first method, samples are collected and the concentration of DON or individual DON components are monitored over time. To measure DON flux rates using ^{15}N tracer techniques, all of the DIN forms (NH_4^+, NO_3^-, and NO_2^-) must be removed, and the DON pool must be isolated with a high efficiency. At present, there are three basic approaches used to isolate DON—wet chemistry, ion retardation, and dialysis.

1. Wet Chemical Isolation

Axler and Rueter (1986) introduced the wet chemical approach, and various permutations have been applied by later researchers (Slawyk and Raimbault, 1995; Bronk and Ward, 1999). In this approach, NH_4^+ is removed by raising the pH slightly, thus effecting a change from soluble protonated NH_4^+, to the more volatile NH_3 via diffusion in a heated oven (Slawyk and Raimbault, 1995) or vacuum distillation (Bronk and Ward, 1999). Nitrate in the sample is converted to NH_3 with DeVarda's alloy, with the NH_3 again removed through volatilization (Slawyk and Raimbault, 1995; Bronk and Ward, 1999). Both of these techniques can suffer from the artifact of losing labile DON as a result of base hydrolysis (Bronk and Ward, 2000). The problem in the isolation is likely the lengthy diffusion step undertaken to remove NH_4^+ and NO_3^-/NO_2^- from solution. My own lab has investigated a suite of other protocols to remove NO_3^-/NO_2^-, including vanadium (VIII; Cox, 1980; Garside, 1982), titanium (TiIII, Cresser, 1977; Cox, 1980), and other DeVarda's alloy approaches (Page *et al.*, 1982). The breakdown and loss of DON is a perpetual concern due to the rigorous reducing conditions necessary to effect the loss of NO_3^-. For example, some researchers use diffusion in a heated oven as a way of removing labile DON before isolation of NO_3^- (Sigman *et al.*, 1997). Potential artifacts during wet chemical DON isolation and the different types of DON release rates and their calculation protocols were recently reviewed by Bronk and Ward (2000) and are not considered here.

2. Ion Retardation

The ion retardation method uses a resin (BioRad AG 11 A8) that retards the flow of charged particles. Originally developed for desalting blood samples, the resin can quantitatively remove salts, including NH_4^+, NO_3^-, and NO_2^-, allowing DON to be isolated in the eluate (Bronk and Glibert, 1991, 1993b; Hu and Smith, 1998; Nagao and Miyazaki, 1999). Unfortunately, DOW Chemical, the company that manufactured the resin marketed by BioRad and other distributors, changed the manufacturing process of the resin such that the recently produced resin retains variable amounts of DON. This DON retention is believed to be due to an accumulation of an organic film on the resin beads during manufacturing (BioRad, pers. commun.) To overcome this problem, AG 11 A8 resin can be manufactured and purified

by buying another resin (Dowex anion exchange resin, BioRad AG1-X8) and then chemically altering it to produce AG 11 A8 as described in Hatch *et al.* (1957).

3. Dialysis

Another technique that has been considered for isolating DON is dialysis. Feuerstein *et al.* (1997) developed a method to isolate DON in freshwater samples, which uses rotary evaporation to preconcentrate the DON followed by dialysis (100-Da cutoff) to remove DIN; no data on marine samples were presented. Drawbacks of the dialysis approach are that the amount of time it takes to remove DIN (100 h for freshwater; 216 h for marine samples) is excessive, the removal is never absolute, and the risk of bacterial or N contamination is substantial. My own lab has experimented with microdialysis to desalt isolated DON before mass spectrometric analysis, but found that the pores did not maintain their integrity at high ionic strengths.

C. Literature Values of DON Release Rates in Aquatic Environments

DON release rates can vary widely within and between systems as reviewed in Tables IV and V. In most cases, these rates were measured using whole water samples, and the specific processes that produced the measured rates are unknown (see Section III.A).

1. Bulk DON

The mean rate of DON release is similar for both oceanic and coastal systems at ~40 ng-at N $L^{-1}h^{-1}$ though the range is large (Table IV), These rates are compared to rates of gross N uptake. Gross N uptake is the total amount of N taken up by cells regardless of whether its ultimate fate was PN production or DON production (Bronk *et al.*, 1994). This is in contrast to a net N uptake rate, which is the rate traditionally measured with ^{15}N tracer techniques that only includes PN production (Bronk *et al.*, 1994). As a percentage of gross N uptake, DON release appears similar in oceanic and coastal environments with 41 $\pm$ 20 and 39 $\pm$ 26% of gross N uptake released as DON, respectively (Table IV). Mean rates of release tend to be higher in estuarine environments, ~72 ng-at N $L^{-1}h^{-1}$, but again the range is large. Based on the limited data available, the percentage of gross N uptake released as DON in estuarine systems appears to be lower than the other systems at 23 $\pm$ 8% (Table IV). Collectively these data suggest that DON release is a significant flux through marine and aquatic systems.

Table V

Summary of Published Release Rates of Individual Organic N Compounds in the Field

Location	Date	Compound released	Release rate (ng-at N L^{-1} h^{-1})	Method	Reference
Oceanic					
Bering Sea	NP	Urea	73.8 ± 30.6	^{15}N and ^{14}C	Hansell and Goering, 1989
Caribbean Sea	November 1988				
Southern California Bight		Urea	11.17[a]	^{14}C	Cho *et al.*, 1996
Southern California Bight (upper 5 m)	September	Urea	0.002 to 0.014[a]	^{14}C	Cho and Azam, 1995
Southern California Bight (upper 5 m)	September	Urea	0.002 to 0.045[a]	^{14}C	Cho and Azam, 1995
Coastal					
Long Island Sound	October 1983	Alanine	1.3[b]	[^{3}H]ala	Fuhrman, 1987
Long Island Sound	October 1983	Alanine	30[c]	[^{3}H]ala	Fuhrman, 1987
Long Island Sound	October 1983	Alanine	< 0.1[d]	[^{3}H]ala	Fuhrman, 1987
Long Island Sound	November 1984	ala, glu, gly, ser	9.9[b]	[^{3}H]ala	Fuhrman, 1987
Long Island Sound	November 1984	ala, glu, gly, ser	17.7[c]	[^{3}H]ala	Fuhrman, 1987
Long Island Sound	November 1984	ala, glu, gly, ser	6.2[d]	[^{3}H]ala	Fuhrman, 1987
Estuarine					
Chesapeake Bay	Spring	Urea	480 ± 200	^{15}N or $^{15}N/^{14}C$	Lomas *et al.*, in press
Chesapeake Bay	Summer	Urea	670 ± 180	^{15}N or $^{15}N/^{14}C$	Lomas *et al.*, in press
Chesapeake Bay	Winter	Urea	1630 ± 820	^{15}N or $^{15}N/^{14}C$	Lomas *et al.*, in press
Chesapeake Bay, mesohaline	May 1988	Urea	0 to 377	$^{15}N/^{14}C$	Bronk *et al.*, 1998

(*Continues*)

Table V *(Continued)*

Location	Date	Compound released	Release rate (ng-at N L^{-1} h^{-1})	Method	Reference
Chesapeake Bay, mesohaline	August 1988	Jrea	164 to 794	$^{15}N/^{14}C$	Bronk *et al.* 1998
Chesapeake Bay mesohaline	October 1988	Urea	0 to 1478	$^{15}N/^{14}C$	Bronk *et al.* 1998

Note. Data was taken directly from tables, estimated from graphs, or obtained from the author's directly. Data are presented as mean ± standard deviation.
[a] Bacterial release.
[b] <202 μm fraction.
[c] <202 μm fraction + added (125–150) copepods.
[d] <0.22 μm fraction + added (125–150) copepods.

As seen in Table IV, the percentage of gross N uptake that can be released as DON can at times be quiet high (i.e., 90%). Slawyk *et al.* (2000) contend that such high percentages of release are "impossible," though I disagree with both their assumptions and their calculations. Analogous to the release of DOC as a percentage of primary production, the percentage of release directly from phytoplankton is likely fairly low, as seen in many of the culture studies presented in Table IV. One would expect that this percentage can increase substantially, however, when other trophic levels act on the phytoplankton such as during sloppy feeding and viral infection (see Carlson, Chapter 4). Though these high rates may not be sustainable, they are clearly possible.

Rates of DON release that result from either NH_4^+or NO_3^- incorporation can be measured using ^{15}N tracer techniques. Of the studies presented in Table IV, a higher percentage of gross NO_3^- uptake is released as DON relative to incubations where NH_4^+ is the substrate in 7 of 11 cases. Vertical profiles of DON release rates vary. In the Gulf of Lions, DON release is generally higher in surface waters and lower at depth (Diaz and Raimbault, 2000). In Monterey Bay, the percentage of N released as DON increased with depth, suggesting that deeper in the water column, a smaller percentage of the N taken up is incorporated into sinking particles (Bronk and Ward, 1999). The fate of N uptake also appears to change. In Monterey Bay, the primary fate of N uptake is particle production in March but DON production in September (Bronk and Ward, 1999). These data suggest that the DON pool acts as an intermediate between DIN assimilation and the net formation of particles for export and will thus affect C flow in Monterey Bay.

In the Choptank River, a subestuary of Chesapeake Bay, rates of total DON release are significantly higher in a <202-μm fraction relative to the <1.2-μm plankton likely due to feeding processes associated with the larger size fraction (Bronk and Glibert, 1993b). Evidence for feeding induced DON release in the

<202-μm fraction includes a low ratio of LMW DON to total DON release, an increase in DON release rates at night when grazing tends to be higher, and a doubling of phaeopigment concentrations during the 36-h experiment, which are an indicator of active grazing. In contrast, rates of LMW DON release in the <1.2-μm plankton are not significantly different from rates of total DON release and rates of DON release decrease by over 95% in the dark, suggesting that passive release from autotrophs is a more important release process. In another study in Chesapeake Bay, the average rates of DON release are remarkably constant from season to season, although, within a diel period, there is considerable variability. DON release also often appears to decrease at night, although the difference is not statistically significant (Bronk *et al.,* 1998).

2. Urea

Urea has been shown to be excreted by chryptomonads, herbivorous marine zooplankton, oceanic and lake microzooplankton, bivalve mulluscs, marine and freshwater teleost fish, and freshwater crabs (Antia *et al.,* 1991).

In the Bering Sea, *in situ* production of urea is approximately equal to the consumption of urea (Hansell and Goering, 1989). In the central channel of Chesapeake Bay, rates of urea regeneration are generally less than rates of NH_4^+ regeneration, but, at the highest rates measured, urea regeneration can contribute 100% of the phytoplankton N requirement (Bronk *et al.,* 1998). Lomas *et al.* (in press) reviewed rates of urea regeneration in Chesapeake Bay and found that mean baywide surface urea regeneration rates are highest but most variable during the fall. In the Southern California Bight, urea decomposition is significant deeper in the water column, particularly at the base of the euphotic zone, and the activity is primarily in the bacterial size fraction (Cho and Azam, 1995). These data suggest that urea is an important intermediate between sinking particles and release of NH_4^+ mediated by bacteria in the mesopelagic.

3. DCAA and DFAA

DCAA and DFAA are other important organic release products. In cultures enriched with DIN, extracellular DFAA often accumulate with the highest concentrations generally present during stationary phase (Poulet and Marine-Jezequel, 1983; Myklestad *et al.,* 1989). Diatoms showed the highest rates of DFAA excretion during exponential growth (Myklestad *et al.,* 1989, and references therein). The types of amino acids released from *Chaetoceros affinis* (diatom) changes during exponential growth relative to stationary growth (Myklestad *et al.,* 1989). In cultures of *Phaeodactylum tricornutum,* DFAA accumulate extracellularly,

particularly glycine, threonine, and serine, which are all important in cellular respiration or are components of cell walls that are likely resistant to decomposition (Marsot *et al.,* 1991).

Amino acid enantiomeric ratios have also been used to infer DOM release by capitalizing on the fact that eukaryotic organisms release exclusively the L enantiomer. The DCAA in refractory DOM generally has a low L/D ratio of 3 to 4 (Lee and Bada, 1977; McCarthy *et al.,* 1998; II.C.3). Significant phytoplankton release, however, can increase the L/D ratio up to 8, making the ratio a useful indicator of new DOM production.

4. Release of DON Relative to DOC

Relatively little is known about the relationship of DOC to DON release. In general, ~5–30% of primary production is directly released as DOM by phytoplankton though the range is very broad (Baines and Pace, 1991; also see Carlson, Chapter 4). In the studies presented here, a mean of 22 to 41% of gross N uptake is released as DON, but as with DOC, the range is very broad (see Section III.C.1).

If phytoplankton maintain a C:N ratio of approximately 6.6, and they are ultimately the primary source for released DOM, then it is reasonable that the C:N of DOM release should be ~6.6 over appropriate space and time scales (see Karl and Björkman, Chapter 6). In Chesapeake Bay, combined DOC and DON release rate data indicate that recently released DOM has an approximate C:N ratio of 3.3 in May, 5.0 in August, and 4.7 in October (Bronk *et al.,* 1998). This low C:N ratio is consistent with an apparent accumulation of N-rich DON in the Bay from May to August as observed in the ambient DOC and DON pools. Carlson *et al.* (2000) reported that DON in excess of background (i.e., winter) concentrations has a C:N ratio of 6.7.

Søndergaard *et al.* (2000) performed mesocosm experiments to investigate DOC and DON accumulation under a range of conditions over time. Following an 11-day time lag, the concentration of DON increases linearly ($r^2 = 0.88$–0.89) with time in all treatments (added N, P, glucose, and various combinations of the three). The average DON production rates for all treatments, except for the high N addition treatment, is 0.28 μM day $^{-1}$and the released DOM has a C:N ratio of 11. In the high N addition treatment (5$\times$ the amount added to the rest of the treatments) the rate of DON production increases to 0.74 μM day^{-1}with a DOC:DON ratio of the released material of 20.

D. Sources of DON: Research Priorities

Clearly there is much work to be done quantifying rates of DON release and, more importantly, systematically defining the mechanisms that produce the

measured rates of release. Along these lines, a quick nondestructive means of isolating DON in quantities sufficient for mass spectrometric analysis remains one of the holy grails of marine N research. Such a method could be used to isolate DON in tracer experiments, as well as provide a way to limit analytical error in the measurement of DON concentrations in areas where inorganic N is high, such as the deep ocean. Other areas that should be a high priority for future research are linking DOC with DON release in laboratory growth experiments and in the field, quantifying the role of viruses in DON release, and defining the rates and pathways involving micro- and macrozooplankton in DON release (i.e., sloppy feeding versus excretion versus fecal pellet dissolution). Most of this latter work is fairly straightforward and doable with existing methods. Quantifying virus mediated release, however, will be challenging, particularly in developing appropriate experimental controls.

IV. SINKS FOR DON

To date, most studies of N uptake in aquatic systems have focused on DIN, and the studies of DON utilization that have been done have focused on labile LMW DON compounds (i.e., DFAA and urea), which are generally present at very low concentrations. Three main sinks for DON will be considered here — heterotrophic uptake, autotrophic uptake, and abiotic photochemical decomposition (Fig. 5). Here I present the evidence for heterotrophic versus autotrophic use of DON and

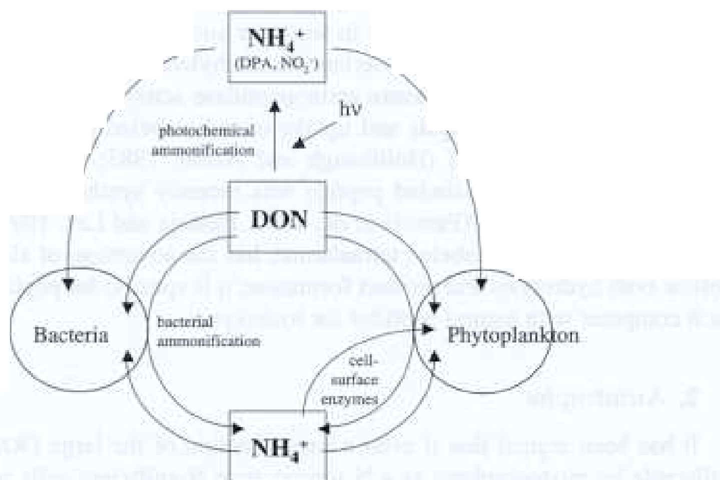

Figure 5 Conceptual diagram of processes involved in dissolved organic nitrogen (DON) utilization in aquatic systems.

the role of cell-surface enzymes, discuss a possible link between DON and harmful algal blooms (HABs), review important considerations in measuring DON uptake, and present a survey of recently published estimates of DON uptake rates. The section concludes with a review of photochemical N release and suggested areas for future research.

A. Heterotrophic versus Autotrophic DON Utilization

Heterotrophic bacteria have traditionally been considered the primary users of DON in marine systems. Several aspects of DOM use by bacteria have recently been reviewed in Williams (2000) and Carlson (Chapter 4). Therefore, I will focus the bulk of my review on the emerging role of DON as a source of N for autotrophs.

1. Heterotrophs

Studies have shown that bacteria can utilize dissolved proteins and DCAA, and that DFAA can support a large fraction of bacterial growth in freshwater and marine systems (see Carlson, Chapter 4). Most bacteria can take up only inorganic or small organic compounds (Antia *et al.,* 1991). Therefore, extracellular hydrolysis is necessary before the bulk of the water column DON can be used for growth by these organisms (see review by Münster and De Haan, 1998). Rates of peptide hydrolysis can determine the supply of free amino acids available for uptake or extracellular oxidation. Similarly, rates of amino acid oxidation may be an important control affecting the supply of NH_4^+. A number of methods have been developed to detect proteolytic activity in seawater and sediments, including peptide-like fluorogenic compounds such as leucine-methylcoumarinylamide (Leu-MCA), which have been used to measure aminopeptidase activity (Hoppe, 1983). Additionally, combined hydrolysis and uptake of radiolabeled proteins and peptides have also been measured (Hollibaugh and Azam, 1983; Keil and Kirchman, 1999). A fluorescently labeled peptide was recently synthesized and tested in seawater and sediments (Pantoja *et al.,* 1997, Pantoja and Lee, 1999). This compound, Lucifer yellow-labeled tetraalanine, has the advantage of allowing one to follow both hydrolysis and product formation; it is specific for peptide hydrolysis as it competes with natural peptides for hydrolysis.

2. Autotrophs

It has been argued that if even a small fraction of the large DON pool were utilizable by phytoplankton as a N source, then N-sufficient cells could exist in waters having undetectable DIN concentrations (Jackson and Williams, 1985). The role that DON plays as a N source for autotrophs, however, is still under

debate, as are the potential mechanisms of utilization—bacterial ammonification and subsequent phytoplankton uptake of the released N or direct incorporation via cell surface enzymes (Fig. 5).

Bacterial degradation of DON followed by phytoplankton uptake of the released compounds has been demonstrated by a number of researchers (Berman *et al.,* 1991; Antia *et al.,* 1991; Ietswaart *et al.,* 1994; Lisa *et al.,* 1995; Palenik and Hensen, 1997; Berman *et al.,* 1999). When the decomposition results in NH_4^+ production, the process is known as ammonification. Direct uptake of DON, without bacterial mediation, was considered to be relatively minor. Research over the past decade, however, requires that this assumption be reevaluated. A number of phytoplankton species have been shown to possess cell surface amine oxidases, which can cleave amino groups from amino acids and primary amines (Palenik and Morel, 1990a,b, 1991; Fig. 6). The resulting alpha-keto acids (from amino acids) or aldehydes (from primary amines) are released as potential C sources for bacteria. This scenario illustrates that, though studies with ^{14}C-labeled organic compounds result in transfer of the label to the bacterial fraction, these results cannot necessarily be extrapolated to include utilization of the associated amino N. Mulholland *et al.* (1998) quantified extracellular amino acid oxidase activity in natural waters from a number of oceanic and estuarine systems using a fluorescent analog of lysine (Pantoja and Lee, 1994). The highest rates of oxidase activity were observed in mesocosms during bloom-like conditions and in samples enriched with *Trichodesmium.*

The resurgence in interest in autotrophic DON utilization has fostered a return to classical culture work (see Antia *et al.,* 1991). One of the common problems with

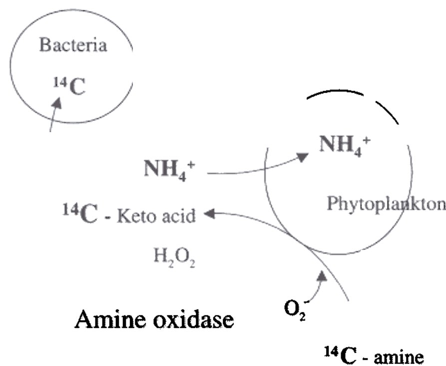

Figure 6 Conceptual diagram of phytoplankton amine oxidase activity (adapted from the work of Palenik and Morel, 1991). The enzyme catalyzes the decomposition of an amine at the surface of a phytoplankton cell resulting in the release of ammonium (NH_4^+), a keto acid, and hydrogen peroxide (H_2O_2). The amine is shown labeled with ^{14}C to illustrate that in a tracer experiment, the amine will appear to be used by the bacterial fraction, while the N may actually be utilized by the phytoplankton.

much of the early culture work, however, was that the concentrations of organic N compounds offered to phytoplankton as sole N sources were much higher (at times two to three orders of magnitude higher) than the concentrations of these compounds present in the environment. Though the studies show that a suite of organic N compounds can be a N source for phytoplankton, it is believed that at the very low concentrations of these compounds present in the environment, bacteria, with their superior surface to volume ratio and uptake capabilities, outcompete phytoplankton for their use. For example, John and Flynn (1999) quantified DFAA uptake by the toxic dinoflagellate *Alexandrium fundyense* and found that, though it can use DFAA as a N source, DFAA cannot support substantial growth at the concentrations found in the environment. This study reinforces the necessity of using environmentally relevant concentrations in cultures.

Recent culture studies have shown that *Aureococcus* and *Nannochloris* sp. can grow on glutamic acid as its sole N source (Dzurica *et al.,* 1989). A host of organic N compounds, including hypoxanthine, acetamide and formamide, can also support growth in the ubiquitous coccolithophore, *Emiliania huxleyi,* although the substrates were added at 100 μM levels (Palenik and Henson, 1997). They suggest that small amides are transported into the cell and then degraded to produce NH_4^+ through the use of amide-specific enzymes. Results from other studies of *E. huxleyi* suggest that organic N use might be strain specific. For example, some strains grow well on amino acids (Flynn, 1990) while others do not (Iestwaart *et al.,* 1994). Palenik and Koke (1995) found that N starvation in *E. huxleyi* induces a cell-surface protein (NPR1) that is present when cells are growing on organic N forms (urea and purines) but not when cells are growing on DIN, raising the question of its possible role as an organic N transporter. A number of phytoplankton species from Lake Kinneret, *Pediastrum* (Chlorophyta), *Cyclotella* (diatom), and *Aphanizomenon ovalisporum* (cyanobacteria), also grow well on a number of organic N compounds, including urea, ornithine, lysine, glucosamine, hypoxanthine, and quanine (Berman and Chava, 1999). Again, however, experiments were done with 100 μM substrate additions such that relating the results to natural waters is questionable.

3. Potential Link between DON and Harmful Algal Blooms

Much of the work on DON utilization in the recent past has been tied to DON's potential as a N source to phytoplankton that can form HABs. There is increasing evidence linking DON additions with the increase in harmful algal species (Paerl, 1988; Berg *et al.,* 1997; Carlsson *et al.,* 1998). In general, diatom abundance tends to correlate with high NO_3^- concentrations (Malone, 1980; Kokkinakis and Wheeler, 1988; Probyn *et al.,* 1990), while low NO_3^- concentrations and high rates of NH_4^+ or DON addition tend to correlate with high microflagellate abundance (Probyn, 1985; Paerl, 1988; Lomas and Glibert, 1999; Carlsson *et al.,* 1998; Glibert

and Terlizzi, 1999). Dinoflagellates, in particular, are characterized by diverse nutritional strategies (Schnepf and Elbrächter, 1992; see review of mixotrophy by Caron, 2000), and a number of dinoflagellate species can use organic nutrients, such as urea and amino acids, both directly (Butler *et al.*, 1979; Berg *et al.*, 1997) and indirectly, via cell-surface enzymes (Palenik and Morel, 1990a,b; Pantoja and Lee, 1994; Mulholland *et al.*, 1998). Three toxic species that have received considerable attention are the brown tide *Aureococcus anophagefferens* (a pelegophyte), *Gymnodinium breve* (a dinoflagellate), and *Pfiesteria piscicida*.

A. anophagefferens has been prevalent along the Northeast Atlantic coast for over 15 years (Bricelj and Lonsdale, 1997). A number of studies have implicated DON in initiating the blooms (Dzurica *et al.*, 1989; Berg *et al.*, 1997; LaRoche *et al.*, 1997) with particular emphasis on urea utilization (Dzurica *et al.*, 1989; Berg *et al.*, 1997). Berg *et al.* (1997) found that organic N comprised 70% of the total N utilized, with the largest portion of N utilization supplied by urea, during an *A. anophagefferens* bloom off Long Island. In contrast, Gobler and Sañudo-Wilhelmy (2001) found that urea additions did not increase the relative abundance of *A. anophagefferens* while glucose additions did. They suggest that DON additions with higher C:N ratios than urea (i.e., amino acids or amino sugars) may be more likely to trigger a brown tide bloom. Brown tides off Long Island are found to commonly occur in drought years when NO_3^- inputs are reduced and DON concentrations are high relative to DIN (LaRoche *et al.*, 1997). Glibert and Terlizzi (1999) found that high urea levels ($>1.5\ \mu M$) cooccur with dinoflagellate blooms in aquaculture ponds. *G. breve*, like other dinoflagellates, can also take up a variety of organic N compounds (e.g., vitamins, amino acids) as N sources for growth (Steidinger *et al.*, 1998). In cultures of *G. breve*, cell yields increase dramatically when glycine, leucine, and aspartic acid are added (Shimizu *et al.*, 1995). Likewise, the kleptoplastidic (when functional chloroplasts are retained from algal prey) *Pfiesteria piscicida* can use DIN, urea, and glutamate in culture (Lewitus *et al.*, 1999).

B. Methods for Estimating Biotic DON Uptake

DON is difficult to study as a N source because it is composed of a large number of compounds and the exact composition is unknown (Gardner and Stephens, 1978; Sharp, 1983; Antia *et al.*, 1991). As a result, measurements of DON uptake rates have largely been limited to a few compounds which have commercially available ^{15}N, ^{14}C, or ^{3}H tracers such as amino acids or urea (Fuhrman, 1987; Hansell and Goering, 1989; Wheeler and Kirchman, 1986; Cochlan and Harrison, 1991; Antia *et al.*, 1991). Bronk and Glibert (1993a) developed a method for manufacturing ^{15}N-labeled DON produced *in situ*, which involves incubating a whole water sample with ^{15}N-labeled NH_4^+ or NO_3^-. The recently released $DO^{15}N$

is then isolated using ion retardation resin (see Section III.B.2) and subsequently used as a tracer to quantify DON uptake rates. Much of the recent work focusing on the bulk DON pool used a bioassay approach, where changes in ambient and added DON are monitored over time (Seitzinger and Sanders, 1997). Bioassay approaches are particularly useful in determining the biological availability of more recalcitrant organic N compounds, such as humic substances (Carlsson and Granéli, 1993; Carlsson *et al.,* 1995).

C. Literature Values of DON Uptake in Aquatic Environments

Consideration of organic N uptake is slowly becoming a routine part of many field programs. Here, uptake rates of bulk DON (i.e., the total DON pool), urea, DCAA and DFAA, humic substances, and other DON compounds are discussed.

1. Bulk DON

Most of the work done on bulk DON utilization has been in freshwater systems using a bioassay approach. This work suggests that 12 to 72% of the DON pool is bioavailable on the order of days to weeks. In the Delaware and Hudson Rivers, 40–72% of the DON is consumed during 10- to 15-day dark bioassays, and DON consumption results in both an increase in PN and the release of DIN (Seitzinger and Sanders, 1997). These data suggest that the bioavailable DON can be utilized within estuaries with residence times on the order of weeks to months. In systems where residence times are shorter, riverine DON will be a source of bioavailable N to coastal waters.

Stepanauskas *et al.* (1999a) measured the concentration and bioavailability of three MW DOM fractions in samples collected seasonally in Swedish wetlands. The percentage of bulk DON represented by the different fractions ranges from a mean of 23% for the HMW fraction to a low of 6% for LMW DON. They found that bioavailable DON is higher in seawater than in freshwater and that bioavailability does not correlate with the C:N ratio of the DOM. The percentage of the different fractions that are bioavailable in seawater cultures are 12 ± 4, 7 ± 3, 5 ± 4, and $16 \pm 8\%$ for bulk, HMW, intermediate, and LMW DON, respectively. In additional studies in wetlands, the addition of natural DON stimulates cell-specific AMPase activity; refractory and humic-rich DOM causes a stronger stimulation than other forms believed to be more labile (Stepanauskas *et al.,* 1999b). AMPase activity is twofold higher in seawater, relative to freshwater, indicating that hydrolysis and turnover of terrestrial DON may increase when it enters the coastal ocean (Stepanauskas *et al.,* 1999b).

In two streams in Sweden, 19–55% of the bulk DON is bioavailable in short-term bioassays (Stepanauskas *et al.*, 2000). Only 5–18% of the DON is identified as urea, DCAA, or DFAA, suggesting that bacteria also utilize other organic N compounds. Potential DON bioavailability is positively correlated with the concentration of DCAA and the proportion of L-enantiomers in amino acids. In 7- to 8-day bioassay experiments in the Gulf of Riga, an average of 77% (8–136%) of the bacterial N biomass accumulation is a result of DCAA and DFAA uptake, and 13% of the DON is bioavailable during the study (Jørgensen *et al.*, 1999). Bronk and Glibert (1993a) used ^{15}N-labeled DON produced *in situ* in Chesapeake Bay and found that during the decline of the spring bloom, uptake rates of DON are higher than uptake rates of NH_4^+ and NO_3^-. In August, rates of DON uptake are again higher than uptake rates of NO_3^-, though not higher than NH_4^+.

2. Urea

In general, phytoplankton are believed to be the primary users of urea in marine systems (Price and Harrison, 1988, Table VI). More recent studies, however, have called this belief into question (Tamminen and Irmisch, 1996). In the Thames Estuary, the addition of a broad procaryotic inhibitor reduces dark uptake rates of amino acids by $49 \pm 20\%$ and urea by $86 \pm 25\%$, suggesting that, contrary to popular belief, autotrophs use a significant fraction of the amino acids and that bacterial uptake of urea is substantial (Middelburg and Niewenhuize, 2000). The whole water microbial community and the heterotrophic bacterial community alone appear to prefer amino acids, with NH_4^+ and urea next, and NO_3^- as the least preferred N substrate. In the bioassay study described in the previous section, Jørgensen *et al.* (1999) also found that urea uptake by bacteria can be as important as DFAA uptake.

In the Chesapeake Bay plume, urea contributes 60 to 80% of the N uptake measured throughout most of the year (Glibert *et al.*, 1991). Lomas *et al.* (in press) reviewed urea uptake rates for over a decade in Chesapeake Bay and found that urea is consistently an important N source for the plankton community, and that the highest mean baywide rates are observed during the summer.

Illustrating the close coupling between urea uptake and urea regeneration, Hansell and Goering (1989) found that urea uptake rates based on urea disappearance are an average of 140% greater than those based on rates of N accumulation in the Bering Sea. Because urea regeneration is prevalent in their samples, correcting for isotope dilution increases measured uptake rates by an average of 54%.

3. DCAA and DFAA

Bacteria are generally considered the primary users of DCAA and DFAA. As noted for urea above, changes in the size of the DFAA pool are generally small even when rates of uptake and release are substantial, indicating that uptake and release

Table VI

Summary of Published Uptake Rates for Individual Organic N Compounds and the Bulk DON Pool

Location	Sampling date	Sampling depth (m)	Fraction	Uptake rate (ng-at N R^{1} h^{-1})	% Total N uptake (%)	Substrates included in total N uptake	Method	Reference
Urea								
North Sea	July–August 1994	10 and 40	WW	4.9 ± 5.6	23.6 ± 17	N4, N3, U	^{15}N	Riegman and Noodeloos, 1998
North Sea	March–April 1994	10	WW	0.3 ± 0.3	9.9 ± 9.6	N4, N3, U	^{15}N	Riegman *et al.*, 1998
Straits of Georgia, Canada	July–Aug 1984	Upper 15	WW	7.37 to 25.55			^{15}N	Cochlan *et al.*, 1991
South Atlantic—oceanic[a]	March 1994	50% Io	WW	2.6 ± 1.4	14.0	N4, N3, U	^{15}N	Metzler *et al.*, 1997
South Atlantic—oceanic[a]	March 1994	1% Io	WW	0.5 ± 0.3	13.5	N4, N3, U	^{15}N	Metzler *et al.*, 1997
South Atlantic—inshore[a]	March 1994	50% Io	WW	55.9 ± 34.7	12.4	N4, N3, U	^{15}N	Metzler *et al.*, 1997
South Atlantic—inshore[a]	March 1994	1% Io	WW	21.5 ± 17.4	22.7	N4, N3, U	^{15}N	Metzler *et al.*, 1997
North of Antarctic Peninsula	November 1992	Surface	WW	0.5 to 1.0	5.1 to 23.6	N4, N3, U	^{15}N	Bury *et al.*, 1995
Bellingshausen Sea	Nov–Dec 1992	Upper 100	WW	1.4 to 9.4	5 to 21	N4, N3, U	^{15}N	Waldron *et al.*, 1995
Chesapeake Bay plume	February 1985	Surface	WW	7.8 to 71.0[b]	24.7 to 57.5	N4, N3, U, DFAA	^{15}N	Glibert *et al.*, 1991
Chesapeake Bay plume	June, Aug 1985	Surface	WW	30 to 660	11.0 to 63.0	N4, N3, U, DFAA	^{15}N	Glibert *et al.*, 1991
Chesapeake Bay plume	April 1986	Surface	WW	7.5 to 139.0	8.2 to 19.2	N4, N3, U, DFAA	^{15}N	Glibert *et al.*, 1991

Chesapeake Bay, mesohaline	May 1988	Surface	WW	176.2 ± 68.2	8.1 ± 3	N4, N3, U	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	August 1988	Surface	WW	228.0 ± 197.8	37.1 ± 27.6	N4, N3, U	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	October 1988	Surface	WW	11.0 ± 2.9	14.1 ± 11.9	N4, N3, N2, U	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	August 1991	Surface	WW	142.3 ± 70.8	16.9 ± 7.9	N4, N3, N2, U, $DO^{15}N$	^{15}N	Bronk and Glibert, 1993a
Chesapeake Bay	1973, 1988–1994	Surface	WW	24 to 332			^{15}N	Lomas *et al.*,in press
Chesapeake Bay	1973, 1988–1994	Deep	WW	28 to 104			^{15}N	Lomas *et al.*,in press
Shinnecock Bay, Long Island	July 1995	Surface	WW	3.5 to 28.6[c]	58 to 64	N4, N3, U, lys, glu, AE	^{15}N	Berg *et al.*, 1997
Thames Estuary	February 1999	Surface	WW	< 0.1 to 7.0	< 3	N4, N3, U, DFAA	^{15}N	Middelburg and Nieuwenhuize, 2000
Culture of *Pfiesteria piscicida*	Low light			2.00 ± 0.90	< 1	N4, N3, U, glu	^{15}N	Lewitus *et al.*, 1999
Culture of *Pfiesteria piscicida*	High light			7.90 ± 2.90	< 1	N4, N3, U, glu	^{15}N	Lewitus *et al.*, 1999
			Mean ± std	**63.5 ± 92.8**	**18.8 ± 15.4**			

(*Continues*)

Table VI (*(Continued*)

Location	Sampling date	Sampling depth (m)	Fraction	Uptake rate (ng-at N R^{1} h^{-1})	% Total N uptake (%)	Substrates included in total N uptake	Method	Reference
DCAA								
Santa Rosa Sound, FL		Surface	B	~7.9	14.1	N4, N3, DC and FAA DNA	CC	Jørgensen *et al.*, 1993
Gulf of Mexico	April–May 1991	Surface	B	37.6 ± 35.4	46.3	N4, N3, DC and FAA DNA	CC	Jørgensen *et al.*, 1994
Santa Rosa Sound, FL	April–May 1991	Surface	B	30.7 ± 3.2	56.3	N4, N3, DC and FAA, DNA	CC	Jørgensen *et al.*, 1994
Eleven Mile Creek, FL	April–May 1991	Surface	B	55.8 ± 19.6	34.4	N4, N3, DC and FAA, DNA	CC	Jørgensen *et al.*, 1994
			Mean ± std	**33.0 ± 19.8**	**37.8 ± 18.2**			
DFAA/DPA								
Gulf of Riga	May and July	Surface	B	0.9 to 30.8[d]			^{14}C	Jørgensen *et al.*, 1999
Central Arctic	July–August 1994	Upper 50	B	1.30 to 4.20			^{3}H	Rich *et al.*, 1997
Chesapeake Bay plume	February 1985	Surface	WW	1.0 to 3.8[e]	1.1 to 4.9	N4, N3, U, DFAA	^{15}N	Glibert *et al.*, 1991
Chesapeake Bay plume	June and Aug 1985	Surface	WW	3.0 to 92.5[e]	1.4 to 7.1	N4, N3, U, DFAA	^{15}N	Glibert *et al.*, 1991
Chesapeake Bay plume	April 1986	Surface	WW	2.6 to 23.1[e]	2.7 to 4.1	N4, N3, U, DFAA	^{15}N	Glibert *et al.*, 1991
Shinnecock Bay, Long Island	July 1995	Surface	WW	0.6 to 7.1[f]	11 to 16	N4, N3, U, lys, glu, AE	^{15}N	Berg *et al.*, 1997

Long Island Sound	May 1983	Surface	WW	10.0[g]			^{3}H	Fuhrman, 1987
Long Island Sound	July 1984	Surface	WW	35.3[h]			^{3}H	Fuhrman, 1987
Long Island Sound	November 1983	Surface	WW	3.8[i]			^{3}H	Fuhrman, 1987
Thames Estuary	February 1999	Surface	WW	6.0 to 150.0	3 to 93	N4, N3, U, DFAA[j]	^{15}N	Middelburg and Nieuwenhuize, 2000
Santa Rosa Sound, FL		Surface	B	~39.4	70.4	N4, N3, DC and FAA, DNA	^{14}C	Jørgensen *et al.*, 1993
Flax Pond, NY		Surface	B	~73.7	58.6	N4, N3, DC and FAA, DNA	^{14}C	Jørgensen *et al.*, 1993
Gulf of Mexico	April–May 1991	Surface	B	5.03 ± 2.12	6.2	N4, N3, DC and FAA, DNA	^{14}C	Jørgensen *et al.*, 1994
Santa Rosa Sound, FL	April–May 1991	Surface	B	4.23 ± 0.26	7.8	N4, N3, DC and FAA, DNA	^{14}C	Jørgensen *et al.*, 1994
Eleven Mile Creek, FL	April–May 1991	Surface	B	4.50 ± 1.32	2.8	N4, N3, DC and FAA, DNA	^{14}C	Jørgensen *et al.*, 1994
Culture of *Pfiesteria piscicida*	Low light			1000 ± 370	24.8	N4, N3, U, glu	^{15}N	Lewitus *et al.*, 1999
Culture of *Pfiesteria piscicida*	High light			950 ± 400	36.7	N4, N3, U, glu	^{15}N	Lewitus *et al.*, 1999
			Mean ± std	**134.8 ± 317.3**	**23.3 ± 24.3**			

(*Continues*)

Table VI (*Continued*)

Location	Sampling date	Sampling depth (m)	Fraction	Uptake rate (ng-at N R^1 h^{-1})	% Total N uptake (%)	Substrates included in total N uptake	Method	Reference
Bulk DON								
Gulf of Riga	May and July 1996	Surface	B	5.8 to 56.9			CC	Jørgensen *et al.*, 1999
eastern North Pacific	June 1992	Surface	B	22.5 ± 29.2^k			CC	Cherrier *et al.*, 1996
eastern North Pacific	October 1992	Surface	B	65.0 ± 12.5^k			CC	Cherrier *et al.*, 1996
Akkeshi Bay, Japan	March–Nov 1998	Surface	B	4.3 to 15.0			^{15}N	Hasegawa *et al.*, 2000b
Chesapeake Bay, mesohaline	May 1990	Surface	WW	376.3 ± 65.1	55.5 ± 5.8	N4, N3, $DO^{15}N$	^{15}N	Bronk and Glibert, 1993a
Chesapeake Bay, mesohaline	August 1990	Surface	WW	252.4 ± 131.1	27.7 ± 10.[illegible]	N4, N3, N2, U, $DO^{15}N$	^{15}N	Bronk and Glibert, 1993a
Lake Kinneret, Israel (freshwater)	September 1997	Surface	B	44.4			CC	Berman *et al.*, 1999
			Mean ± std	**114.5 ± 142.2**	**41.6 ± 19.7**			
D-DNA								
Santa Rosa Sound, FL		Surface	B	~8.7	15.5	N4, N3, DC and FAA, DNA	^3H	Jørgensen *et al.*, 1993
Flax Pond, NY		Surface	B	~1.1	0.9	N4, N3, DC and FAA, DNA	^3H	Jørgensen *et al.*, 1993
Gulf of Mexico	April–May 1991	Surface	B	3.70 ± 0.53	4.5	N4, N3, DC and FAA, DNA	^3H	Jørgensen *et al.*, 1994; Kroer *et al.*, 1994

Santa Rosa Sound, FL	April–May 1991	Surface	B	4.50 ± 0.00	8.3	N4, N3, DC and FAA, DNA	H	Jørgensen *et al.*, 1994; Kroer *et al.*, 1994
Eleven Mile Creek, FL	April–May 1991	Surface	B	101.19 ± 12.7	41.6	N4, N3, DC and FAA, DNA	^3H	Jørgensen *et al.*, 1994; Kroer *et al.*, 1994
			Mean ± std	**23.8 ± 43.3**	**14.2 ± 16.3**			

Note. Data were taken directly from tables, estimated from graphs, or obtained from the author's directly. Substrates are ammonium (N4), nitrate (N3), nitrite (N2), urea (U), dissolved free amino acids (DFAA), and algal extract (AE). Data are presented as mean ± standard deviation. When ranges are presented, the mean uptake rates were calculated using the median value in the range.

[a] Under mixed water column conditions.

[b] Rates received from the author.

[c] Rates are pmax for short-term (minutes) to 60-min incubations.

[d] Converted to N using the average C:N ratio of the DFAA used (glu, gly, ser, ala), which is 3.25.

[e] DFAA measured were glu, gly, ala, and ser.

[f] Combined pmax rates for glu, lys, and algal extract.

[g] DFAA measured were glu and ala.

[h] DFAA measured were glu, gly, ala, and leu.

[i] DFAA measured were gly, ala, and leu.

[j] Used an ^{15}N-labeled amino acid mixture.

[k] Rates are for bioassays used phytoplankton extract supplied at 2× the ambient concentration of DOC.

processes are closely coupled (Fuhrman, 1987). In Long Island Sound, DFAA supply >10% of the C and N used to fuel bacterial growth, and DFAA uptake and release rates tend to be highest near noon and lowest at night, suggesting a link to autotrophs (Fuhrman, 1987). The four amino acids measured (glutamic acid, serine, glycine, alanine) can supply 44 to 131% of the calculated bacterial N demand.

In other studies, DFAA and DCAA have been shown to supply ~50% of the bacterial N demand in estuarine and coastal systems (Keil and Kirchman 1991a, 1993; Middelboe *et al.*, 1995). In the subarctic Pacific and Delaware estuary, DFAAs are used preferentially over DCAAs unless DFAA concentrations are very low (Keil and Kirchman, 1991a). In 14 bioassays performed, 51 ± 45% of the bacterial N demand is met by DFAA, with 18 ± 24% met by DON other than DFAA. In the Northern Sargasso Sea, protein is the dominant form of DON fueling bacterial production, supporting 20 to 65% of the estimated bacterial N demand in the surface (Keil and Kirchman, 1999). Middelboe *et al.* (1995) also found that DFAA and DCAA sustains up to 34 and 24% of the bacterial N demand, respectively, during exponential growth. As DFAA and NH_4^+ concentrations decrease during stationary phase, the importance of DCAA as both a C and an N source increases.

In the Mississippi plume, rapid DFAA turnover occurs coincident with rapid NH_4^+ regeneration rates, suggesting that DFAA are important substrates for bacterial NH_4^+ regeneration in the plume (Cotner and Gardner, 1993). Similar findings where DFAA turnover exceeds bacterial N demand have been observed in another study in the plume (Gardner *et al.*, 1993), in Chesapeake Bay (Fuhrman, 1990), and in the subarctic Pacific (Kirchman *et al.*, 1989; Keil and Kirchman, 1991a).

The role of DFAA as a N source for phytoplankton was reviewed in Flynn and Butler (1986) and Antia *et al.* (1991). Though laboratory studies show that some phytoplankton can grow on DFAA, uptake of DFAA by phytoplankton is considered to be insignificant in the field; as noted above, recent research on cell-surface enzymes suggests that phytoplankton use of DFAA may be greater than previously thought (see Section IV.A.2). In a salt marsh phytoplankton community, addition of organic N, including glycine, glutamic acid, and an amino acid mixture, results in increased phytoplankton growth (Lewitus *et al.*, 2000). The physiological response of the phytoplankton community to organic N additions, in the presence and absence of antibiotics, suggests that the stimulation caused by organic N additions results directly from uptake of the organic substrates and indirectly through bacterial decomposition.

The newly recognized Archaea also appear to use DFAA. In studies in the Mediterranean Sea and the Pacific Ocean near California, ~60% of the Archaea exhibit measurable DFAA uptake at nanomolar levels (Ouverney and Fuhrman, 2000).

There is increasing recognition that the utilization of DCAA and DFAA may be affected by abiotic reactions. Glucosylation and adsorption processes appear to be

important in making labile compounds more refractory. Rates of protein utilization decrease when the protein is adsorbed to submicrometer particles (Nagata and Kirchman, 1996). This is potentially a very important mechanism because the surface area of colloids in the surface ocean likely exceeds that of bacteria (Schuster *et al.,* 1998). Accordingly, a given amino acid released from a phytoplankton cell is much more likely to come into contact with colloidal material, rendering it less biologically available, than to come into direct contact with a bacterial cell. These studies suggest that competition between abiotic adsorption onto colloids and bacterial uptake can have large implications for the cycling of DOM, particularly small labile moieties such as amino acids. An estimated ~11–55% of the DFAA detectable by HPLC may be adsorbed to colloidal DOM in oceanic surface waters (Schuster *et al.,* 1998). Natural bacterial populations degraded ~92% of dissolved unprotected proteins in 72–90 h in one study (Borch and Kirchman, 1999). Protein adsorbed to or present within liposomes, designed to mimic protein that is adsorbed or trapped within particles similar to those produced by protists, however, has substantially lower degradation rates. The fecal pellets of some flagellates are believed to be similar in structure to liposomes (Nagata and Kirchman, 1992), and viral lysis can also produce liposome-like structures (Shibata *et al.,* 1997). Reduction in the degradation rates of organics associated with liposome-like structures may explain the presence of membrane proteins in the deep ocean DOM pool (Tanoue *et al.,* 1996; McCarthy *et al.,* 1998).

On the flip side, adsorption of DFAA can also make refractory organics more bioavailable. Adsorption of DFAA to dextran and phytoplankton-derived colloidal DOM results in approximately three times more efficient utilization of dextran or colloidal DOM by marine bacteria when compared to dextran or DOM without adsorbed DFAA (Schuster *et al.,* 1998).

4. Humic Substances

Humic substances constitute a large reservoir of organic C and N in both aquatic and terrestrial systems (Mantoura *et al.,* 1978). Humic substances have long been recognized for their ability to chelate organometallic substances, thereby making trace metals more available to phytoplankton (Prakash, 1971; Prakash *et al.,* 1973) and sequestering toxic heavy metals (Barber, 1973; Toledo *et al.,* 1982). Biologically, humic substances have traditionally been considered unavailable for assimilation due to their HMW and structural complexity. More recent studies of HMW organic compounds, however, have revealed that they are not as refractory as once thought (Moran and Hodson, 1994; Amon and Benner, 1994; Gardner *et al.,* 1996).

Despite these advances, the role of marine humic substances remains unclear. It has been postulated that some phytoplankton, specifically the dinoflagellates, may be able to utilize N bound to humic substances (Carlsson and Granéli, 1993).

Experiments in which natural humic substances, isolated from river water, are added to an assemblage of coastal phytoplankton reveal that growth and biomass formation are stimulated (Carlsson *et al.,* 1993). The literature suggests that the N associated with humic substances can be removed via one of three mechanisms: through microbial activity (Müller-Wegener, 1988), via excision by phytoplankton cell-surface enzymes (Palenik and Morel, 1990a; see Section IV.A.2), or through photodegradation to LMW compounds by exposure to UV radiation (Gellar, 1986; Kieber *et al.,* 1990; Mopper *et al.,* 1991; see Section IV.D).

5. Other Organic Compounds

Additional studies that measure uptake of other organic N compounds such as purines (Douglas, 1983), pyrimidines (Knutsen, 1972), and amines (Neilson and Larsson, 1980; Wheeler and Hellebust, 1981) show that though phytoplankton and bacteria can utilize these compounds, the uptake rates are quite low (reviewed in Antia *et al.,* 1991). There is still a debate as to whether D-DNA is actually used as a source of N for bacteria; D-DNA is approximately 16% N and so it has the potential to be a N source. Paul *et al.* (1988) found evidence that D-DNA is used as a source of nucleic acids for bacteria and that it is degraded to provide phosphate needed by the cell. Jørgensen *et al.* (1993) measured uptake rates of DCAA, DFAA, and D-DNA in seawater cultures, and found that D-DNA is used primarily as a source of N. When DCAA, DFAA, and D-DNA are combined, they provide 14 to 49% of the net bacterial N uptake measured in that study. Using turnover times of unidentified HMW DON, estimated with $\delta^{15}N$ data, DON concentrations, and rates of primary production, Benner *et al.* (1997) estimated that DON remineralization can support 30–50% of daily phytoplankton N demand in the equatorial Pacific region.

D. Photochemical Decomposition as a Sink for DON

Recent findings in freshwater and marine systems indicate that photochemical processes can effect the release of labile N moieties from DOM (Bushaw *et al.,* 1996). Numerous studies have shown that photochemical reactions occur when DOM from freshwater or marine environments is exposed to natural sunlight. The resulting photoproducts include carbon monoxide, carbon dioxide, various carbonyl compounds, and likely many others (see reviews by Moran and Zepp, 2000, and Mopper and Kieber, Chapter 9). Some of these photoproducts can be lost by direct transfer to the atmosphere, while others can be assimilated rapidly by natural bacterial populations (Kieber *et al.,* 1989; Geller, 1986; Lindell *et al.,* 1995). With respect to N, we know that substances containing organic N can play an important role in the impact of UV radiation on aquatic biogeochemical cycles (de Mora *et al.,* 2000).

To date, most of the studies of N photoproduction have focused on fresh or brackish water systems (Table VII). Studies have documented the photoproduction of NH_4^+, DFAA, DCAA, DPA, and NO_2^- (Table VII), but the process is not ubiquitous (Bertilsson *et al.,* 1999; Koopmans and Bronk, in press). DON and isolated humic substances can be a source of labile N when irradiated with sunlight, and wavelengths in the ultraviolet (UV) region (280–400 nm) produce the N photoproducts most efficiently (Bushaw *et al.,* 1996). Humic substances are likely important substrates for photoproduction because their aromaticity and color allow them to absorb UV light, making them more photochemically reactive than other classes of marine DOM. Furthermore, an estimated 50 to 75% of the N associated with humic substances exists as DFAA, amino sugars, and other N-rich compounds that are likely sources of the labile N forms produced photochemically (Valiela and Teal, 1979; Rice, 1982; Thurman, 1985; Stevenson, 1994).

In a river and bayou in Louisiana, an estimated 9 to 20% of the TON in the photic zone was converted to NH_4^+ each day (Wang *et al.,* 2000). Koopmans and Bronk (in press) measured N photoproduction from DOM isolated from surficial groundwaters. Photochemical production of NH_4^+ was observed in 4 of 5 irradiated estuarine surface water samples, but in only 2 of 13 groundwater samples. In contrast, the photochemically mediated loss of NH_4^+ was observed in 7 of 13 groundwater samples, likely due to incorporation into DOM. These data suggest that photochemical reactions may be a sink as well as a source of available N.

In a cross-system comparison, photoproduction experiments were performed in parallel with ^{15}N uptake experiments (Bronk *et al.,* unpublished data). Photochemical ammonification supplied an average of 13, 13, and 7% of the NH_4^+ taken up in the Eastern Tropical North Pacific, South Atlantic Bight, and two rivers in Georgia, respectively. When photoproduction is detected, it supplies up to 38% of the DPA utilized and up to 33% of the NO_2^- taken up. Photochemical ammonification is a relatively minor source of NH_4^+ in all three environments with rates being 2 to 6% of biotic NH_4^+ regeneration rates, measured with the ^{15}N isotope dilution technique (Glibert *et al.,* 1982). In a study in Lake Maracaibo, photochemical ammonification rates are ~30% of the total near surface rates of NH_4^+ regeneration (Gardner *et al.,* 1998).

E. Sinks for DON: Research Priorities

Research on DON utilization is poised for rapid development. Some specific areas where additional study should prove fruitful would be to address questions of the differential flow of the C and N fractions of DOM in parallel. Combining the new enzymatic approaches with dual labeled substrates (^{13}C, ^{15}N, ^{18}O, etc.)

Table VII

Rates of Photochemical Release from Dissolved Organic Nitrogen (DON) in Whole Water or Various DON Fractions

Location	Date	Substrate	Photoproduction rate (ng-at N L^1 h^{-1})	Reference
Production of NH_4^+				
Boreal Pond, Manitoba	June	Isolated fulvic acids	370 ± 10	Bushaw *et al.*, 1996
Boreal Pond, Manitoba	July	Whole water	150 ± 10	Bushaw *et al.*, 1996
Boreal Pond, Manitoba	August	Isolated fulvic acids	65 ± 10	Bushaw *et al.*, 1996
Okeefenokee Swamp, GA		Whole water	340 ± 30	Bushaw *et al.*, 1996
Satilla River, GA		Isolated fulvic acids	50 ± 15	Bushaw *et al.*, 1996
Oyster River, NH		Isolated fulvic acids	320	Bushaw *et al.*, 1996
Lake Maracaibo, Venezuela	September 1995	Whole water	0 to 220	Gardner *et al.*, 1998
River catchments, Sweden	June–Aug 1996	Whole water	ND	Bertilsson *et al.*, 1999
Groundwater, Sweden	June–Aug 1996	Whole water	ND	Bertilsson *et al.*, 1999
Lake Skarshult, Sweden	July 1994	Whole water	ND	Jørgensen *et al.*, 1998
Pearl River, LA		< 1000 Dalton DOM	330	Wang *et al.*, 2000
Bayou Trepagnier, LA	August 1997	< 1000 Dalton DOM	1200 to 1700	Wang *et al.*, 2000
Bayou Trepagnier, LA	January 1999	< 1000 Dalton DOM	1900	Wang *et al.*, 2000
Skidaway River, GA	August 1995	2.8× Concentrated humics	ND	Bushaw-Newton and Moran, 1999
Skidaway River, GA	February 1996	2.8× Concentrated humics	7 ± 4.9[a]	Bushaw-Newton and Moran, 1999
Skidaway River, GA	February 1996	28× Concentrated humics	60 ± 3[a]	Bushaw-Newton and Moran, 1999
Satilla River, GA	October 1996	2.8× Concentrated humics	58 ± 3[a]	Bushaw-Newton and Moran, 1999

(Continues)

Table VII (*Continued*)

Location	Date	Substrate	Photoproduction rate (ng-at N L^{-1} h^{-1})	Reference
Eastern Tropical North Pacific	July 1995	Whole water	5.4 ± 4.4	Bronk *et al.*, unpublished data
South Atlantic Bight	March 1999	Whole water	35.3 ± 39.3	Bronk *et al.*, unpublished data
Altamah and Savannah rivers	Mar, July, Oct 1998	Whole water	10.8 ± 15.1	Bronk *et al.*, unpublished data
		Mean ± std	**350.0 ± 559.8**[b]	
		Mean ± std	**136.5 ± 139.4**[c]	
Production of dissolved free and combined amino acids				
Lake Skarshult, Sweden	July 1994	Whole water	63	Jørgensen *et al.*, 1998
Production of DPA				
Skidaway River, GA	August 1995	2.8 × Concentrated humics	ND	Bushaw-Newton and Moran, 1999
Skidaway River, GA	February 1996	2.8 × Concentrated humics	ND	Bushaw-Newton and Moran, 1999
Skidaway River, GA	February 1996	28× Concentrated humics	41 ± 7.1[a]	Bushaw-Newton and Moran, 1999
Satilla River, GA	October 1996	2.28× Concentrated humics	9 ± 8.5[a]	Bushaw-Newton and Moran, 1999
Eastern Tropical North Pacific	July 1995	Whole water	6.1 ± 9.4	Bronk *et al.*, unpublished data
Altamah and Savannah rivers	Mar, July, Oct 1998	Whole water	8.7 ± 12	Bronk et al., unpublished data
		Mean ± std	**16.2 ± 16.6**	
Production of NO_2^-				
Coastal seawater, NC	May	Isolated humics	1.4	Kieber *et al.*, 1999
Albermarle sound, NC	May	Isolated humics	6.7	Kieber *et al.*, 1999
Marsh, NC	May	Isolated humics	1.9	Kieber *et al.*, 1999
Cape Fear Estuary, NC	May	Isolated humics	4.9	Kieber *et al.*, 1999

(*Continues*)

Table VII (*Continued*)

Location	Date	Substrate	Photoproduction rate (ng-at N L^{-1} h^{-1})	Reference
Eastern Tropical North Pacific	July 1995	Whole water	4.8 ± 4.4	Bronk *et al.*, unpublished data
Altamah and Savannah rivers	Mar, July, Oct 1998	Whole water	0.3 ± 0.9	Bronk *et al.*, unpublished data
			Mean ± std 3.3 ± 2.5	

Note. Data are presented as mean ± standard deviation unless otherwise noted. ND: not detected.
[a] Standard errors.
[b] Including all data.
[c] Excluding the Bayour Trepagnier data.

will likely show that the fate of the separate elements in DOM are different trophic levels (for example, see Fig. 6). It may also show that mixotrophy is more widespread than presently recognized. Along these same lines, quantifying where the DON is going, into autotrophic versus heterotrophic biomass, is extremely important to determining how these flows are modeled. Combining tracer techniques with flow cytometric sorting is one very promising way to discriminate between autotrophic and heterotrophic uptake (Lipschultz, 1995). The increasing availability of flow cytometers and the higher sorting speeds they can reach should make this approach much more widespread in the future. Finally, the long-term goal of bringing molecular techniques to bear on issues of elemental cycling is beginning to pay off. Quantitative PCR-type approaches will continue to be refined, holding out the tantalizing possibility of estimating flux rates without the perturbations inherent in traditional incubation techniques.

V. DON TURNOVER TIMES

Considering the heterogeneous nature of the DON pool, interpreting DON turnover times can be difficult. Turnover times for organic N cover a broad range from minutes for DFAA (Fuhrman, 1990) to hundreds of years for the bulk DON pool (Vidal *et al.,* 1999; Table VIII). In the Chesapeake Bay plume, DFAAs cycle rapidly with turnover times of 0.5 to 1.0 h in spring and summer and ~3 h in winter (Fuhrman, 1990). When considering the bulk DON pool, Abell *et al.* (2000) estimated turnover times, based on the surface concentrations of bioavailable TON in the mixed layer, to be 18 years when both shallow or

deep isopycnal degradation estimates are used. The residence time of DON in the surface waters of the equatorial Atlantic is estimated at 2.5 years (Vidal *et al.*, 1999). Harrison *et al.* (1992) estimated a maximum DON turnover time of 333 days (0.003 day^{-1}) in the northeastern Pacific by measuring changes in DON concentrations between cruises. Considering the enormous range of turnover times, one tends to wonder whether turnover times for the bulk DON pool really tell us much.

One danger in interpreting DON turnover times estimated with ^{15}N tracers is the convention that the shorter the turnover time, the more labile the compound. For example, Bronk and Ward (1999) found that DON turnover times, estimated with release rates measured in $^{15}NH_4^+$ incubations, are shorter than those measured in incubations with $^{15}NO_3^-$. These data imply that DON resulting from NH_4^+ uptake is more labile than that resulting from NO_3^- uptake. In reality the compounds produced and released are likely the same in both cases because the first step after NO_3^- is taken up by phytoplankton is the reduction to NH_4^+. The lability should be the same, regardless of the substrate, because the compounds released should be the same.

VI. SUMMARY

Traditionally, DON has been viewed as a large refractory pool that is unimportant to microbial nutrition. Research over the past decade has transformed this view, however, and the DON pool is emerging as a dynamic component of the DOM and N cycles. It is increasingly included as a core measurement in field programs and sophisticated chemical analyses are beginning to define its structure, chemical properties, sources, and sinks. I have attempted to describe recent findings in each of these areas, which I summarize below.

1. Concentration and Composition of the DON Pool

The lowest DON concentrations are generally found in the deep ocean with the highest observed in rivers (Fig. 1). DON generally accounts for the largest percentage of the TDN pool (~60%) in most systems. Though much work still needs to be done to define the global distributions of DON, the general trends emerging are that upwelling at the equator, in both the Atlantic and Pacific, fuels DON production. The DON produced is then exported to the north and south into the oligotrophic gyres. Concentrations tend to decrease near the poles, though seasonal accumulations in spring are likely, and increase near the continental margins. Vertical profiles of DON generally show a surface enrichment, and DON concentrations tend to be inversely correlated with NO_3^- concentrations as depth increases. Concentrations of DON and NO_3^- are also often inversely correlated over time in surface waters. Recent studies estimate that up to 80% of the net NO_3^- drawdown in a number of

Table VIII

Turnover Time Estimates of Dissolved Organic Nitrogen (DON) and Organic N Compounds

Location	Date	Compound considered	Turnover time	Units	Method	Reference
Oceanic						
Northeastern Pacific	NP	DON	0.91	Years	CC	Harrison *et al.*, 1992
Equatorial Atlantic (15S–25N)	Oct–Nov 1995	DON	0.4 to 13.2[a]	Years	CC	Vidal *et al.*, 1999
Equatorial Atlantic (15S–15N)	Oct–Nov 1995	DON	12.7 ± 26.1[a]	Years	CC	Vidal *et al.* 1999
Equatorial Atlantic (35–15S)	Oct–Nov 1995	DON	2.1 to 300[a]	Years	CC	Vidal *et al.* 1999
Caribbean Sea	November 1988	DON	40.7 ± 10.4	Days	^{15}N	Bronk *et al.*, 1994
Southern California Bight	October 1992	DON	11 to 62	Days	^{15}N	Bronk *et al.*, 1994
Northern Sargasso Sea	July 1990, Feb 1991	Protein	0.38 to 3.42	Days	^{14}C	Keil and Kirchman, 1999
Northern Sargasso Sea	July 1990	Modified protein[b]	9.04 to 32.71	Days	^{14}C	Keil and Kirchman, 1999
Northern Sargasso Sea	February 1991	Modified protein[b]	9.04 to 32.71	Days	^{14}C	Keil and Kirchman, 1999
Northern Sargasso Sea	July 1990, Feb 1991	DFAA	0.03 to 0.29	Days	^{3}H	Keil and Kirchman, 1999
Central Arctic	July-Aug 1994	DFAA	~2.72	Days	^{3}H	Rich *et al.*, 1997
Coastal						
Monterey Bay	March 1993	DON	5.0 ± 2.4	Days	^{15}N	Bronk and Ward, 1999
Monterey Bay	September 1993	DON	8.2 ± 2.4	Days	^{15}N	Bronk and Ward, 1999
Southern California Bight	October 1992	DON	24 to 85	Days	^{15}N	Bronk *et al.*, 1994
Mississippi River plume	February 1991	DFAA	0.013 to 0.073[c]	Days	^{3}H	Cotner and Gardner, 1993

(Continues)

Table VIII (*Continued*)

Location	Date	Compound considered	Turnover time	Units	Method	Reference
Mississippi River plume	September 1991	DFAA	0.02 to 0.14[c]	Days	^3H	Cotner and Gardner, 1993
Santa Rosa Sound, FL		D-DNA	0.2 to 0.43	Days	^3H	Jørgensen *et al.*, 1993
Flax Pond, NY		D-DNA	0.64 to 9.7	Days	^3H	Jørgensen *et al.*, 1993
Estuarine						
Chesapeake Bay	April 1989 and 1990	DON	6.0 to 91.0	Days	^{15}N	Bronk *et al.*, 1994
Chesapeake Bay, mesohaline	August 1991	DON	2.0 to 6.0	Days	^{15}N	Bronk *et al.*, 1993a
Chesapeake Bay, mesohaline	May 1988	DON	0.27 ± 0.23	Days	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	August 1988	DON	2.01 ± 1.13	Days	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	October 1988	DON	2.53 ± 2.54	Days	^{15}N	Bronk *et al.*, 1998
Choptank River[d]	August 1990	DON	33.8	Days	^{15}N	Bronk *et al.*, 1993b
Choptank River[d]	August 1990	LMW DON	15.9	Days	^{15}N	Bronk *et al.*, 1993b
Chesapeake Bay, mesohaline	May 1988	Urea	0.12 ± 0.03	Days	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	August 1988	Urea	0.33 ± 0.33	Days	^{15}N	Bronk *et al.*, 1998
Chesapeake Bay, mesohaline	October 1988	Urea	1.00 ± 0.30	Days	^{15}N	Bronk *et al.*, 1998
Thames Estuary	February 1999	Urea	4.2 to 69.0	Days	^{15}N	Middelburg and Nieuwenhuize, 2000
Chesapeake Bay	1973	Urea	3.17 ± 0.63	Days	^{15}N	Lomas *et al.*, in press
Chesapeake Bay	1988–1997	Urea	1.10 ± 0.71	Days	^{15}N	Lomas *et al.*, in press

(*Continues*)

Table VIII (*Continued*)

Location	Date	Compound considered	Turnover time	Units	Method	Reference
Thames Estuary	February 1999	Algal amino acid mix	0.2 to 1.9	Days		Middelburg and Nieuwenhuize, 2000
Hudson River plume	September 1985				^3H	Furhman, 1990
Chesapeake Bay plume	February 1985	glu, gly, ala	0.060 to 0.210	Days	^3H	Furhman, 1990
Chesapeake Bay plume	June 1985	glu, gly, ser, ala	0.009 to 0.090	Days	^3H	Furhman, 1990
Chesapeake Bay plume	August 1985	glu, gly, ser, ala	0.017 to 0.170	Days	^3H	Furhman, 1990
Chesapeake Bay plume	April 1986	glu, gly, ser, ala	0.016 to 0.240	Days	^3H	Furhman, 1990

Note. Data are presented as mean ± standard deviation. NP: not presented.
[a] Estimated with DON concentrations and vertical flux estimates.
[b] Glucosylated (i.e., aged) protein as in Keil and Kirchman (1993).
[c] In general, turnover times increased with salinity.
[d] Subestuary of Chesapeake Bay.

systems accumulates as DON. In the most general sense, a generic DON pool is shaping up to look like this: Identifiable LMW compounds such as urea, DCAA, and DFAA make up ~5 to 10% of the total DON pool each. Roughly 30% of the pool is HMW (>1 kDa). Of that HMW fraction, ~20–30% is hydrolyzable amino acids with the remainder being amide in form. This leaves a substantial fraction of the pool yet to be identified

2. Sources of DON

With respect to sources of DON, this review focuses on biotic water column processes that result in DON production from phytoplankton and N_2 fixers (passive diffusion, active release, sloppy feeding, and viral lysis), bacteria (passive diffusion, release of exoenzymes, bactivory, and viral lysis), and micro- and macrozooplankton (fecal pellet dissolution and excretion; Fig. 3). Rates of DON release summarized here suggest that the magnitude of release is similar in oceanic and coastal environments but slightly higher in estuarine systems. The percentage of the rate of gross N uptake released as DON was highest in oceanic systems (~40%) and lowest in estuaries (~23%), though clearly more data are needed before these generalizations can be considered robust.

3. Sinks for DON

With respect to DON sinks, this review focuses on heterotrophic uptake, autotrophic uptake, and photochemical N decomposition. Though heterotrophs have been traditionally considered the primary users of DON, there is increasing

recognition that DON can be an important source of N for phytoplankton. The recent work on phytoplankton cell surface enzymes has provided a mechanism by which autotrophs can utilize the N associated with DON without developing transport mechanisms for a wide range of compounds. Much of the interest in DON uptake of late has been encouraged by a number of studies that have documented a link between increases in DON concentrations and blooms of harmful algae.

Rates of DON utilization vary widely across systems and even within systems. The work summarized here suggests that the large DON pool is more bioavailable than previously thought. Work to date (much of which was done in freshwater systems with dark bioassays) suggests that 12 to 72% of the DON pool is bioavailable on the time scale of days to weeks. Three key substrates within the DON pool are urea, DCAA, and DFAA. In studies where the uptake of these substrates are compared to other N compounds, urea averages 19% of total measured N uptake with 38 and 23% contributed by DCAA and DFAA, respectively.

Nitrogen photoproduction has been demonstrated in a number of environments, and it can be an important mechanism for converting DON into labile compounds available for uptake by either phytoplankton or bacteria. Photochemical ammonification has been the most studied with an average rate of 136 ng-at N $L^{-1}h^{-1}$ with some extremely high rates documented. Rates of DPA and NO_2^-photoproduction have tended to be lower, though only a small number of studies have been done.

ACKNOWLEDGMENTS

I thank N. O. G. Jørgensen for his thought provoking review, S. Seitzinger for editorial advice, two anonymous reviewers for insightful comments, D. Karl for help with DNA/RNA calculations, and C. Carlson and D. Hansell for their patience. This work was supported by Georgia Sea Grant (NA06RG0029) and the National Science Foundation (OCE-0095940). This paper is VIMS Contribution 2400 from the Virginia Institute of Marine Science, College of William and Mary.

REFERENCES

Abell, J., Emerson, S., and Renaud, P. (2000). Distributions of TOP, TON, and TOC in the North Pacific subtropical gyre: Implications for nutrient supply in the surface ocean and remineralization in the upper thermocline. *J. Mar. Res.* **58,** 203–222.

Abdul-Rashid, M. (1990). Ph.D. thesis, University of Liverpool.

Admiraal, W., Peletier, H. and Laane, R. P. M. (1986). Nitrogen metabolism of marine planktonic diatoms: Excretion, assimilation and cellular pools of free amino acids in seven species with different cell size. *J. Exp. Mar. Biol. Ecol.* **98,** 241–263.

Agusti, S., Satta, M. P., Mura, M. P., and Benavent, E. (1998). Dissolved esterase activity as a tracer of phytoplankton lysis: Evidence of high phytoplankton lysis rates in the northeastern Mediterranean. *Limnol. Oceanogr.* **43,** 1836–1849.

Aiken, G. R. (1988). A critical evaluation of the use of macroporous resins for the isolation of aquatic humic substances. *In* "Humic Substances and Their Role in the Environment" (F. H. Frimmel and R. F. Christman, Eds.), pp. 15–28. Wiley, New York.

Alberts, J. J., and Takács, M. (1999). Importance of humic substances for carbon and nitrogen transport into southeastern United States estuaries. *Organ. Geochem.* **30,** 385–395.

Alonso, M. C., Rodriguez, V., Rodriguez, J., and Borrego, J. J. (2000). Role of ciliates, flagellates and bacteriophages on the mortality of marine bacteria and on dissolved-DNA concentrations in laboratory experimental systems. *J. Exp. Mar. Biol. Ecol.* **244,** 239–252.

Altabet, M. A. (1988). Variations in nitrogen isotopic composition between sinking and suspended particles: Implications for nitrogen cycling and particle transformations in the open ocean. *Deep Sea Res.* **35,** 535–554.

Aluwihare, L., and Repeta, D. (1999). A comparison of the chemical characteristics of oceanic DOM and extracellular DOM produced by marine algae. *Mar. Ecol. Prog. Ser.* **186,** 105–117.

Aluwihare, L., Repeta, D., and Chen, R. (1997). A major biopolymeric component to dissolved organic carbon in surface seawater. *Nature* **387,** 166–169.

Amon, R. M. W., and Benner, R. (1994). Rapid cycling of high-molecular-weight dissolved organic matter in the ocean. *Nature* **369,** 549–551.

Amon, R., Fitznar, H. P., and Benner, R. (2001). Linkages among the bioreactivity, chemical composition, and diagenetic state of marine dissolved organic matter. *Limnol. Oceanogr.* **46,** 287–297.

Antia, N. J., Harrison, P. J., and Oliveira, L. (1991). Phycological reviews: The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology, and ecology. *Phycologia* **30,** 1–89.

Armstrong, F. A. J., and Tibbitts, S. (1968). Photochemical combustion of organic matter in sea water for nitrogen, phosphorus, and carbon determination. *J. Mar. biol. Assoc. UK* **48,** 143–152.

Armstrong, F. A. J., Williams, P. M., and Strickland, J. D. H. (1966). Photo-oxidation of organic matter in sea water by ultra-violet radiation, analytical and other applications. *Nature* **211,** 481–483.

Axler, R. P., and Reuter, J. E. (1986). A simple method for estimating the ^{15}N content of DOM (DO^{15}N) in N cycling studies. *Can. J. Fish. Aquat. Sci.* **43,** 130–133.

Baines, S. P., and Pace, M. L. (1991). The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems. *Limnol. Oceanogr.* **36,** 1078–1090.

Barber, R. T. (1973). Organic ligands and phytoplankton growth in nutrient-rich seawater. *In* "Trace Metals and Metal–Organic Interactions in Natural Waters" (P. C. Singer, Ed.), pp. 321–338. Ann Arbor Sci., Ann Arbor, MI.

Bates, N. R., and Hansell, D. A. (1999). A high resolution study of surface layer hydrographic and biogeochemical properties between Chesapeake Bay and Bermuda. *Mar. Chem.* **64,** 1–16.

Benner, R., Biddanda, B., Black, B., and McCarthy, M. (1997). Abundance, size distribution, and stable carbon and nitrogen isotopic compositions of marine organic matter isolated by tangential-flow ultrafiltration. *Mar. Chem.* **57,** 243–263.

Benner, R., Chin-Leo, G., Gardner, W., Eadie, B., and Cotner, J. (1992a). The fates and effects of riverine and shelf-derived DOM on Mississippi river plume/Gulf shelf processes. *In* Nutrient Enhanced Coastal Ocean Productivity, pp. 84–94. Sea Grant Program, Texas A&M University, Galveston, TX.

Benner, R., Pakulski, J. D., McCarthy, M., Hedges, J. I., and Hatcher, P. G. (1992b). Bulk chemical characteristics of dissolved organic matter in the ocean. *Science* **255,** 1561–1564.

Benner, R. H. (2002). Composition and Reactivity. *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and C.A. Carlson, Eds.), pp. 58–90. Academic Press, San Diego.

Berg, G. M., Glibert, P. M., Lomas, M. W., and Burford, M. A. (1997). Organic nitrogen uptake and growth by the chrysophyte *Aureococcus anophagefferens* during a brown tide event. *Mar. Biol.* **129,** 377–387.

Berges, J. A., and Falkowski, P. G. (1996). Cell-associated proteolytic enzymes from marine phytoplankton. *J. Phycol.* **32,** 566–574.

Berman, T., Bechemin, C., and Maestrini, S. Y. (1999). Release of ammonium and urea from dissolved organic nitrogen in aquatic ecosystems. *Aquat. Microb. Ecol.* **16,** 295–302.

Berman, T., and Chava, S. (1999). Algal growth on organic compounds as nitrogen sources. *J. Plankton Res.* **21,** 1391–1421.

Berman, T., Chava, S., Kaplan, B., and Wynne, D. (1991). Dissolved organic substrates as phosphorus and nitrogen sources for axenic batch cultures of freshwater green algae. *Phycologia* **30,** 339–345.

Bertilsson, S., Stepanauskas, R., Cuadros-Hansson, R., Granéli, W., Wikner, J., and Tranvik, L. (1999). Photochemically induced changes in bioavailable carbon and nitrogen pools in a boreal watershed. *Aquat. Microb. Ecol.* **19,** 47–56.

Biddanada, B., and Benner, R. (1997). Carbon, nitrogen and carbohydrate fluxes during the production of particulate and dissolved organic matter by marine plankton. *Limnol. Oceanogr.* **42,** 506–518.

Billen, G. (1991). Protein degradation in aquatic environments. *In* "Microbial Enzymes in Aquatic Environments" (R. J. Chrost, Ed.), pp. 123–143. Springer-Verlag, New York.

Bjørnsen, P. K. (1988). Phytoplankton exudation of organic matter: Why do healthy cells do it? *Limnol. Oceanogr.* **33,** 151–155.

Borch, N. H., and Kirchman, D. L. (1999). Protection of protein from bacterial degradation by submicron particles. *Aquat. Microb. Ecol.* **16,** 265–272.

Branch, G. M., and Griffiths, C. L. (1988). The Benguela ecosystem part V. The coastal zone. *Oceanogr. Mar. Biol. Annu. Rev.* **26,** 395–486.

Bratbak, G., Heldal, M., Naess, A., and Roeggen, T. (1993). Viral impact on microbial communities. *In* "Trends in Microbial Ecology" (R. Guerrero and C. Pedros-Alio, Eds.), pp. 299–302. Spanish Society for Microbiology, Barcelona, Spain.

Bratbak, G., Jacobsen, A., and Heldal, M. (1998). Viral lysis of *Phaeocystis pouchetii* and bacterial secondary production. *Aquat. Microb. Ecol.* **16,** 11–16.

Bratbak, G., Thingstad, F., and Heldal, M. (1994). Viruses and the microbial loop. *Microb. Ecol.* **28,** 209–221.

Bratbak, G., and Thingstad, T. F. (1985). Phytoplankton-bacteria interactions: An apparent paradox? Analysis of a model system with both competition and commensalism. *Mar. Ecol. Prog. Ser.* **25,** 23–30.

Bricelj, V. M., and Lonsdale, D. J. (1997). *Aureococcus anophagefferens*: Causes and ecological consequences of brown tides in U.S. mid-Atlantic coastal waters. *Limnol. Oceanogr.* **42,** 1023–1038.

Bronk, D. A. (1999). Rates of NH_4^+ uptake, intracellular transformation, and dissolved organic nitrogen release in two clones of marine *Synechococcus* spp. *J. Plankton Res.* **21,** 1337–1353.

Bronk, D. A., and Glibert, P. M. (1991). A ^{15}N tracer method for the measurement of dissolved organic nitrogen release by phytoplankton. *Mar. Ecol. Prog. Ser.* **77,** 171–182.

Bronk, D. A., and Glibert, P. M. (1993a). Application of a ^{15}N tracer method to the study of dissolved organic nitrogen uptake during spring and summer in Chesapeake Bay. *Mar. Biol.* **115,** 501–508.

Bronk, D. A., and Glibert, P. M. (1993b). Contrasting patterns of dissolved organic nitrogen release by two size fractions of estuarine plankton during a period of rapid NH_4^+ consumption and NO_2^- production. *Mar. Ecol. Prog. Ser.* **96,** 291–299.

Bronk, D. A., Glibert, P. M., and Ward, B. B. (1994). Nitrogen uptake, dissolved organic nitrogen release, and new production. *Science* **265,** 1843–1846.

Bronk, D. A., Glibert, P. M., Malone, T. C., Banahan, S., and Sahlsten, E. (1998). Inorganic and organic nitrogen cycling in Chesapeake Bay: Autotrophic versus heterotrophic processes and relationships to carbon flux. *Aquat. Microb. Ecol.* **15,** 177–189.

Bronk, D. A., Lomas, M., Glibert, P. M., Schukert, K. J., and Sanderson, M. P. (2000). Total dissolved nitrogen analysis: Comparisons between the persulfate, UV and high temperature oxidation method. *Mar. Chem.* **69,** 163–178.

Bronk, D. A., and Ward, B. B. (1999). Gross and net nitrogen uptake and DON release in the euphotic zone of Monterey Bay, California. *Limnol. Oceanogr.* **44,** 573–585.

Bronk, D. A., and Ward, B. B. (2000). Magnitude of DON release relative to gross nitrogen uptake in marine systems. *Limnol. Oceanogr.* **45,** 1879–1883.

Brown, M. R. (1991). The amino acid and sugar composition of 16 species of microalgae used in mariculture. *J. Exp. Mar. Biol. Ecol.* **145,** 79–99.

Burdige, D. J. (2002). Sediment Pore Waters. *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and C.A. Carlson, Eds.), pp. 611–663. Academic Press, San Diego.

Bury, S. J., Owens, N. J. P., and Preston, T. (1995). ^{14}C and ^{15}N uptake by phytoplankton in the marginal ice zone of the Bellingshausen Sea. *Deep-Sea Res. II* **42,** 1225–1252.

Bushaw, K. L., Zepp, R. G., Tarr, M. A., Schulz-Jander, D., Bourbonniere, R. A., Hodson, R., Miller, W. L., Bronk, D. A., and Moran, M. A. (1996). Photochemical release of biologically labile nitrogen from dissolved organic matter. *Nature* **381,** 404–407.

Bushaw-Newton, K. L., and Moran, M. A. (1999). Photochemical formation of biologically available nitrogen from dissolved humic substances in coastal marine systems. *Aquat. Microb. Ecol.* **18,** 285–292.

Butler, E. I., Knox, S., and Liddicoat, M. I. (1979). The relationship between inorganic and organic nutrients in seawater. *J. Mar. Biol. Assoc. UK* **59,** 239–250.

Capone, D. G. (2000). The marine nitrogen cycle. *In* "Microbial Ecology of the Oceans" (D. L. Kirchman, Ed.), pp. 455–494. Wiley, New York.

Capone, D., Ferrier, M., and Carpenter, E. (1994). Amino acid cycling in colonies of the planktonic marine cyanobacterium *Trichodesmium thiebautii*. *Appl. Environ. Microbiol.* **60,** 3989–3995.

Capone, D., Zehr, J., Paerl, H., Bergman, B., and Carpenter, E. (1997). *Trichodesmium,* a globally significant marine cyanobacterium. *Science* **276,** 1221–1229.

Carlson, C. A. (2002). Production and removal processes. *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and C.A. Carlson, Eds.), pp. 91–151. Academic Press, San Diego.

Carlson, C. A., and Ducklow, H. W. (1995). Dissolved organic carbon in the upper ocean of the central equatorial Pacific Ocean, 1992: Daily and fine scale vertical variations. *Deep-Sea Res. II* **42,** 639–656.

Carlson, C. A., Ducklow, H. W., and Michaels, A. F. (1994). Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature* **371,** 405–408.

Carlson, C. A., Hansell, D. A., Peltzer, E. T., and Smith, Jr., W. O. (2000). Stocks and dynamics of dissolved and particulate organic matter in the Southern Ross Sea, Antarctica. *Deep Sea Res. II* **42,** 3201–3225.

Carlsson, P., Edling, H., and Bechemin, C. (1998). Interactions between a marine dinoflagellate (*Alexandrium catenella*) and a bacterial community utilizing riverine humic substances. *Aquat. Microb. Ecol.* **16,** 65–80.

Carlsson, P., and Granéli, E. (1993). Availability of humic bound nitrogen for coastal phytoplankton. *Estuarine Coastal Shelf Sci.* **36,** 433–447.

Carlsson, P., Granéli, E., Tester, P., and Boni, L. (1995). Influences of riverine humic substances on bacteria, protozoa, phytoplankton, and copepods in a coastal plankton community. *Mar. Ecol. Prog. Ser.* **127,** 213–221.

Carlsson, P., Segatto, A. Z., and Granéli, E. (1993). Nitrogen bound to humic matter of terrestrial origin—A nitrogen pool for coastal phytoplankton? *Mar. Ecol. Prog. Ser.* **97,** 105–116.

Caron, D. A. (2000). Symbiosis and mixotrophy among pelagic microorganisms. *In* "Microbial Ecology of the Oceans" (D. L. Kirchman, Ed.), pp. 495–523. Wiley-Liss, New York.

Cherrier, J., Bauer, J. E., and Druffel, E. R. M. (1996). Utilization and turnover of labile dissolved organic matter by bacterial heterotrophs in eastern North Pacific surface waters. *Mar. Ecol. Prog. Ser.* **139,** 267–279.

Cho, B., Park, M., Shim, J., and Azam, F. (1996). Significance of bacteria in urea dynamics in coastal surface waters. *Mar. Ecol. Prog. Ser.* **142,** 19–26.

Cho, B. C., and Azam, F. (1995). Urea decomposition by bacteria in the Southern California Bight and its implications for the mesopelagic nitrogen cycle. *Mar. Ecol. Prog. Ser.* **122,** 21–26.

Chrost, R. J. (1991). Environmental control of the synthesis and activity of aquatic microbial ectoenzymes. *In* "Microbial Enzymes in Aquatic Environments" (R. J. Chrost, Ed.), pp. 25–59. Springer, New York.

Cochlan, W. P., and Harrison, P. J. (1991). Kinetics of nitrogen (nitrate, ammonium, and urea) uptake by the picoflagellate *Micromonas pusilla* (Prasinophyceae). *J. Exp. Mar. Biol. Ecol.* **153,** 129–141.

Collos, Y. (1986). Time-lag algal growth dynamics: Biological constraints on primary production in aquatic environments. *Mar. Ecol. Prog. Ser.* **33,** 193–206.

Collos, Y., Descolas-Gros, C., and Mornet, F. (1996). Diel variation in dissolved organic nitrogen in a coastal pond: Relationships with carbon and nitrogen metabolism. *J. Exp. Mar. Biol. Ecol.* **202,** 177–189.

Collos, Y., Dohler, G., and Biermann, I. (1992). Production of dissolved organic nitrogen during uptake of nitrate by *Synedra planctonica*: Implications for estimating new production in the oceans. *J. Plankton Res.* **14,** 1025–1029.

Conover, R. J., and Gustavson, K. R. (1999). Sources of urea in arctic seas: zooplankton metabolism. *Mar. Ecol. Prog. Ser.* **179,** 41–54.

Conover, R. J., Mumm, N., Bruecker, P., and MacKenzie, S. (1999). Sources of urea in arctic seas: Seasonal fast ice? *Mar. Ecol. Prog. Ser.* **179,** 55–69.

Cornell, S., Rendell, A., and Jickells, T. (1995). Atmospheric inputs of dissolved organic nitrogen to the oceans. *Nature* **376,** 243–246.

Cotner, J. B., and Gardner, W. S. (1993). Heterotrophic bacterial mediation of ammonium and dissolved free amino acid fluxes in the Mississippi River plume. *Mar. Ecol. Prog. Ser.* **93,** 75–87.

Cowan, S. W., Schirmer, T., Rummel, G., Steiert, M., Chosh, R., Pauptit, R. A., Jansonius, J. N., and Rosenbusch, J. P. (1992). Crystal structures explain functional properties of two *E. coli* porins. *Nature* **358,** 727–733.

Cox, R. D. (1980). Determination of nitrate and nitrite at the parts per billion level by chemiluminescence. *Anal. Chem.* **52,** 332–335.

Cresser, M. S. (1977). Nitrate determination by reduction to ammonia and gas-phase ultraviolet adsorption spectrometry. *Analyst* **102,** 99–103.

Dagg, M. J. (1974). Loss of prey body contents during feeding by an aquatic predator. *Ecology* **55,** 903–906.

Daly, K. L., Wallace, D. W. R., Smith, J., W. O., Skoog, A., Lara, R., Gosselin, M., Falck, E., and Yager, P. L. (1999). Non-Redfield carbon and nitrogen cycling in the Arctic: Effects of ecosystem structure and dynamics. *J. Geophys. Res.* **104,** 3185–3199.

De Mora, S., Demers, S., and Vernet, M. (2000). "The Effects of UV Radiation in the Marine Environment." Cambridge University Press, Cambridge.

Derenne, S., Largeau, C., and Taulelle, F. (1992). Occurrence of non-hydrolysable amides in the macromolecular constituents of *Scenedesmus quadricauda* cell wall as revealed by ^{15}N NMR: Origin of n-alkylnitriles in pyprolysates of ultralaminae-containing kerogens. *Geochim. Cosmochim. Acta* **57,** 851–857.

Diaz, F., and Raimbault, P. (2000). Nitrogen regeneration and dissolved organic nitrogen release during spring in a NW Mediterranean coastal zone (Gulf of Lions): Implications for the estimation of new production. *Mar. Ecol. Prog. Ser.* **197,** 51–65.

Douglas, A. E. (1983). Uric acid utilization in *Platymonas convolutae* and symbiotic *Convoluta roscoffensis*. *J. Mar. Biol. Assoc. UK* **63,** 435–447.

Dzurica, S., Lee, C., and Cosper, E. M. (1989). Role of environmental variables, specifically organic compounds and micronutrients, in the growth of the chrysophyte *Aureococcus anaphagefferens*. *In* "Novel Phytoplankton Blooms" (E. M. Cosper, V. M. Bricelj, and E. J. Carpenter, Eds.), pp. 229–252. Spriner-Verlag, Berlin.

Ferrier-Pagès, C., Karner, M., and Rassoulzadegan, F. (1998). Release of dissolved amino acids by flagellates and ciliates grazing on bacteria. *Oceanol. Acta* **21,** 485–494.

Feuerstein, T., Ostrom, P., and Ostrom, N. (1997). Isotope biogeochemistry if dissolved organic nitrogen: A new technique and application. *Org. Geochem.* **27,** 363–370.

Flynn, K. J. (1990). Composition of intracellular and extracellular pools of amino acids, and amino acid utilization of microalgae of different sizes. *J. Exp. Mar. Biol. Ecol.* **139,** 151–166.

Flynn, K. J., and Berry, L. S. (1999). The loss of organic nitrogen during marine primary production may be significantly overestimated when using ^{15}N substrates. *Proc. R. Soc. London B* **266,** 641–647.

Flynn, K. J., and Butler, I. (1986). Nitrogen sources for the growth of microalgae: role of dissolved free amino acids. *Mar. Ecol. Prog. Ser.* **34,** 281–304.

Flynn, K. J., and Davidson, K. (1993). Predator–prey interactions between *Isochrysis galbana* and *Oxyrrhis marina.* II. Prelease of non-protein amines and faeces during predation of *Isochrysis. J. Plankton Res.* **15,** 893–905.

Fogg, G. E. (1966). The extracellular products of algae. Oceanogr. *Mar. Biol. Ann. Rev.* **4,** 195–212.

Fogg, G. E. (1983). The ecological significance of algal extracellular products of phytoplankton photosynthesis. *Bot. Mar.* **26,** 3–14.

Fu, T., and Pocklington, R. (1983). Quantitative adsorption of organic matter from seawater on solid mattrices. *Mar. Chem.* **13,** 255–264.

Fuhrman, J. (1987). Close coupling between release and uptake of dissolved free amino acids in seawater studied by an isotope dilution approach. *Mar. Ecol. Prog. Ser* **37,** 45–52.

Fuhrman, J. (1990). Dissolved free amino acid cycling in an estuarine outflow plume. *Mar. Ecol. Prog. Ser.* **66,** 197–203.

Fuhrman, J. (1992). Bacterioplankton roles in cycling of organic matter: The microbial loop. *In* "Primary Productivity and Biogeochemical Cycles in the Sea" (P. G. Falkowski and A. D. Woodhead, Eds.), pp. 361–381. Plenum Press, New York.

Fuhrman, J. A. (1999). Marine viruses and their biogeochemical and ecological effects. *Nature* **399,** 541–548.

Fuhrman, J. A. (2000). Impact of viruses on bacterial processes. *In* "Microbial Ecology of the Oceans" (D. L. Kirchman, Ed.), pp. 327–350. Wiley-Liss, New York.

Fuhrman, J. A., and Noble. (1995). Viruses and protists cause similar bacterial mortality in coastal seawater. *Limnol. Oceanogr.* **40,** 1236–1242.

Gagosian, R. B., and Lee, C. (1981). Processes controlling the distribution of biogenic organic compounds in seawater. *In* "Marine Organic Chemistry: Evolution, Composition, Interactions and Chemistry of Organic Matter in Seawater" (E. K. Duursma and R. Dawson, Eds.), pp. 91–124. Elsevier, Amsterdam.

Galloway, J. N., Schlesinger, W. H., Levy, H., Michaels, A. F., and Schnoor, J. L. (1995). Large changes in oceanic nutrient inventories from glacial to interglacial periods. *Nature* **376,** 755–758.

Gardner, W., Benner, R., Amon, R., Cotner, J., Cavaletto, J., and Johnson, J. (1996). Effects of high molecular weight dissolved organic matter on the nitrogen dynamics on the Mississippi River plume. *Mar. Ecol. Prog. Ser.* **133,** 287–297.

Gardner, W. S., Cavaletto, J. F., Bootsma, H. A., Lavrentyev, P. J., and Tanvone, F. (1998). Nitrogen cycling rates and light effects in tropical Lake Maracaibo, Venezuela. *Limnol. Oceanogr.* **43,** 1814–1825.

Gardner, W. S., Cotner, J. B., and Herche, L. R. (1993). Chromatographic measurement of nitrogen mineralization rates in marine coastal waters with ^{15}N. *Mar. Ecol. Prog. Ser.* **93,** 65–73.

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

Garside, C. (1982). A chemiluminescent technique for the determination of nanomolar concentrations of nitrate and nitrite in seawater. *Mar. Chem.* **11,** 159–167.

Geller, A. (1986). Comparison of mechanisms enhancing biodegradability of refractory lake water constituents. *Limnol. Oceanogr.* **31,** 755–764.

Gibb, S. W., Mantoura, R. F. C., Liss, P. S., and Barlow, R. G. (1999). Distributions and biogeochemistries of methylamines and ammonium in the Arabian Sea. *Deep-Sea Res. II* **46,** 593–615.

Glibert, P. M., and Bronk, D. A. (1994). Release of dissolved organic nitrogen by marine diazotrophic cyanobacteria *Trichodesmium* spp. *Appl. Environ. Microbiol.* **36,** 3996–4000.

Glibert, P. M., Garside, C., Fuhrman, J. A., and Roman, M. R. (1991). Time-dependent coupling of inorganic and organic nitrogen uptake and regeneration in the plume of the Chesapeake Bay estuary and its regulation by large heterotrophs. *Limnol. Oceanogr.* **36,** 895–909.

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

Glibert, P. M., and Terlizzi, D. E. (1999). Cooccurrence of elevated urea levels and dinoflagellate blooms in temperate estuarine aquaculture ponds. *Appl. Environ. Microbiol.* **65,** 5594–5596.

Gobler, C. J., Hutchins, D. A., Fisher, N. S., Cosper, E. M., and Sañudo-Wilhelmy, S. A. (1997). Release and bioavailability of C, N, P, Se, and Fe following viral lysis of a marine chrysophyte. *Limnol. Oceanogr.* **42,** 1492–1504.

Gobler, C. J., and Sañudo-Wilhelmy, S. A. (2001). Effects of organic carbon, organic nitrogen, inorganic nutrients, and iron additions on the growth of phytoplankton and bacteria during a brown tide bloom. *Mar. Ecol. Prog. Ser.* **209,** 19–34.

Gordeev, V. V., Martin, J. M., Sidorov, I. S., and Sidorova, M. V. (1996). A reassessment of the Eurasian River input of water sediment, major elements, and nutrients to the Arctic Ocean. *Am. J. Sci.* **296,** 664–691.

Hammer, K. D., and Kattner, G. (1986). Dissolved free amino acids in the marine environment: a carbon to nitrogen shift during diatom blooms. *Mar. Ecol. Prog. Ser.* **31,** 35–45.

Hansell, D., and Waterhouse, T. (1997). Controls on the distributions of organic carbon and nitrogen in the eastern Pacific Ocean. *Deep-Sea Res.* **44,** 843–857.

Hansell, D. A. (1993). Results and observations from the measurement of DOC and DON in seawater using a high-temperature catalytic oxidation technique. *Mar. Chem.* **41,** 195–202.

Hansell, D. A. (2002). DOC in the Global Ocean Carbon Cycle. *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and C.A. Carlson, Eds.), pp. 685–715. Academic Press, San Diego.

Hansell, D. A., and Carlson, C. A. (2001). Biogeochemistry of total organic carbon and nitrogen in the Sargasso Sea: Control by convective overturn. *Deep Sea Res. II,* **48,** 1649–1667.

Hansell, D. A., and Feely, R. A. (2000). Atmospheric intertropical convergence impacts surface ocean carbon and nitrogen biogeochemistry in the western tropical Pacific. *Geophys. Res. Lett.* **27,** 1013–1016.

Hansell, D. A., Williams, P. M., and Ward, B. B. (1993). Measurements of DOC and DON in the Southern California Bight using oxidation by high temperature combustion. *Deep-Sea Res.* **40,** 219–234.

Hansell, P. A., and Goering, J. J. (1989). A method for estimating uptake and production rates for urea in seawater using ^{14}C urea and ^{15}N urea. *Can. J. Fish. Aquat. Sci.* **46,** 198–202.

Harrison, W. G., Harris, L. R., Karl, D. M., Knauer, G. A., and Redalje, D. G. (1992). Nitrogen dynamics at the VERTEX time-series site. *Deep-Sea Res.* **39,** 1535–1552.

Harvey, G. R., and Boran, D. A. (1985). Geochemistry of humic substances in seawater. *In* "Humic Substances in Soil Sediment and Water" (G. R. Aiken, D. M. McKnight, R. L. Wershaw, and P. MacCarthy, Eds.). pp. 223–247. Wiley, New York.

Harvey, G. R., Boran, D. A., and Chesal, L. A. (1983). The structure of marine fulvic and humic acids. *Mar. Chem.* **12,** 119–132.

Hasegawa, T., Koike, I., and Mukai, H. (2000a). Release of dissolved organic nitrogen by size-fractionated natural planktonic assemblages in coastal waters. *Mar. Ecol. Prog. Ser.* **198,** 43–49.

Hasegawa, T., Koike, I., and Mukai, H. (2000b). Estimation of dissolved organic nitrogen release by micrograzers in natural plankton assemblages. *Plankton Biol. Ecol.* **47,** 23–30.

Hasagawa, T., Koike, I., and Mukai, H. (2000c). Dissolved organic nitrogen dynamics in coastal waters and the effect of copepods. *J. Exp. Mar. Biol. Ecol.* **244,** 219–238.

Hatch, M. J., Dillon, J. A., and Smith, H. B. (1957). Preparation and use of snake-cage polyelectrolytes. *Ind. Eng. Chem.* **49,** 1812–1818.

Hatcher, P. G., and Spiker, E. C. (1988). Selective degradation of plant biomolecules. *In* "Humic Substances and Their Role in the Environment" (F. H. Frimmel and R. F. Christman, Eds.). pp. 59–74. Wiley, New York.

Hedges, J. I. (1988). Polymerization of humic substances in natural environments. *In* "Humic Substances and Their Role in the Environment" (F. H. Frimmel and R. F. Christman, Eds.). pp. 45–58. Wiley, New York.

Hedges, J. I., and Hare, P. E. (1987). Amino acid adsorption by clay minerals in distilled water. *Geochim. Cosmochim. Acta* **51,** 255–259.

Hessen, D. O., and Tranvik, L. J. (1998). "Aquatic Humic Substance: Ecology and Biogeochemistry." Springer, Berlin.

Hoffman, M., and Decho, A. W. (2000). proteolytic enzymes in the marine bacterium *Pseudoalteromonas atlantica*: Post-secretional activation and effects of environmental conditions. *Aquat. Microb. Ecol.* **23,** 29–39.

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

Hooper, J. K., and Hughes, M. J. (1992). Purification and characterization of a membrane-bound protease from *Chlamydomonas reinhardtii*. *Plant Physiol.* **99,** 932–937.

Hopkinson, C., Buffam, I., Hobbie, J., Vallino, J., Perdue, M., Eversmeyer, B., Prahl, F., Covert, J., Hodson, R., Moran, M. A., Smith, E., Baross, J., Crump, B., Findlay, S., and Foreman, K. (1998). Terrestrial inputs of organic matter to coastal ecosystems: An intercomparison of chemical characteristics and bioavailability. *Biogeochemistry.* **43,** 211–234.

Hopkinson, C., Fry, B., and Nolin, A. (1997). Stoichiometry of dissolved organic matter dynamics on the continental shelf of the northeastern USA. *Cont. Shelf Res.* **17,** 473–489.

Hoppe, H. G. (1983). Significance of exoenzymatic activities in the ecology of brackish water: Measurements by means of methylumbelliferyl-substrates. *Mar. Ecol. Prog. Ser.* **11,** 299–308.

Hu, S. H., and Smith, W. O. (1998). The effects of irradiance on nitrate uptake and dissolved organic nitrogen release by phytoplankton in the Ross Sea. *Cont. Shelf Res.* **18,** 971–990.

Hubberten, U., Lara, R. J., and Kattner, G. (1995). Refractory organic compounds in polar waters: Relationship between humic substances and amino acids in the Arctic and Antarctic. *J. Mar. Res.* **53,** 137–149.

Ietswaart, T., Schneider, P. J., and Prins, R. A. (1994). Utilization of organic nitrogen sources by two phytoplankton species and a bacterial isolate in pure and mixed cultures. *Appl. Environ. Microbiol.* **60,** 1554–1560.

Ishiwatari, R. (1992). Macromolecular material (humic substances) in the water column and sediments. *Mar. Chem.* **39,** 151–166.

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

Jenkinson, I. R., and Biddanda, B. A. (1995). Bulk-phase viscoelastic properties of seawater: Relationship with plankton components. *J. Plankton Res.* **17,** 2251–2274.

John, E. H., and Flynn, K. J. (1999). Amino acid uptake by the toxic dinoflagellate *Alexandrium fundyense*. *Mar. Biol.* **133,** 11–19.

Jones, K., and Stewart, W. D. P. (1969). Nitrogen turnover in marine and brackish habitats. III. The production of extracellular nitrogen by *Calothrix scopulorum*. *J. Mar. Biol. Assoc. UK* **49,** 475–488.

Jørgensen, N. O. G., Kroer, N., and Coffin, R. B. (1994). Utilization of dissolved nitrogen by heterotrophic bacterioplankton: Effect of substrate C/N ratio. *Appl. Env. Microbiol.* **60.** 4124–4133.

Jørgensen, N. O. G., Kroer, N., Coffin, R. B., Yang, X.-H., and Lee, C. (1993). Dissolved free amino acids, combined amino acids, and DNA as sources of carbon and nitrogen to marine bacteria. *Mar. Ecol. Prog. Ser.* **98,** 135–148.

Jørgensen, N. O. G., Tranvik, L. J., and Berg, G. M. (1999). Occurrence and bacterial cycling of dissolved nitrogen in the Gulf of Riga, the Baltic Sea. *Mar. Ecol. Prog. Ser.* **191,** 1–18.

Jørgensen, N. O. G., Tranvik, L., Edling, H., Granéli, W., and Lindell, M. (1998). Effects of sunlight on occurrence and bacterial turnover of specific carbon and nitrogen compounds in lake water. *FEMS Microbiol. Ecol.* **25,** 217–227.

Jumars, P. A., Penry, D. L., Baross, J. A., Perry, M. J., and Frost, B. W. (1989). Closing the microbial loop: Dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion, and absorption in animals. *Deep-Sea Res.* **36,** 483–495.

Kähler, P., Bjørnsen, P. K., Lochte, K., and Antia, A. (1997). Dissolved organic matter and its utilization by bacteria during spring in the Southern Ocean. *Deep-Sea Res. II* **44,** 341–353.

Kähler, P., and Koeve, W. (2001). Marine dissolved organic matter: Can its C:N ratio explain carbon overconsumption. *Deep Sea Res. II* **48,** 49–62.

Karl, D. M., and Bailiff, M. D. (1989). The measurement and distribution of dissolved nucleic acids in aquatic environments. *Limnol. Oceanogr.* **34,** 543–558.

Karl, D. M., and Björkman, K. M. (2002). Dynamics of Phosphorus. *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and C.A. Carlson, Eds.), pp. 249–366. Academic Press, San Diego.

Keil, R. G., and Kirchman, D. L. (1991a). Contribution of dissolved free amino acids and ammonium to the nitrogen requirements of heterotrophic bacterioplankton. *Mar. Ecol. Prog. Ser.* **73,** 1–10.

Keil, R. G., and Kirchman, D. L. (1991b). Dissolved combined amino acids in marine waters as determined by a vapor-phase hydrolysis method. *Mar. Chem.* **33,** 243–259.

Keil, R. G., and Kirchman, D. L. (1993). Dissolved combined amino acids: Chemical form and utilization by marine bacteria. *Limnol. Oceanogr.* **38,** 1256–1270.

Keil, R. G., and Kirchman, D. L. (1994). Abiotic transformations of labile protein to refractory protein in sea water. *Mar. Chem.* **45,** 187–196.

Keil, R. G., and Kirchman, D. L. (1999). Utilization of dissolved protein and amino acids in the northern Sargasso Sea. *Aquat. Microb. Ecol.* **18,** 293–800.

Karl, D. M., Christian, J. R., Dore, J. E., and Letelier, R. M. (1996). Microbiological oceanography in the region west of the Antarctic peninsula: Microbial dynamics, nitrogen cycle, and carbon flux. *In* "Foundations for Ecological Research West of the Antarctic Peninsula, Antarctic Research Series" (R. M. Ross, E. E. Hofmann, and L. B. Quetin, Eds.), Vol. 70, pp. 303–332. American Geophysical Union, Washington, DC.

Karl, D. M., Letelier, R., Hebel, D. V., Bird, D. F., and Winn, C. D. (1992). *Trichodesmium* blooms and new nitrogen in the North Pacific Gyre. *In* "Marine Pelagic Cyanobacteria: *Trichodesmium* and Other Diazotrophs" (E. J. Carpenter, D. G. Capone, and J. G. Reuter, Eds.), pp. 219–237. Kluwer Academic, Dordrecht, The Netherlands.

Karl, D., Letelier, R., Tupas, L., Dore, J., Christian, J., and Hebel, D. (1997). The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* **388,** 533–538.

Kerner, M., and Spitzy, A. (2001). Nitrate regeneration coupled to degradation of different size fractions of DON by the picoplankton in the Elbe Estuary. *Microb. Ecol.* **41,** 69–81.

Kieber, R. J., Li, A., and Seaton, P. J. (1999). Production of nitrite from the photodegradation of dissolved organic matter in natural waters. *Environ. Sci. Technol.* **33,** 993–998.

Kieber, D. J., McDaniel, J., and Mopper, K. (1989). Photochemical source of biological substrates in sea water: Implications for carbon cycling. *Nature* **341,** 637–639.

Kieber, R. J., Zhou, X., and Mopper, K. (1990). Formation of carbonyl compounds from UV-induced photodegradation of humic substances in natural waters: Fate of riverine carbon in the sea. *Limnol. Oceanogr.* **35,** 1503–1515.

Kirchman, D. L., Ducklow, H. W., McCarthy, J. J., and Garside, C. (1994). Biomass and nitrogen

uptake by heterotrophic bacteria during the spring bloom in the North Atlantic Ocean. *Deep-Sea Res. II* **41,** 879–895.

Kirchman, D. L., Keil, R. G., and Wheeler, P. A. (1989). The effect of amino acids on ammonium utilization and regeneration by heterotrophic bacteria in the subarctic Pacific. *Deep-Sea Res.* **36,** 1763–1776.

Kirchman, D. L., Lancelot, C., Fasham, M., Legendre, L., Radach, G., and Scott, M. (1993). Dissolved organic matter in biogeochemical models of the ocean. *In* "Towards a Model of Ocean Biogeochemical Processes," Vol. 40, pp. 209–225. Springer-Verlag, Berlin.

Knutsen, G. (1972). Uptake of uracil by synchronous *Chlorella fusca. Phys. Planet.* **27,** 300–309.

Koike, I., and Tupas, L. (1993). Total dissolved nitrogen in the Northern North Pacific assessed by a high-temperature combustion method. *Mar. Chem.* **41,** 209–214.

Kokkinakis, S. A., and Wheeler, P. A. (1988). Uptake of ammonium and urea in the northeast Pacific: Comparison between netplankton and nanoplankton. *Mar. Ecol. Prog. Ser.* **43,** 113–124.

Koopmans, D. J., and Bronk, D. A. (in press). Photochemical production of inorganic nitrogen from dissolved organic nitrogen in waters of two estuaries and adjacent surficial groundwaters. *Aquat. Microbial. Ecol.*

Kroer, N., Jorgensen, N. O. G., and Coffin, R. B. (1994). Utilization of dissolved nitrogen by heterotrophic bacterioplankton: A comparison of three ecosystems. *Appl. Env. Microbiol.* **60,** 4116–4123.

Lampert, W. (1978). Release of dissolved organic carbon by grazing zooplankton. *Limnol. Oceanogr.* **23,** 831–834.

Lampitt, R. S., Noji, T., and von Bodungen, B. (1990). What happens to zooplankton faecal pellets? Implications for material flux. *Mar. Biol.* **104,** 15–23.

Lara, C., Rodriguez, R., and Guerrero, M. G. (1993). Sodium-dependent nitrate transport and energetics of cyanobacteria. *J. Phycol.* **29,** 389–395.

Lara, R. J., Hubberten, U., Thomas, D. N., Baumann, M. E. M., and Kattner, G. (1997). Dissolved organic matter studies in enclosed systems: Application of hydrophobic fractionation for the assessment of organic nitrogen dynamics. *J. Mar. Syst.* **13,** 155–161.

LaRoche, J., Nuzzi, R., Waters, R., Wyman, K., Falkowski, P. G., and Wallace, D. W. R. (1997). Brown Tide blooms in Long Island's coastal waters linked to interannual variability in groundwater flow. *Global Change Biol.* **3,** 397–410.

Larsson, U., and Hagström, Å. (1979). Phytoplankton exudate release as an energy source for the growth of pelagic bacteria. *Mar. Biol.* **52,** 199–206.

Lee, C., and Bada, J. L. (1977). Dissolved amino acids in the equatorial Pacific, the Sargasso Sea, and Biscayne Bay. *Limnol. Oceanogr.* **22,** 502–510.

Letelier, R. M., and Karl, D. M. (1996). Role of *Trichodesmium* spp. in the productivity of the subtropical North Pacific Ocean. *Mar. Ecol. Prog. Ser.* **133,** 263–273.

Lewitus, A. J., Koepfler, E. T., and Pigg, R. J. (2000). Use of dissolved organic nitrogen by a salt marsh phytoplankton bloom community. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **55,** 441–456.

Lewitus, A. J., Willis, B. M., Hayes, K. C., Burkholder, J. M., Glasgow, J., H. B., Glibert, P. M., and Burke, M. K. (1999). Mixotrophy and nitrogen uptake by *Pfiesteria piscicida* (Dinophyceae). *J. Phycol.* **35,** 1430–1437.

Libby, P., and Wheeler, P. (1997). Particulate and dissolved organic nitrogen in the central and eastern equatorial Pacific. *Deep-Sea Res.***44,** 345–361.

Lindell, M. J., Granéli, W., and Tranvik, L. J. (1995). Enhanced bacterial growth in response to photochemical transformation of dissolved organic matter. *Limnol. Oceanogr.* **40,** 195–199.

Lipschultz, F. (1995). Nitrogen-specific uptake rates of marine phytoplankton isolated from natural populations of particles by flow cytometry. *Mar. Ecol. Prog. Ser.* **123,** 245–258,

Lipschultz, F., and Owens, J. P. (1996). An assessment of nitrogen fixation as a source of nitrogen to the North Atlantic Ocean. *Biogeochemistry* **35,** 261–274.

Lisa, T., Piedras, P., Cardenas, J., and Pineda, M. (1995). Utilization of adenine and quanine as nitrogen sources by *Chlamydomonas reinhardtii* cells. *Plant Cell Environ* **18,** 583–588.

Loh, A. N., and Bauer, J. E. (2000). Distribution, partitioning and fluxes of dissolved and particulate organic C, N and P in the eastern North Pacific and Southern Oceans. *Deep-Sea Res. I* **47,** 2287–2316.

Lomas, M. W., and Glibert, P. M. (1999). Temperature regulation of nitrate uptake: A novel hypothesis about nitrate uptake and reduction in cool-water diatoms. *Limnol. Oceanogr.* **44,** 556–572.

Lomas, M. W., Glibert, P. M., Berg, G. M., and Burford, M. (1996). Characterization of nitrogen uptake by natural populations of *Aureococcus anaphagefferens* (Chrysophyceae) as a function of incubation duration, substrate concentration, light, and temperature. *J. Phycol.* **32,** 907–916.

Lomas, M. W., Trice, T. M., Glibert, P. M., Bronk, D. A., and McCarthy, J. J. (in press). Temporal and spatial dynamics of urea concentrations in Chesapeake Bay: Biological versus physical forcing. *Estuaries*

López-Veneroni, D., and Cifuentes, L. A. (1992). Dissolved organic nitrogen distribution and transport in the continental shelf of the northwest Gulf of Mexico. "*In* Nutrient Enhanced Coastal Ocean Productivity," pp. 57–68. NOAA

López-Veneroni, D., and Cifuentes, L. A. (1994). Transport of dissolved organic nitrogen in Mississippi River Plume and Texas-Louisiana continental shelf near-shore waters. *Estuaries* **17,** 796–808.

Lytle, C. R., and Perdue, E., M. (1981). Free, proteinaceous, and humic-bound amino acids in river water containing high concentrations of aquatic humics. *Environ. Sci. Technol.* **15,** 224–228.

Maita, Y., and Yanada, M. (1990). Vertical distribution of total dissolved nitrogen and dissolved organic nitrogen in seawater. *Geochem. J.* **24,** 245–254.

Malone, T. C. (1980). Size-fractionated primary production. *In* "Primary Production in the Sea." Brookhaven Symp. Biol. 31, pp. 301–319. Plenum Press, New York.

Mann, K. H. (1982). "Ecology of Coastal Waters. A System Approach," pp. 322. Blackwell Scientific, Oxford.

Mantoura, R. F. C., Dickson, A., and Riley, J. P. (1978). The complexation of materials in natural waters. *Estuarine Coastal Mar. Sci.* **6,** 387–408.

Marsot, P., Cembella, A. D., and Colombo, J. C. (1991). Intracellular and extracellular amino acid pools of the marine diatom *Phaeodactylum tricornutum* (Bacillariophyceae) grown on unenriched seawater in high cell density dialysis culture. *J. Phycol* **27,** 478–491.

Martinez, J., and Azam, F. (1993). Aminopeptidase activity in marine chroococcoid cyanobacteria. *Appl. Environ Microbiol.* **59,** 3701–3707.

Mason, C. A., and Engli, T. (1993). Dynamics of microbial growth in the decelerating and stationary phase of batch culture. *In* "Starvation in Bacteria" (S. Kjelleberg, Ed.), pp. 81–102. Plenum Press, New York.

McCarthy, J. J. (1970). A urease method for urea in seawater. *Limnol. Oceanogr.* **15,** 309–313.

McCarthy, M., Hedges, J., and Benner, R. (1996). Major biochemical composition of dissolved high molecular weight organic matter in seawater. *Mar. Chem.* **55,** 281–297.

McCarthy, M., Pratum, T., Hedges, J., and Benner, R. (1997). Chemical composition of dissolved organic nitrogen in the ocean. *Nature* **390,** 150–154.

McCarthy, M. D., Hedges, J. I., and Benner, R. (1998). Major bacterial contribution to marine dissolved organic nitrogen. *Science* **281,** 231–234.

McKnight, D. M., and Aiken, G. R. (1998). Sources and age of aquatic humus. *In* "Aquatic Humic Substances" (D. O. Hessen and L. J. Tranvik, Eds.). pp. 9–39. Springer-Verlag, Berlin.

Menzel, D. W., and Vaccaro, R. F. (1964). The measurement of dissolved organic and particulate carbon in seawater. *Limnol. Oceanogr.* **9,** 138–142.

Metzler, P., Glibert, P., Gaeta, S., and Ludlam, J. (1997). New and regenerated production in the South Atlantic off Brazil. *Deep-Sea Res.* **44,** 363–384.

Metzler, P., Glibert, P., Gaeta, S., and Ludlam, J. (2000). Contrasting effects of substrate and grazer manipulations on picoplankton in oceanic and coastal waters off Brazil. *J. Plankton Res.* **22,** 77–90.

Meybeck, M. (1993). C, N, P, and S in rivers: From sources to global inputs. *In* "Interactions of C, N, P, and S Biogeochemical Cycles and Global Change" (R. Wollast, F. T. Mackenzie, and L. Chou, Eds.). pp. 163–193. Springer-Verlag, Berlin.

Middelboe, M., Borch, N. H., and Kirchman, D. L. (1995). Bacterial utilization of dissolved free amino acids, dissolved combined amino acids and ammonium in the Delaware Bay estuary: Effects of carbon and nitrogen limitation. *Mar. Ecol. Prog. Ser.* **128,** 109–120.

Middelboe, M., Jørgensen, N. O. G., and Kroer, N. (1996). Effects of viruses on nutrient turnover and growth efficiency of noninfected marine bacterioplankton. *Appl. Environ Microbiol.* **62,** 1991–1997.

Middelburg, J. J., and Nieuwenhuize, J. (2000). Nitrogen uptake by heterotrophic bacteria and phytoplankton in the nitrate-rich Thames estuary. *Mar. Ecol. Prog. Ser.* **203,** 13–21.

Miller, C. A., and Glibert, P. M. (1998). Nitrogen excretion by the calanoid copepod *Acartia tonsa*: Results from mesocosm experiments. *J. Plankton Res.* **20,** 1767–1780.

Mopper, K., and Kieber, D. J. (2002). Photochemistry and cycling of carbon, sulfur, nitrogen, and phosphorus. *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and Carlson, C. A., Eds.), pp. 455–507. Academic Press, San Diego.

Mopper, K., and Lindroth, P. (1982). Diel and depth variations in dissolved free amino acids and ammonium in the Baltic Sea determined by shipboard HPLC analysis. *Limnol. Oceanogr.* **27,** 366–347.

Mopper, K., Zhou, X., Kieber, R. J., Kieber, D. J., Sikorski, R. J., and Jones, R. D. (1991). Photochemical degradation of dissolved organic carbon and its impact on the oceanic carbon cycle. *Nature* **353,** 60.

Moran, M. A., and Hodson, R. E. (1994). Support of bacterioplankton production by dissolved humic substances from three marine environments. *Mar. Ecol. Prog. Ser.* **110,** 241–247.

Moran, M. A., and Zepp, R. G. (2000). UV radiation effects on microbes and microbial processes. *In* "Microbial Ecology of the Oceans" (D. L. Kirchman, Ed.), pp 201–228. Wiley-Liss, New York.

Mortazavi, B., Iverson, R. L., Landing, W. M., Lewis, F. G., and Huang, W. (2000). Control of phytoplankton production and biomass in a river-dominated estuary: Apalachicola Bay, Florida, USA. *Mar. Ecol. Prog. Ser.* **198,** 19–31.

Mulholland, M. R., Glibert, P. M., Berg, G. M., Van Heukelem, L., Pantoja, S., and Lee, C. (1998). Extracellular amino acid oxidation by microplankton: A cross-system comparison. *Aquat. Microb. Ecol.* **15,** 141–152.

Müller-Wegener, U. (1988). Interaction of humic substances with biota. *In* "Humic Substances and Their Role in the Environment" (F. H. Frimmel and R. F. Christman, Eds.). pp. 179–192. Wiley, New York.

Münster, U., and De Haan, H. (1998). The role of microbial extracellular enzymes in the transformation of dissolved organic matter in humic waters. *In* "Aquatic Humic Substances" (D. O. Hessen and L. J. Tranvik, Eds.), pp. 199–257. Springer-Verlag, Berlin.

Murray, A. G. (1995). Phytoplankton exudation: Exploitation of the microbial loop as a defense against algal viruses. *J. Plankton Res.* **17,** 1079–1094.

Murray, A. G., and Eldridge, P. M. (1994). Marine viral ecology: Incorporation of bacteriophage into the microbial planktonic food web paradigm. *J. Plankton Res.* **16,** 627–641.

Myklestad, S., Holm-Hansen, O., Varum, K. M., and Volcani, B. E. (1989). Rate of release of extracellular amino acids and carbohydrates from the marine diatom *Chaetoceros affinis*. *J. Plankton Res.* **11,** 763–773.

Nagao, F., and Miyazaki, T. (1999). A modified ^{15}N tracer method and new calculation for estimating release of dissolved organic nitrogen by freshwater planktonic algae. *Aquat. Microb. Ecol.* **16,** 309–314.

Nagata, T. (2000). Production mechanisms of dissolved organic matter. *In* "Microbial Ecology of the Oceans" (D. L. Kirchman, Ed.), pp. 121–152. Wiley, New York.

Nagata, T., and Kirchman, D. L. (1992). Release of macromolecular organic complexes by heterotrophic marine flagellates. *Mar. Ecol. Prog. Ser.* **83,** 233–240.

Nagata, T., and Kirchman, D. L. (1996). Bacterial degradation of protein adsorbed to model submicron particles in seawater. *Mar. Ecol. Prog. Ser.* **132,** 241–248.

Nausch, M. (1996). Microbial activities on *Trichodesmium* colonies. *Mar. Ecol. Prog. Ser.* **141,** 173–181.

Neilson, A. H., and Larsson, T. (1980). The utilization of organic nitrogen for growth of algae: Physiological aspects. *Physiol. Plant.* **48,** 542–553.

Ogawa, H., Fukuda, R., and Koike, I. (1999). Vertical distributions of dissolved organic carbon and nitrogen in the Southern Ocean. *Deep-Sea Res. I* **46,** 1809–1826.

Ohki, K. (1999). A possible role of temperate phage in the regulation of *Trichodesmium* biomass. *In* "Marine Cyanobacteria" (L. Charpy and A. W. D. Larkum, Eds.), Vol. 19, pp. 287–292. Bulletin de l'Institute Oceanographique, Monaco.

Ohlendieck, U., Stuhr, A., and Siegmund, H. (2000). Nitrogen fixation by diazotrophic cyanobacteria in the Baltic Sea and transfer of the newly fixed nitrogen to picoplankton organisms. *J. Mar. Syst.* **25,** 213–219.

O'Neil, J. M., Metzler, P. M., and Glibert, P. M. (1996). Ingestion of $^{15}N_2$ -labelled *Trichodesmium* sp. and ammonium regeneration by the harpacticoid copepod *Macrosetella gracilis*. *Mar. Biol.* **125,** 89–96.

O'Neil, J. M., and Roman, M. R. (1992). Grazers and associated organisms of *Trichodesmium*. *In* "Marine Pelagic Cyanobacteria: *Trichodesmium* and Other Diazotrophs" (E. J. Carpenter, D. G. Capone, and J. G. Reuter, Eds.), pp. 61–73. Kluwer Academic, Dordrecht.

Ouverney, C. C., and Fuhrman, J. A. (2000). Marine planktonic archaea take up amino acids. *Appl. Env. Microbiol.* **66,** 4829–4833

Paerl, H. W. (1988). Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol. Oceanogr.* **33,** 823–847.

Page, A. L., Miller, R. H., and Keeney, D. R. (1982). "Methods of Soil Analysis" pp. 1159. Soil Science Society of America, Inc., Madison.

Palenik, B., and Henson, S. E. (1997). The use of amides and other organic nitrogen sources by the phytoplankton *Emiliana huxleyi*. *Limnol. Oceanogr.* **42,** 1544–1551.

Palenik, B., and Koke, J. A. (1995). Characterization of a nitrogen-regulated protein identified by cell surface biotinylation of a marine phytoplankton. *Appl. Env. Microbiol.* **61,** 3311–3315.

Palenik, B., and Morel, F. M. M. (1990a). Amino acid utilization by marine phytoplankton: A novel mechanism. *Limnol. Oceanogr.* **35,** 260–269.

Palenik, B., and Morel, F. M. M. (1990b). Comparison of cell-surface L-amino acid oxidases form several marine phytoplankton. *Mar. Ecol. Prog. Ser.* **59,** 195–201.

Palenik, B., and Morel, F. M. M. (1991). Amine oxidases of marine phytoplankton. *App. Environ. Microbiol.* **57,** 2440–2443.

Pantoja, S., and Lee, C. (1994). Cell-surface oxidation of amino acids in seawater. *Limnol. Oceanogr.* **39,** 1718–1726.

Pantoja, S., and Lee, C. (1999). Peptide decomposition by extracellular hydrolysis in coastal seawater and salt marsh sediment. *Mar. Chem.* **63,** 273–291.

Pantoja, S., Lee, C., and Marecek, J. F. (1997). Hydrolysis of peptides in seawater and sediment. *Mar. Chem.* **57,** 25–40.

Parsons, T. R., Maita, Y., and Lalli, C. (1984). "A Manual of Chemical and Biological Methods for Seawater Analysis." Pergamon Press, Oxford.

Paul, J. H., DeFlaun, M. F., Jeffrey, W. H., and David, A. W. (1988). Seasonal and diel variability in dissolved DNA and in microbial biomass and activity in a subtropical estuary. *Appl. Environ. Microbiol.* **54,** 718–727.

Paul, J. H., Jeffrey, W. H., and DeFlaun, M. F. (1987). Dynamics of extracellular DNA in the marine environment. *Appl. Environ. Microbiol.* **53,** 170–179.

Poulet, S. A., and Martin-Jezequel, V. (1983). Relationships between dissolved free amino acids, chemical composition and growth of the marine diatom *Chaetoceros debile*. *Mar. Biol.* **77,** 93–100.

Poutanen, E. L., and Morris, R. J. (1985). Comparison of the structures of humic acids from marine sediments and degraded field diatoms by ^{13}C– and ^{1}H-NMR spectroscopy. *Mar. Chem.* **17,** 115–126.

Prakash, A. (1971). Terrigenous organic matter and coastal phytoplankton fertility. *In* "Fertility of the Sea" (J. D. Costlow, Ed.), pp. 351–368. Gordon and Breach, New York.

Prakash, A., M.A., R., Jensen, A., and Rao Subba, D. V. (1973). Influence of humic substances on the growth of marine phytoplankton: Diatoms. *Limnol. Oceanogr.* **18,** 516–524.

Price, N., and Harrison, P. (1987). Comparison of methods for the analysis of dissolved urea in seawater. *Mar. Biol.* **94,** 307–317.

Price, N. M., and Harrison, P. J. (1988). Urea uptake by Sargasso Sea phytoplankton: Saturated and *in situ* uptake rates. *Deep-Sea Res.* **35,** 1579–1593.

Probyn, T. A. (1985). Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling systems. *Mar. Ecol. Prog. Ser.* **22,** 249–258.

Probyn, T. A., Waldron, H. N., and James, A. G. (1990). Size-fractionated measurements of nitrogen uptake in ages upwelled waters: Implications for pelagic food webs. *Limnol. Oceanogr.* **35,** 202–210.

Pujo-Pay, M., Conan, P., and Raimbault, P. (1997). Excretion of dissolved organic nitrogen my phytoplankton assessed by wet oxidation and N-15 tracer procedures. *Mar. Ecol. Prog. Ser.* **153,** 99–111.

Raimbault, P., Slawyk, G., Boudjellal, B., Coatanoan, C., Conan, P., Coste, B., Carcia, N., Moutin, T., and Pujo-Pay, M. (1999). Carbon and nitrogen uptake and export in the equatorial Pacific at 150°W: Evidence for an efficient regenerated production cycle. *J. Geophys. Res.* **104,** 3341–3356.

Rice, D. L. (1982). The detritus nitrogen problem: New observations and perspectives from organic geochemistry. *Mar. Ecol. Prog. Ser.* **9,** 153–162.

Rich, J., Gosselin, M., Sherr, E., Sherr, B., and Kirchman, D. L. (1997). High bacterial production, uptake and concentrations of dissolved organic matter in the Central Arctic ocean. *Deep-Sea Res. II* **44,** 1645–1663.

Riegman, R., Flameling, I. A., and Noordeloos, A. A. M. (1998). Size-fractionated uptake of ammonium, nitrate and urea and phytoplankton growth in the North Sea during spring 1994. *Mar. Ecol. Prog. Ser.* **173,** 85–94.

Riegman, R., and Noordeloos, A. A. M. (1998). Size-fractionated uptake of nitrogenous nutrients and carbon by phytoplankton in the North Sea during summer 1994. *Mar. Ecol. Prog. Ser.* **173,** 95–106.

Roy, S., Harris, R. P., and Poulet, S. A. (1989). Inefficient feeding by *Calanus helgolandicus* and *Temora longicornis* on *Coscinodiscus wailesii* : Quantitative estimation using chlorophyll-type pigments and effects on dissolved free amino acids. *Mar. Ecol. Prog. Ser.* **52,** 145–153.

Sakano, S., and Kamatani, A. (1992). Determination of dissolved nucleic acids in seawater by the fluorescence dye, ethidium bromide. *Mar. Chem.* **37,** 239–255.

Sakshaug, E., and Holm-Hansen, O. (1977). Chemical composition of *Skeletonema costatus* (Grev.) Cleve and *Pavlova (Monochrysis) lutheri* (Droop) Green as a function of nitrate-, phosphate-, and iron-limited growth. *J. Exp. Mar. Biol. Ecol.* **29,** 1–34.

Sanders, R., and Jickells, T. (2000). Total organic nutrients in Drake Passage. *Deep-Sea Res. I* **47,** 997–1014.

Schnef, E., and Elbräcter, M. (1992). Nutritional strategies of dinoglagellates. A review with emphasis on cell biological aspects. *J. Protistol.* **28,** 3–24

Schnitzer, M. (1985). Nature of nitrogen in humic substances. *In* "Humic Substances in Soil, Sediment, and Water" (G. R. Aiken, D. M. McKnight, and R. L. Wershaw, Eds.), pp. 303–328. Wiley, New York.

Schuster, S., Arrieta, J. M., and Herndl, G. J. (1998). Adsorption of dissolved free amino acids on colloidal DOM enhances colloidal DOM utilization but reduces amino acid uptake by orders of magnitude in marine bacterioplankton. *Mar. Ecol. Prog. Ser.* **166,** 99–108.

Seitzinger, S., and Sanders, R. (1997). Contribution of dissolved organic nitrogen from rivers to estuarine eutrophication. *Mar. Ecol. Prog. Ser.* **159,** 1–12.

Seitzinger, S., and Sanders, R. (1999). Atmospheric inputs of dissolved organic nitrogen stimulate estuarine bacteria and phytoplankton. *Limnol. Oceanogr.* **44,** 721–730.

Sellner, K. G. (1992). Trophodynamics of marine cyanobacteria blooms. *In* "Marine Pelagic Cyanobacteria: *Trichodesmium* and Other Diazotrophs" (E. J. Carpenter, D. G. Capone, and J. G. Reuter, Eds.), pp. 75–95. Kluwer Academic Publishers, The Netherlands.

Sellner, K. G., and Nealley, E. W. (1997). Diel fluctuations in dissolved free amino acids and monosaccharides in Chesapeake Bay dinoflagellate blooms. *Mar. Chem.* **56,** 193–200.

Sharp, J. H. (1973). Total organic carbon in seawater—comparison of measurements using persulfate oxidation and high temperature combustion. *Mar. Chem.* **1,** 211–229.

Sharp, J. H. (1983). The distribution of inorganic nitrogen and dissolved and particulate organic nitrogen in the sea. *In* "Nitrogen in the Marine Environment" (D. G. Capone and E. J. Carpenter, Eds.), pp. 101–120. Plenum Press, New York.

Sharp, J. H. (2002). Analytical Methods for Total DOM Pool *In* "Biogeochemistry of Marine Dissolved Organic Matter" (D. A. Hansell and Carlson, C. A., Eds.), pp. 35–58. Academic Press, San Diego.

Sharp, J. H., Rinker, K. R., Savidge, K. B., Abell, J., Benaim, J. Y., Bronk, D. A., Burdige, D. J., Cauwet, G., Chen, W., Doval, M. D., Hansell, D., Hopkinson, C., Kattner, G., Kaumeyer, N., McGlathery, K. J., Merriam, J., Morley, J., Nagel, K., Ogawa, H., Pollard, C., Raimbault, P., Seitzinger, S., Spyres, G., Tirendi, F., Walsh, T. W. and Wong, C. S. (in press). A preliminary methods comparison for measurement of dissolved organic nitrogen in seawater. *Mar. Chem.*

Shibata, A., Kogure, K., Koike, I., and Ohwada, K. (1997). Formation of submicron colloidal particles from marine bacteria by viral infection. *Mar. Ecol. Prog. Ser.* **155,** 303–307.

Shimizu, Y., Watanabe, N., and Wrensford, G. (1995). Biosynthesis of brevetoxins and heterotrophic metabolism in *Gymnodinium breve*. *In* "Harmful Marine Algal Blooms" (P. Lassus, G. Arzul, E. Erard, P. Gentien, P., and C. Marcaillou, Eds.), Lavoisier, Intercept, Ltd.

Sigman, S. D., Altabet, M. A., Michner, R., McCorkle, D. C., Fry, B., and Holmes, R. M. (1997). Natural abundance-level measurement of the nitrogen isotopic composition of oceanic nitrate: An adaptation of the ammonia diffusion method. *Mar. Chem.* **57,** 227–242.

Slawyk, G., and Raimbault, P. (1995). Simple procedure for simultaneous recovery of dissolved inorganic and organic nitrogen in ^{15}N-tracer experiments and improving the isotopic mass balance. *Mar. Ecol. Prog. Ser.* **124,** 289–299.

Slawyk, G., Raimbault, P., and Garcia, N. (1998). Measuring gross uptake of ^{15}N-labeled nitrogen by marine phytoplankton without particulate matter collection: Evidence for low ^{15}N losses to the dissolved organic nitrogen pool. *Limnol. Oceanogr.* **43,** 1734–1739.

Slawyk, G., Raimbault, P., and Garcia, N. (2000). Use of ^{15}N to measure dissolved organic nitrogen release by marine phytoplankton. *Limnol. Oceanogr.* **45,** 1884–1886.

Smith, D. C., Simon, M., Alldredge, A. L., and Azam, F. (1992). Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature* **359,** 139–141.

Smith, S. V., Hollibaugh, J. T., Dollan, S. J., and Vink, S. (1991). Tomales Bay metabolism: C-N-P stoichiometry and ecosystem heterotrophy at the land-sea interface. *Estuarine Coastal Shelf Sci.* **33,** 223–257.

Søndergaard, M., Williams, P. J. le. B., Cauwet, G., Riemann, B., Robinson, C., Terzic, S., Woodward, E. M. S., and Worm, J. (2000). Net accumulation and flux of dissolved organic carbon and dissolved organic nitrogen in marine plankton communities. *Limnol. Oceanogr.* **45,** 1097–1111.

Steidinger, K. A., Vargo, G. A., Tester, P. A., and Tomas, C. R. (1998). Bloom dynamics and physiology of *Gymnodinium breve* with emphasis on the Gulf of Mexico. *In* "Physiological Ecology of Harmful

Algal Blooms" (D. M. Anderson, A. D. Cembella, and G. M. Hallegraeff, Eds.), Springer-Verlag, Berlin

Stepanauskas, R., Edling, H., and Tranvik, L. J. (1999b). Differential dissolved organic nitrogen availability and bacterial aminopeptidase activity in limnic and marine waters. *Microb. Ecol.* **38,** 264–272.

Stepanauskas, R., Jørgensen, N. O. G., Eigaard, O. R., and Zvikas, A. (in press). Riverine nutrients in the Baltic Sea. *Ecological Monographs.*

Stepanauskas, R., Laudon, H., and Jørgensen, N. O. G. (2000). High DON bioavailability in boreal streams during a spring flood. *Limnol. Oceanogr.* **45,** 1298–1307.

Stepanauskas, R., Leonardson, L., and Tranvik, L. J. (1999a). Bioavailability of wetland-derived DON to freshwater and marine bacterioplankton. *Limnol. Oceanogr.* **44,** 1477–1485.

Stevenson, F. J. (1994). "Humus Chemistry." Wiley, New York.

Strom, S. L. (2000). Bacterivory: Interactions between bacteria and their grazers. *In* "Microbial Ecology of the Oceans" (Kirchman, D. L., Ed.), pp. 351-386. Wiley-Liss, New York.

Strom, S. L., Benner, R., Ziegler, S., and Dagg, M. J. (1997). Planktonic grazers are a potentially important source of marine dissolved organic carbon. *Limnol. Oceanogr.* **42,** 1364–1374.

Stuermer, D. H., Peters, K. E., and Kaplan, I. R. (1978). Source indicators of humic substances and proto-kerogen: Stable isotope ratios, elemental compositions, and electron spin resonance spectra. *Geochim. Cosmochim. Acta* **42,** 989–997.

Suttle, C. A. (1994). The significance of viruses to mortality in aquatic microbial communities. *Microb. Ecol.* **28,** 237–243.

Suzuki, Y., and Sugimura, Y. (1985). A catalytic oxidation method for the determination of total nitrogen dissolved in seawater. *Mar. Chem.* **16,** 83–97.

Tamminen, T., and Irmisch, A. (1996). Urea uptake kinetics of a midsummer planktonic community on the SW coast of Finland. *Mar. Ecol. Prog. Ser.* **130,** 201–211.

Tamminen, T., and Seppälä, J. (1999). Nutrient pools, transformations, ratios, and limitations in the Gulf of Riga, the Baltic Sea, during four successional stages. *J. Mar. Systems* **23,** 83–106.

Tanoue, E., Ishii, M., and Midorikawa, T. (1996). Discrete dissolved and particulate proteins in oceanic waters. *Limnol. Oceanogr.* **41,** 1334–1343.

Tanoue, E., Nishiyama, S., Kamo, M., and Tsugita, A. (1995). Bacterial membranes: Possible source of a major dissolved protein in seawater. *Geochim. Cosmochim. Acta* **59,** 2643–2648.

Therkildsen, M., Isaksen, M. F., and Lonstein, B. A. (1997). Urea production by the marine bacteria *Delaya venusta* and *Pseudomonas stutzeri* grown in a minimal medium. *Aquat. Microb. Ecol.* **13,** 213–217.

Thurman, E. M. (1985). "Organic Geochemistry of Natural Waters." Niyhoff/Junk, Boston.

Tobias, C. R., Harvey, J. W., and Anderson, I. C. (2001). Quantifying groundwater discharge through fringing wetlands to estuaries: Seasonal variability, methods comparison, and implications for wetland-estuary exchange. *Limnol. Oceanogr.* **46,** 604–615.

Toggweiler, J. R. (1989). Is the downward dissolved organic matter (DOM) flux important in carbon transport? *In* "Productivity in the Ocean: Past and Present" (W. H. Berger, V. S. Smetacek, and G. Wefer, Eds.). pp. 65–83. Wiley, New York.

Toledo, A. P. P., D'Aquino, V. A., and Tundisi, J. G. (1982). Influence of humic acid on growth and tolerance to cupric ions in *Melosira italica* (subsp. *antarctica*). *Hydrobiology* **87,** 247–254.

Tsugita, A., Uchida, T., Mewes, H. W., and Atake, T. (1987). A rapid vapor-phase acid (hydrochloric acid and trifluoroacetic acid) hydrolysis for peptide and protein. *J. Biochem.* **102,** 1593–1597.

Tupas, L., and Koike, I. (1990). Amino acid and ammonium utilization by heterotrophic marine bacteria grown in enriched seawater. *Limnol. Oceanogr.* **35,** 1145–1155.

Turk, V., Rehnstam, A.-S., Lundberg, E., and Hagström, Å. (1992). Release of bacterial DNA by marine nanoflagellates, an intermediate step in phosphorus regeneration. *Appl. Env. Microb.* **58,** 3744–3750.

Urban-Rich, J. (1999). Release of dissolved organic carbon from copepod fecal pellets in the Greenland Sea. *J. Exp. Mar. Biol. Ecol.* **232,** 107–124.

Valderrama, J. C. (1981). The simultaneous analysis of total nitrogen and total phosphorus in natural waters. *Mar. Chem.* **10,** 109–122.

Valiela, I., Costa, J., Foreman, K., Teal, J. M., Howes, B., and Aubrey, D. (1990). Transport of groundwater-borne nutrients from watersheds and their effects on coastal waters. *Biogeochemistry* **10,** 177–197.

Valiela, I., and Teal, J. M. (1979). The nitrogen budget of a salt marsh ecosystem. *Nature* **280,** 652–656.

Vidal, M., Duarte, C. M., and Agusti, S. (1999). Dissolved organic nitrogen and phosphorus pools and fluxes in the central Atlantic Ocean. *Limnol. Oceanogr.* **44,** 106–115.

Villareal, T. A., Altabet, M. A., and Culver-Rymsza, K. (1993). Nitrogen transport by vertically migrating diatom mats in the North Pacific Ocean. *Nature* **363,** 709–712.

Waldron, H. N., Attwood, C. G., Probyn, T. A., and Lucas, M. I. (1995). Nitrogen dynamics in the Bellingshausen Sea during the Austral spring of 1992. *Deep-Sea Res. II* **42,** 1253–1276.

Wang, W., Tarr, M. A., Bianchi, T. S., and Engelhaupt, E. (2000). Ammonium photoproduction from aquatic humic and colloidal matter. *Aquat. Geochem.* **6,** 275–292.

Ward, B. B., and Bronk, D. A. (2001). Net nitrogen uptake and DON release in surface waters: Importance of trophic interactions implied from size fractionation experiments. *Mar. Ecol. Prog. Ser.* **219,** 11–24.

Weinbauer, M. G., and Peduzzi, P. (1995). Effect of virus-rich high molecular weight concentrates of seawater on the dynamics of dissolved amino acids and carbohydrates. *Mar. Ecol. Prog. Ser.* **127,** 245–253.

Wheeler, P. A., and Hellebust, J. A. (1981). Uptake and concentration of alkylamines by a marine diatom. *Plant. Physiol.* **67,** 367–372.

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

Wheeler, P. A., Watkins, J. M., and Hansing, R. L. (1997). Nutrients, organic carbon and organic nitrogen in the upper water column of the Arctic Ocean: Implications for the sources of dissolved organic carbon. *Deep-Sea Res. II* **44,** 1571–1592.

Williams, P. J. le. B. (2000). Heterotrophic bacteria and the dynamics of dissolved organic material. *In* "Microbial Ecology of the Oceans" (Kirchman, D. L., Ed), pp. 153–200. Wiley-Liss, New York.

Williams, R., and Poulet, S. A. (1986). Relationships between the zooplankton, phytoplankton, particulate matter, and dissolved free amino acids in the Celtic Sea. *Mar. Biol.* **90,** 279–284.

Wommack, K. E., and Colwell, R. R. (2000). Virioplankton: Viruses in aquatic ecosystems. *Microbiol. Mol. Biol. Rev.* **64,** 69–114.