03	0.03
	7	0.10	0.09
	9	0.05	0.05
	10	0.09	0.09
	19	0.06	0.31
	Depth integrated	0.06	0.06
September	1	0.11	0.20
	10	0.35	0.55
	20	0.17	0.32
	30	0.08	0.19
	40	0.21	0.28
	Depth integrated	0.21	0.33

Wheeler (1995) found that rates of NH_4^+ uptake and regeneration were approximately in balance under most conditions. When regeneration rates exceeded uptake rates, Dickson and Wheeler (1995) suggested that uptake rates might have been underestimated due to loss of ^{15}N label to the DON pool or bacteria. Our September results support this hypothesis. In September, the ratio of depth-integrated net NH_4^+ uptake to regeneration was 0.30 (Table 1). When gross uptake rates, which take into account DON release, were used in the comparison, the ratio increased to a more balanced 0.86 (Table 1).

Though there were many differences between the two cruises, consistencies were also observed. Ambient nitrogen concentrations were not dramatically different between March and September (Fig. 2). During both cruises, rates of NH_4^+ regeneration were higher at night by a factor of two, likely due to increased grazing at night (Fig. 7). NO_3^- uptake rates (specific, net, and gross) were 3–10 times higher during the day than at night (Figs. 4–6). While water mass differences obscure diel patterns between these two experiments, we attribute some of the difference to the different energy demand involved in NH_4^+ and NO_3^- assimilation and the predominantly autotrophic use of NO_3^-. Similar day/night difference in NO_3^- uptake were observed in the northeastern subarctic Pacific by Wheeler and Kokkinakis (1990) and Cochlan et al. (1991).

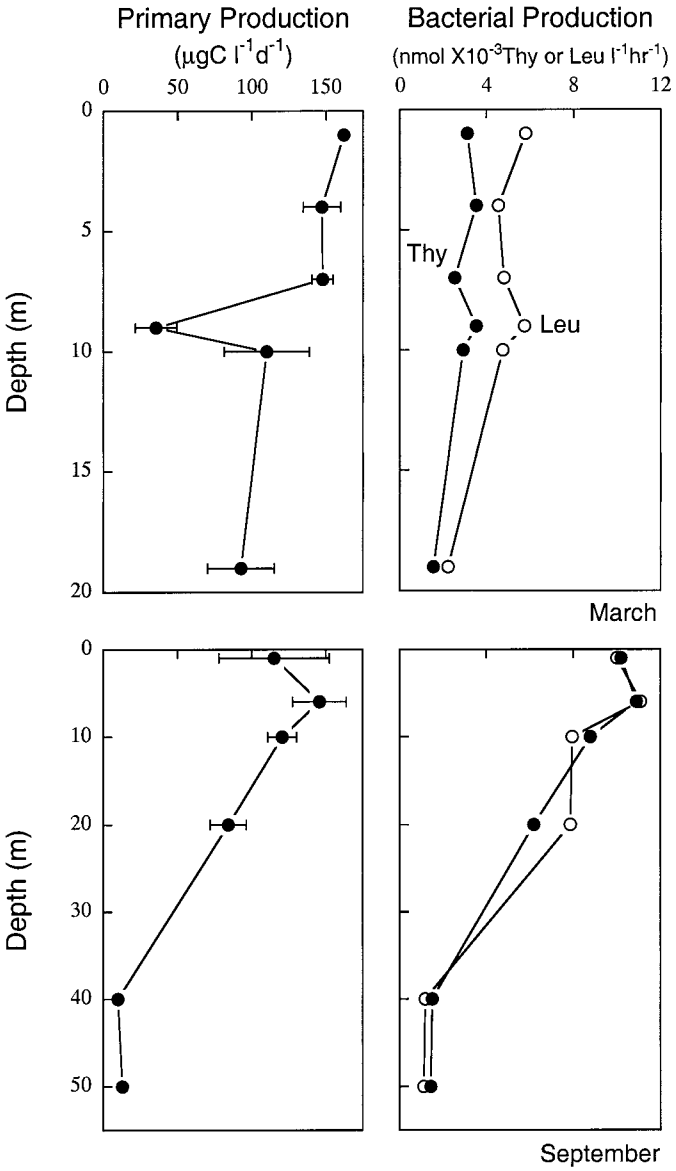

Fig. 10. Rates of primary production (●) and bacterial production, measured with tritiated thymidine (●) and leucine (○) in March and September in Monterey Bay. Data are plotted with error bars indicating standard deviations; where error bars are not shown, errors are smaller than the symbols.

Potential mechanisms responsible for nitrogen release—During these cruises, DON release represented a significant nitrogen flux within the euphotic zone in Monterey Bay. We suggest that the magnitude of DON production we observed was linked to grazing pressures in March and to a combination of grazing and physiological stress in September. We also suggest that a recently hypothesized protective mechanism used by diatoms could explain the rates of DON release due to NO_3^- uptake we observed at the base of the euphotic zone (Lomas and Glibert 1999).

In March, several lines of evidence suggest that grazing was significant. First, DON release resulting from NH_4^+ uptake and NH_4^+ regeneration were all higher at night than during the day; grazing rates tend to increase at night (Dagg et al. 1989). Second, the large peak in DON release resulting from NH_4^+ uptake at night also coincided with the peak in NH_4^+ regeneration (Figs. 5, 6); high rates of NH_4^+ regeneration are often associated with high grazing activity (Goldman et al. 1985). Furthermore, although we do not have direct information on phytoplankton community composition for either cruise, the phytoplankton community in Monterey Bay is generally dominated by diatoms during the seasons in which both of these cruises occurred (Garrison 1979; Chavez 1996). Diatoms are especially susceptible to breakage during grazing, thus resulting in DON release via sloppy feeding (Dagg 1974; Lampert 1978). Third, high grazing rates are

also suggested by the large changes in Chl *a* concentrations. Although grazing alone is unlikely to be solely responsible for the 50% decrease observed from the night sampling to the following morning, it was likely a contributing factor.

In September, we suggest that grazing was still significant and that the plankton community was also more physiologically stressed. Evidence for grazing was, again, the substantial increase in NH_4^+ regeneration from day to night. Second, concentrating the larger size fraction (>10 μm) resulted in significantly higher rates of both DON release and NH_4^+ regeneration. These higher rates would likely result from concentration of the grazers themselves or grazers and their larger phytoplankton prey.

Evidence for a physiologically stressed population in September is, first, the lower specific uptake rates, which suggest that the phytoplankton were assimilating nitrogen more slowly (Fig. 4). Second, the C : N ratio of carbon to gross nitrogen uptake was 6.4, suggesting phytoplankton were taking up carbon and nitrogen approximately in the ratio required to build phytoplankton biomass; we note that the comparison is complicated by not having gross carbon uptake rates. When net nitrogen uptake rates were used, however, the calculated ratio increased to 21.3. This suggests that cells were taking up carbon and nitrogen in the ratio they required but were not able to assimilate the nitrogen into biomass. As a result, the cells were releasing much more DON than they were incorporating into biomass, which implies some physiological stress. This finding also suggests that rates of DON uptake were low, such that the $DO^{15}N$ that was released was not rapidly reassimilated but remained in the dissolved pool to be measured.

During both cruises, we observed very low rates of net NO_3^- uptake at the base of the euphotic zone. Low NO_3^- uptake rates are often observed at the base of the euphotic zone and are generally attributed to the low light and resulting decrease in photosynthetically produced reductant available for NO_3^- assimilation. For example, White and Dugdale (1997) also observed very low net uptake rates at the base of the euphotic zone in Monterey Bay. In both sets of experiments reported here, however, >90% of the NO_3^- taken up at the base of the euphotic zone resulted in DON production. Thus, the very low net uptake we measured at depth was due largely to substantial DON release at depth. White and Dugdale (1997) used 24-h incubations such that their net rates are likely underestimates of total NO_3^- uptake due to the accumulation of ^{15}N in the DON and/or bacterial fraction (Bronk and Glibert 1994).

These observations indicate that deep in the water column, relative to the surface, less nitrogen is incorporated directly into biomass. We suggest three possible scenarios to explain this pattern. First, the larger percentage of nitrogen released at depth may be a reflection of higher grazing pressure at the base of the euphotic zone. Alternatively, or additionally, the difference with depth could reflect differential reincorporation of recently released DON. For example, in September, primary and bacterial production were highest at the surface where ambient DIN concentrations were lower relative to deeper waters. Under these conditions, recently released $DO^{15}N$ would likely be an attractive substrate and may have been taken back up into biomass—a situation we would methodologically view as straight NH_4^+ or NO_3^- uptake. Deeper in the water column, however, inorganic nitrogen was more available, such that DON may not have been in as great a demand by bacteria and phytoplankton and thus remained in the extracellular pool to be measured as release.

A third potential mechanism that could be responsible for the high rates of DON release at the base of the euphotic zone has been proposed by Lomas and Glibert (1999). They hypothesize that diatoms have the ability to take up NO_3^- in excess of their nutritional requirements for use as a sink for high-energy electrons when the cells are exposed to damaging light levels, such as they may encounter when brought to the surface during a deep mixing event. In our experiments, this exposure to a high light environment could have occurred as the water sample was drawn from the Niskin bottle, through a clear Tygon tube, into a darkened incubation bottle.

PN production vs. DON production—In March, though DON release rates were relatively high, most of the DIN taken up resulted in the production of PN, and the PN pool was turning over rapidly (0.33 d). In September, however, PN turnover times were over a factor of five longer than in March, and most of the DIN taken up resulted in DON production. We stress that we did not observe an accumulation of PN or DON during either cruise.

The recognition that an appreciable amount of nitrogen uptake results in the production of dissolved rather than PN affects our understanding of export production. With the exception of isolated sites of downwelling, nitrogen must be packaged into particles of sufficient size and density to sink out of the euphotic zone. Transfer of nitrogen to a dissolved fraction, particularly one with a longer turnover time, will retain nitrogen within the more biologically active surface waters for a longer time. For example, PN turnover times calculated from NH_4^+ and NO_3^- uptake rates ranged from 0.3 to 1.7 d in March and September, respectively. In comparison, turnover times for the total DON pool suggest that transfer of nitrogen to the DON pool would retain that nitrogen within the surface layer as a dissolved component for an estimated 5–8 d during these two cruises. These turnover times, however, are probably not representative of the whole DON pool, which is a heterogeneous mixture of labile moieties, such as amino acids, and refractory compounds. Following the convention used for DOC, the DON pool could be separated into labile, semilabile, and refractory compounds (Carlson and Ducklow 1996). The labile/semilabile DON would be the fraction of the surface DON that is greater than the approximately 4 μM of presumably refractory DON observed below the mixed layer; with the data available, we can not discriminate between the labile and semilabile DON pools. If we use the estimated concentration of the combined labile plus semilabile DON pool, the mean turnover times for DON decrease to 2.0 d in March and 4.2 d in September, with the labile fraction likely turning over even more quickly. Packaging this recently released DON, even the labile compounds, into sinking particles would require the long trek through the microbial food web via bacterial production, or possibly small autotrophs, extending the residence time in the euphotic zone further.

Based on these data, we suggest that the DON pool acts as an intermediate between DIN assimilation and the net formation of particles for export and that it will thus affect carbon flow in Monterey Bay. In the traditional view of nitrogen flux, new nitrogen enters a system via a number of mechanisms, such as upward diffusion, nitrogen fixation, atmospheric nitrogen deposition, etc. The new nitrogen, NO_3^-, is assimilated into PN, usually by the larger phytoplankters (Malone 1980; Probyn et al. 1990), which then sink out of the euphotic zone directly or are packaged into settling particles via grazing processes. In our study, however, a large fraction of the new nitrogen, assumed to be NO_3^-, resulted in the production of DON, which had a longer turnover time in the euphotic zone than PN. We speculate that the retention of nitrogen within the euphotic zone as DON will have two likely consequences. First, retaining the nitrogen in the surface layer will increase the spatial and temporal uncoupling between new nitrogen inputs and resulting particle flux because the longer the nitrogen is retained, the greater the opportunity for advection. As noted above, there are several pieces of evidence that suggest that advection was important in March.

Second, retention of nitrogen as DON would also presumably shunt more nitrogen into the microbial food web. If nitrogen is going into bacterial production, rather than particle flux, then the potential loss of carbon via respiration is increased. Alternatively, Carlson and Ducklow (1996) found that in the Sargasso Sea, labile carbon was respired even when there did not appear to be sufficient nitrogen to produce biomass. Under this scenario, retention of DON in the surface could result in altering the balance between production of bacterial biomass and carbon loss via respiration. The ultimate effect on particle flux would then hinge on the plankton community and the efficiency of packaging bacterial carbon into sinking particles.

Conclusions

The importance of DON release has been hypothesized for some time on the basis of deficits in ^{15}N mass balances as well as experimental and field observations. In the two sets of experiments presented here, we directly measured rates of DON release throughout the euphotic zone. We found that DON release was an important nitrogen flux within the euphotic zone during both cruises and that there was evidence that grazing and possibly physiological stress were mechanisms contributing to the DON release. In March, the primary fate of nitrogen uptake was particle production, while in September, the primary fate of nitrogen uptake was DON. During both cruises, the percentage of nitrogen released as DON increased with depth, which suggests that the percentage of nitrogen incorporated into sinking particles decreased with depth. The mechanisms, whether physical, trophic, and/or physiological, that operate to control the balance between PN vs. DON production are unknown. Defining these mechanisms is an important area for future research, with implications for our understanding of nitrogen cycling, particle export, carbon loss, and elemental mass balances.

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