

REVIEW

Dissolved organic nitrogen: a dynamic participant in aquatic ecosystems

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ABSTRACT: In both marine and freshwaters, the concentration of dissolved organic nitrogen (DON) frequently exceeds that of dissolved inorganic nitrogen (DIN), including ammonium, nitrate, and nitrite. Recent evidence indicates that many organic N compounds are released into the DON pool and taken up from this pool by planktonic microbiota on timescales of hours to days. This observation suggests that many components of the DON pool can play an active role in supplying N nutrition directly or indirectly to phytoplankton and bacteria and, in so doing, may affect the species composition of the ambient microbial assemblage. Here we present an overview of the state of knowledge of DON pools in aquatic environments, focused mainly on data gathered in the last decade. We review information on DON concentrations in freshwater and marine systems, analytical methods for the determination of DON, and the biotic and abiotic sources and sinks of DON. More detailed discussion addresses specific components of the DON pool: urea, dissolved combined and free amino acids, proteins, nucleic acids, amino sugars, and humic substances. The DON pool in natural waters is not inert and can be an important sink and source for N. There is a need for greater appreciation and understanding of the potential role of DON as a dynamic participant in the nitrogen cycle within aquatic ecosystems, particularly in freshwater environments.

KEY WORDS: Dissolved organic nitrogen · Phytoplankton · Bacteria · N nutrition · N cycling · Marine/freshwater ecosystems

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INTRODUCTION

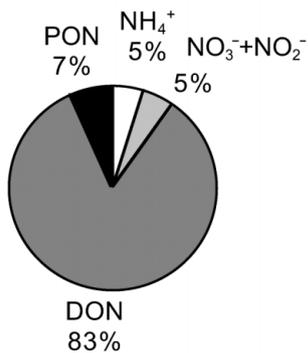
Over 20 yr ago, Antia et al. (1980) wrote: 'we urge oceanographers and marine biologists to stop ignoring the role of dissolved organic nitrogen (DON) in primary production'. Since then, many studies have examined various aspects of DON, both in marine and freshwaters. As a result, the DON pool is increasingly recognized as a dynamic component of the nitrogen (N) and carbon (C) cycles of marine and aquatic systems.

Historically, DON was believed to be composed mainly of refractory compounds resistant to biological degradation and generally unavailable as sources of N nutrition for phytoplankton or bacteria. Nevertheless, there were several early reports of relatively rapid

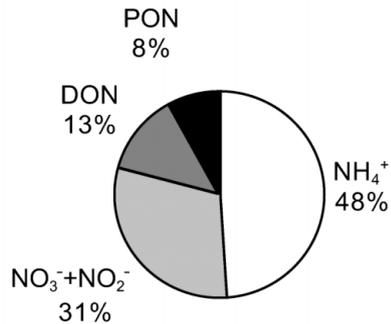
turnover and high flux rates of total DON pools. Turnover times for total DON and for 'labile' DON in the coastal waters of Southern California were estimated as 21 and 17 d respectively; these rates were 13 to 14 times more rapid than DON turnover times in the Central North Pacific Gyre (Jackson & Williams 1985). In Castle Lake, Zehr et al. (1988) reported fast rates of increase in the DON pool in early summer ($0.31 \mu\text{M N d}^{-1}$). In the photic layer of Lake Kizaki, Japan, Takahashi & Saijo (1981) measured daily decomposition rates of DON to be 8.6%, implying a DON pool turnover of about 12 d (Takahashi 2001). Twenty years later, Haga et al. (2001) determined DON residence times in Lake Kizaki ranging from 1.4 to 21 d during May through December, when DON concentrations

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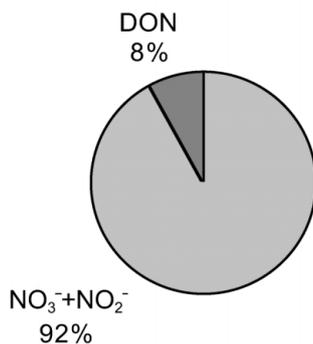
Open Ocean-Surface



Estuarine



Open Ocean-Deep



Coastal

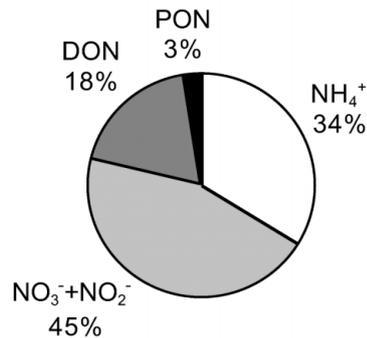


Fig. 1. Average composition of nitrogen pools (except dissolved N₂) in open ocean surface water, open ocean deep water, coastal and estuarine waters (modified from Antia et al. 1991). DON: dissolved organic nitrogen; PON: particulate organic nitrogen

ranged from 3.5 to 10.4 μM N. Such observations are not consistent with the perception of a DON pool composed entirely of recalcitrant compounds.

Subsequent to the comprehensive and detailed review of Antia et al. (1991), some salient new features of N flux into and out of DON pools have become evident. These imply that many DON compounds are cycled more rapidly in aquatic environments than previously recognized. We now know that DON may be released from actively growing phytoplankton, sometimes in appreciable quantities (Bronk et al. 1994, Bronk & Ward 1999, Diaz & Raimbault 2000), possibly via viral lysis or autolysis of bacteria (Fuhrman 1999) and algae (Gobler et al. 1997, Agusti et al. 1998), that elevated concentrations of DON are common in blooms of *Trichodesmium*, the primary N₂ fixer in the ocean (Capone et al. 1994, Glibert & Bronk 1994, Vidal et al. 1999), and that atmospheric inputs of DON to the oceans can be substantial (Cornell et al. 1995, Scudlark et al. 1998).

Sinks for DON have also been studied in more detail over the last decade. Algae (Lewitus et al. 2000), cyanobacteria (Berman 2001), bacteria (Antia et al. 1991, Bronk 2002), archaeobacteria (Ouverney &

Fuhrman 2000) and perhaps even protists (Tranvik et al. 1993) have been shown to exploit various components of the DON pool either directly or after bacterial degradation. The potential of photochemical modification or degradation of DON constituents has also been recognized (Bushaw et al. 1996, Moran & Zepp 2000, Morell & Corredor 2001).

The capacity of some algal species to exploit DON compounds as sources of N has led to the idea that specific DON components can exert selective pressure on the composition of the phytoplankton community (Paerl 1997, Seitzinger & Sanders 1997, Berman & Chava 1999). For example, inputs of DON from rivers heavily impacted by human activity may stimulate eutrophication processes and the proliferation of toxic phytoplankton in estuarine and coastal waters (Granéli et al. 1985, Berg et al. 2001).

In this paper we present an overview of the present state of knowledge of DON in both freshwater and marine environments, focusing mainly on information gathered since the extensive review on this topic by Antia et al. (1991). Recently, a comprehensive review focusing on DON dynamics in marine systems, though not freshwater environments, was published by Bronk (2002).

CONSTITUENTS OF THE DON POOL

A considerable proportion of the total N (TN) pool (excluding dissolved gaseous N₂) in many freshwater, marine, coastal, and estuarine environments is frequently associated with the DON fraction. Indeed, in many natural waters, concentrations of DON are much higher than those of the total dissolved inorganic nitrogen (DIN) fraction, consisting of ammonium (NH₄⁺), nitrate (NO₃⁻), and nitrite (NO₂⁻). 'Average' composition for seawater total dissolved N (TDN) pools is shown in Fig. 1. In the deep ocean, however, DON is a small percentage of TDN.

In freshwaters, the DON fraction often exceeds 50% of the TDN pool and is usually 5 to 10 times higher in concentration than the particulate organic nitrogen (PON) within plankton and seston (Krupka 1989, Wetzel 2001). An example of seasonal data from Lake Kinneret is shown in Fig. 2 (T. Berman & A. Nishri

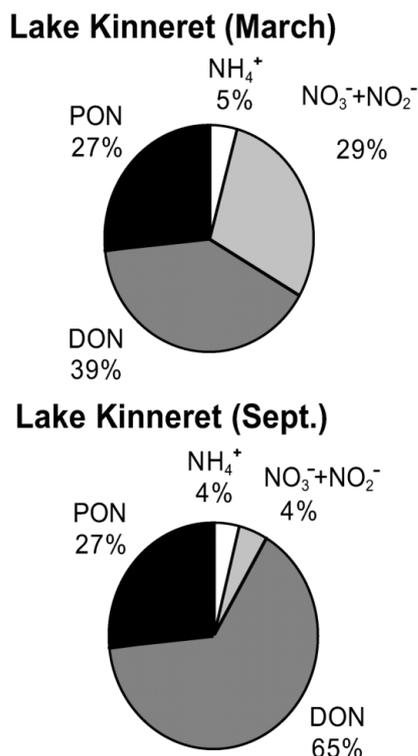


Fig. 2. The distributions of N fractions in the euphotic zone of a monomictic, meso-eutrophic lake (Lake Kinneret). Values are averaged from 1975 through 1994 for a homothermic period, late winter (March), and a stratified period (September; unpubl. data from Kinneret Laboratory database). DON: dissolved organic nitrogen; PON: particulate organic nitrogen

unpubl. data). The DON:PON ratio tends to decrease as lakes become more eutrophic (Wetzel 2001). A detailed summary of the ranges of DON concentrations in marine waters, their global and vertical distribution, seasonal variation and relationships between DON and DIN is given in Bronk (2002). A condensed version of these data is reproduced in Table 1 together with additional data from freshwater environments. The reader is also directed to Tables 2 & 3 in Antia et al. (1991) for details of low molecular weight (LMW) DON compounds, sample locations, and concentrations as reported in the literature prior to 1990.

Much of the DON pool still remains uncharacterized chemically. Operationally, components of the DON pool have been divided into high molecular weight (HMW, usually >1 kDa) and LMW compounds. HMW DON includes proteins (such as enzymes, modified bacterial wall proteins, dissolved combined amino acids [DCAA]), nucleic acids (DNA, RNA) and humic-like substances that have a relatively low N content. There is the added complication that some LMW and HMW DON compounds may be loosely held or adsorbed to humic substances.

Within the last decade the application of ultra-filtration techniques has expanded our knowledge of the HMW DON fraction and added the acronym UDON (ultra-filtered DON) to the literature. Marine HMW DON (i.e. the >1 kDa fraction) has a characteristic chemical composition that is highly conserved across oceanic regions (McCarthy et al. 1997, 1998). Recent studies of this fraction suggest that much of the refractory DON in the oceans probably consists of amide groups in peptidoglycan remnants enriched with D-enantiomers of alanine, asparagine, glutamic acid, and serine (McCarthy et al. 1996, 1997, 1998, Dittmar et al. 2001, Ogawa et al. 2001). Most of this DON appears to be derived from bacterial cell wall material that has undergone modification of its molecular structure, making it resistant to further degradation. Similar material was present in coastal sediments (Pedersen et al. 2001). To the best of our knowledge, no comparable studies have yet been made in freshwater.

A host of organic nitrogen (ON) compounds make up the LMW DON pool, including urea, peptides (part of the DCAA pool), dissolved free amino acids (DFAA), amino sugars, purines, pyrimidines, pteridines, amides, methyl amides and others (Antia et al. 1991). Many of these compounds may be important N substrates for autotrophs and heterotrophs (Bronk 2002).

ANALYTICAL METHODS FOR DON DETERMINATION

A major challenge in the study of DON is the lack of sensitive and precise techniques to quantify total DON concentrations, and those of various known DON constituents. Presently all methods to measure total DON concentrations depend on determining the TDN concentration and then subtracting the separately measured concentrations of DIN (i.e. the sum of NH_4^+ , NO_3^- and NO_2^- concentrations). This approach combines the analytical errors of 3 analyses: TDN, NH_4^+ and ($\text{NO}_3^- + \text{NO}_2^-$).

Three basic methods are currently used to obtain the complete oxidation of all the organic constituents of TDN: (1) Variations of the 'wet chemical' method based on persulphate digestion and oxidation to NO_3^- (Menzel & Vaccaro 1964, Sharp 1973, Nydahl 1978, Valderrama 1981, Bronk et al. 2000). Some earlier studies on freshwater used Kjeldahl digestion with SeO_3 as the catalyst to determine TDN (Mitamura & Saijo 1981). (2) Ultraviolet oxidation to NO_3^- (Armstrong et al. 1966, Armstrong & Tibbitts 1968, Bronk et al. 2000). (3) High temperature oxidation to NO gas and detection by spectrophotometry (Sharp 1973, Suzuki & Sugimura 1985), or chemiluminescence (Walsh 1989, Hansell et al. 1993).

Table 1. Concentrations of total dissolved nitrogen (TDN) and dissolved organic nitrogen (DON) in ocean, coastal, estuarine, riverine, and freshwater systems. Measurement methods were variations of persulfate oxidation (PO), high-temperature oxidation (HTO) or ultraviolet oxidation (UV). HMW: high molecular weight

Location	Depth (m)	TDN ($\mu\text{M N}$)	DON ($\mu\text{M N}$)	Method	Source
Oceanic-surface					
Greenland Sea	<100		4.6 \pm 0.6	PO	Hubberten et al. (1995)
Bering Sea, North Pacific	<30	8.6 \pm 2.9	2.5 \pm 1.9	HTO	Hansell (1993)
Western tropical Pacific (10–20° S)	<50		5.4 \pm 0.3 ^a	UV	Hansell & Feely (2000)
Western tropical Pacific (25–35° S)	<50		4.8 \pm 0.4 ^a	UV	Hansell & Feely (2000)
Santa Monica Basin, Pacific	<100	11.9 \pm 6.2	5.2 \pm 1.9	HTO	Hansell et al. (1993)
Eastern N. Pacific	<85	11.1 \pm 6.4	4.1 \pm 0.5	PO	Loh & Bauer (2000)
Subtropical Pacific (5–21° N)	<50	5.8 \pm 1.4	5.5 \pm 0.9 ^a	UV	Hansell & Waterhouse (1997)
Equatorial Pacific (6° S–2° N)	<50	16.0 \pm 6.1	5.0 \pm 0.7 ^a	UV	Hansell & Waterhouse (1997)
Equatorial Pacific	<40	13.9 \pm 4.0	8.4 \pm 1.0 ^{a,b}	PO	Libby & Wheeler (1997)
Equatorial Pacific (6–15° S)	<100	7.9 \pm 3.5	5.5 \pm 0.7 ^a	UV	Hansell & Waterhouse (1997)
Subtropical Pacific (16–35° S)	<150	4.8 \pm 0.4	4.5 \pm 0.4 ^a	UV	Hansell & Waterhouse (1997)
Subpolar Pacific (35–64° S)	<150	18.3 \pm 6.8	4.3 \pm 0.6 ^a	UV	Hansell & Waterhouse (1997)
Pacific Equatorial Transition	<50	5.8–6.0	5.7–5.9 ^a	UV	Abell et al. (2000)
Pacific Subtropical Gyre	<50	5.3–6.3	5.2–6.2 ^a	UV	Abell et al. (2000)
Pacific Subtropical Transition	<50	4.7–5.5	4.5–5.3 ^a	UV	Abell et al. (2000)
Equatorial Pacific (16° S–1° N)	<200		~3.0–7.0	PO	Raimbault et al. (1999)
Southern California Bight (offshore)	<55	9.7 \pm 2.4	7.0 \pm 0.4	UV	Ward & Bronk (2001)
Southern California Bight (offshore)	<43	10.8 \pm 5.8	6.6 \pm 1.4	UV	Ward & Bronk (2001)
Southern Ocean Polar Front	<200		6.9–11.0	HTO	Kähler et al. (1997)
North of Antarctic Peninsula	Surface		0.8–6.3	UV	Karl et al. (1996)
Pacific Subarctic Frontal	<50	5.3–7.9	5.1–5.2 ^a	UV	Abell et al. (2000)
Southern Ocean	<150	31.2 \pm 3.1	4.6 \pm 1.5	HTO	Ogawa et al. (1999)
Southern Ocean (Stn F)	<94	20.9 \pm 1.1	4.2 \pm 0.2	PO	Loh & Bauer (2000)
Ross Sea Polynya	<150		2.1–6.3	UV	Carlson et al. (2000)
Antarctic waters	<100		3.9 \pm 1.3	PO	Hubberten et al. (1995)
Drake Passage (61–50° S)	<50		3.1–7.3	UV	Sanders & Jickells (2000)
North Atlantic (33–60° N)	Surface		4.4–7.4	HTO	Kähler & Koeve (2001)
Arctic Ocean (shelf)	<55 ^c		3.6 \pm 0.7	PO	Wheeler et al. (1997)
Arctic Ocean (slope)	<100 ^c		5.2 \pm 1.6	PO	Wheeler et al. (1997)
Arctic Ocean (basin)	<100 ^c		5.3 \pm 1.4	PO	Wheeler et al. (1997)
Sargasso Sea	Surface		5.8 \pm 0.8 ^{a,b}	UV	Bates & Hansell (1999)
Sargasso Sea (BATS)	Surface		4.0–5.5	UV	Hansell & Carlson (2001)
Equatorial Atlantic	<100		8.2 \pm 4.8	PO	Vidal et al. (1999)
Pacific (HMW DON >1 kDa) ^d	<100		1.2 \pm 0.2	UV	Benner et al. (1997)
Atlantic (HMW DON >1 kDa) ^d	Surface		1.0	UV	Benner et al. (1997)
Gulf of Mexico (HMW DON >1 kDa) ^d	10		1.2	UV	Benner et al. (1997)
Sargasso Sea	Surface		5.8 \pm 0.8 ^{a,b}	UV	Bates & Hansell (1999)
Sargasso Sea (BATS)	Surface		4.0–5.5	UV	Hansell & Carlson (2001)
Equatorial Atlantic	<100		8.2 \pm 4.8	PO	Vidal et al. (1999)
Oceanic-deep					
NE Pacific	>150	4.82 ^e	4.5 \pm 0.4	UV	Harrison et al. (1992)
Greenland Sea	>100		3.5 \pm 0.8	PO	Hubberten et al. (1995)
Santa Monica Basin	110–800	36.7 \pm 5.7	4.3 \pm 1.2	HTO	Hansell et al. (1993)
Subtropical Pacific (5–21° N)	51–1000	36.9 \pm 5.7	2.7 \pm 0.7 ^a	UV	Hansell & Waterhouse (1997)
Equatorial Pacific (6° S–2° N)	51–1000	38.8 \pm 4.1	2.6 \pm 0.6 ^a	UV	Hansell & Waterhouse (1997)
Equatorial Pacific (6–15° S)	101–3000	37.1 \pm 7.1	2.9 \pm 0.8 ^a	UV	Hansell & Waterhouse (1997)
Subtropical Pacific (16–35° S)	151–3000	28.3 \pm 12.2	3.0 \pm 0.6 ^a	UV	Hansell & Waterhouse (1997)
Subpolar Pacific (35–64° S)	151–3250	31.2 \pm 4.7	2.8 \pm 0.6 ^a	UV	Hansell & Waterhouse (1997)
Pacific Equatorial Transition	~205		2.8	UV	Abell et al. (2000)
Pacific Subtropical Gyre	~305		2.8–3.7	UV	Abell et al. (2000)
Pacific Subtropical Transition	~185		4.4	UV	Abell et al. (2000)
Pacific Subarctic Frontal	~145		3.7	UV	Abell et al. (2000)
Eastern N. Pacific	100–4097	39.0 \pm 5.2	2.4 \pm 0.4	PO	Loh & Bauer (2000)
Southern Ocean Polar Front	200–1500		7.9–9.8	HTO	Kähler et al. (1997)
Southern Ocean	~100–4150	36.1 \pm 2.0	3.9 \pm 1.1	HTO	Ogawa et al. (1999)
Southern Ocean (Stn F)	142–5408	32.2 \pm 5.4	3.5 \pm 0.6	PO	Loh & Bauer (2000)
Ross Sea Polynya	150–600		2.4 \pm 0.3	UV	Carlson et al. (2000)

Table 1 (continued)

Location	Depth (m)	TDN ($\mu\text{M N}$)	DON ($\mu\text{M N}$)	Method	Source
Oceanic-deep (continued)					
Antarctic waters	>100		3.0 ± 1.1	PO	Hubberten et al. (1995)
Sargasso Sea (BATS)	250–1000		2.1–5.0	UV	Hansell & Carlson (2001)
Sargasso Sea (BATS)	1000–4000		3.1 ± 0.4	UV	Hansell & Carlson (2001)
Drake Passage (61–50° S)	>50		1.4–2.9	UV	Sanders & Jickells (2000)
Equatorial Atlantic	110–1000		6.7 ± 4.1	PO	Vidal et al. (1999)
HMW DON >1 kDa ^d	200–2400		0.5–0.56	UV	Benner et al. (1997)
Coastal/Continental shelf					
Gulf of Mexico (Los Angeles–Texas coast)	Surface		1.9–52.5	HTO	López-Veneroni & Cifuentes (1994)
Gulf of Riga, Baltic Sea	Surface	26.7–29.4 ^f	18.0–26.4	PO	Tamminen & Seppälä (1999)
Gulf of Riga, Baltic Sea	2.5–30	15.5–40.2	5.4–23.0 ^g	HTO	Jørgensen et al. (1999)
Georges Bank	Surface		4.8–5.4	UV	Hopkinson et al. (1997)
Georges Bank	200–1500		2.5–3.4	UV	Hopkinson et al. (1997)
Middle Atlantic Bight	Surface		$7.4 \pm 1.1^{\text{a,b}}$	UV	Bates & Hansell (1999)
Monterey Bay	<100	18.5 ± 6.1	1.9 ± 1.6	HTO	Hansell (1993)
Bering Sea, North Pacific	<30	8.6 ± 2.9	2.5 ± 1.9	HTO	Hansell (1993)
Monterey Bay	<20	6.5 ± 1.9	5.2 ± 1.8	PO	Bronk & Ward (1999)
Northeast Greenland Shelf	<70	7.2	5.9 ^h	PO	Daly et al. (1999)
Akkeshi Bay, Japan	Surface	7.7 ± 2.3	6.7 ± 1.0	PO	Hasagawa et al. (2000a)
Japanese bays (2)	Surface	12.0 ± 1.6	8.7 ± 1.6	HTO	Tupas & Koike (1990)
Southern California Bight (nearshore)	<55	10.2 ± 2.5	7.7 ± 1.3	UV	Ward & Bronk (2001)
Estuarine					
Shinnecock Bay, New York	Surface	2.0–4.9	0.6–4.3 ⁱ	PO	Berg et al. (1997), Lomas et al. (1996)
Waquoit Bay, Massachusetts	Surface	140	40.0	NG	Hopkinson et al. (1998)
Chesapeake Bay, mesohaline	Surface	34.1 ± 12.3	21.3 ± 16.0	PO	Bronk et al. (1998)
Chesapeake Bay, mesohaline	Surface	42.5 ± 3.7	22.3 ± 9.2	PO	Bronk & Glibert (1993a)
Chesapeake Bay, mesohaline	Surface	23.1 ± 1.7	22.2 ± 1.6	PO	Bronk & Glibert (1993a)
Chesapeake Bay, mouth	Surface		$16.3 \pm 5.5^{\text{b}}$	UV	Bates & Hansell (1999)
Apalachicola Bay	Surface	23	14.8 ± 1.0	PO	Mortazavi et al. (2000)
Delaware Estuary	Surface		40.8 ± 29.3	PO	Karl (1993)
Elbe Estuary	Surface	72.2 ± 17.6	65.0 ± 12.2	PO	Kerner & Spitzzy (2001)
North Inlet, South Carolina	Surface	19.4–35.3	18.0–30.8	NG	Lewitus et al. (2000)
Tomales Bay	Surface		5.8–12.6	UV	Smith et al. (1991)
Rivers					
Russian rivers draining into Arctic (7)	Surface		27.0 ± 5.0	NG	Gordeev et al. (1996), Wheeler et al. (1997)
Rivers entering the Baltic Sea (5)	Surface	48.9 ± 41.9	29.8 ± 14.8	HTO	Stepanuskas et al. (2002)
Susquehanna River, Maryland	Surface	116	23.0	NG	Hopkinson et al. (1998)
Satilla River, Georgia	Surface	62.6	59.0	NG	Hopkinson et al. (1998)
Parker River, Maryland	Surface	37	26.0	NG	Hopkinson et al. (1998)
Delaware River	Surface		29.7 ± 23.7	HTO	Seitzinger & Sanders (1997)
Hudson River	Surface		33.5	HTO	Seitzinger & Sanders (1997)
Rivers in USA and Europe (17)	Surface			NG	Seitzinger & Sanders (1997)
Choptank River	Surface	41.3	26.9	PO	Bronk & Glibert (1993a)
Georgia and South Carolina Rivers (8) ^j	Surface		35.9 ± 10.7	NG	Alberts & Takács (1999)
Streams in Sweden (2) ^k	Surface		24.3 ± 7.4	HTO	Stepanuskas et al. (2000)
Wetland in Sweden (bulk DON) ^l	Surface		90.0 ± 68.0	PO	Stepanuskas et al. (1999b)
Lagunitas Creek (flows to Tomales Bay)	Surface		3.9–17.9	UV	Smith et al. (1991)
Lakes					
Mendota, USA	0 m	42.3	44.7	NG	Wetzel (2001)
Mendota, USA	20 m		44.2	NG	Wetzel (2001)
Furesø, Denmark			31.4–45.7	NG	Wetzel (2001)
Ysel, Netherlands			42.1–131.4	NG	Wetzel (2001)
Constance, Germany			3.6–10.7	NG	Wetzel (2001)
Lucerne, Switzerland			5.7–12.9	NG	Wetzel (2001)
Rotsee, Switzerland			19.2–47.1	NG	Wetzel (2001)
Wintergreen, USA			35.7–94.3	NG	Wetzel (2001)
Lawrence, USA			5.7–17.1	NG	Wetzel (2001)
Kizaki, Japan		15.9–24.0	4.8–12.5	PO	Takahashi & Saijo (1981)
Biwa, Japan N Basin		7.0–8.0	4.0–7.2	PO	Mitamura & Matsumoto (1981)

(Table continued on next page)

Table 1 (continued)

Location	Depth (m)	TDN ($\mu\text{M N}$)	DON ($\mu\text{M N}$)	Method	Source
Lakes (continued)					
Biwa, Japan S Basin		7.0–15.0	5.4–8.6	PO	Mitamura & Matsumoto (1981)
Okeechobee, USA		67.6	41.2–63.1	PO	Gu et al. (1997)
Plüsee, Germany	0–15	51–104	47.1	PO	Münster & Albrecht (1994)
Plüsee, Germany	20–25	12–259	88.5–187.8	PO	Münster & Albrecht (1994)
Kinneret, Israel—winter	0–15	47.9	26.1	PO	Present study
Kinneret, Israel—spring	0–15	25.6	22.7	PO	Present study
^a Data presented are total organic nitrogen (TON)					
^b TON includes ammonium					
^c Data were converted from g m^{-2} ; mean and SD at stations within each area are reported					
^d Samples from the Pacific, Atlantic, and Gulf of Mexico					
^e Estimated from integrated values throughout the upper 150 m					
^f Sum of the average DON, nitrate and ammonium concentrations					
^g Jørgensen et al. (1999) listed urea separately; it was added back into the DON pool					
^h Median values					
ⁱ Measured during a bloom of <i>Aureococcus anophagefferens</i>					
^j Averages for 8 rivers (Altamaha, Black, Edsto, Ogeechee-Eden, Ogeechee-Oliver, Peedee, Satilla, Savannah, and St. Mary's)					
^k The 2 streams were Lillån and Stridbäcken					
^l The 3 wetlands were Amboke, Isgrannatorp, and Vomb					

The need to improve techniques for measuring DON has long been recognized. To this end, a working group was convened in 1993 to decide how best to proceed and to offer recommendations to the oceanographic community (Hopkinson et al. 1993). Other comparisons of DON methodology were subsequently published (Walsh 1989, Williams 1993, Bronk et al. 2000). A recent cross-laboratory exercise with 29 sets of analyses comparing these methods on 5 marine samples gave a coefficient of variation ranging from 19 to 46%, with the poorest replication of samples from deep ocean waters (Sharp et al. 2002). All the methods gave similar levels of sensitivity and precision. We conclude that present methods are reasonably compatible but that new or improved techniques for determining concentrations of DON with better sensitivity and precision are still needed.

SOURCES OF DON

DON may come from both allochthonous and autochthonous sources. The former includes terrestrial runoff, leaching from plant detritus and soils into streams and rivers, sediments, and atmospheric deposition. Autochthonous sources may include release by exudation from phytoplankton, macrophytes and bacteria, from cell death or viral lysis, or from micro- and macrozooplankton grazing and excretion (Fig. 3).

In the case of streams, rivers, lakes and freshwater reservoirs, much of the DON is often derived from

terrestrial leaching and runoff, and consists mainly of humic substances. Significant inputs of DON to shallow freshwaters and wetlands may be derived from active or passive release from submerged macrophytes (Crowder & Painter 1991) and benthic algae (Jansson 1979). Clearly the composition of DON exported by rivers into lakes, estuaries and coastal waters may be radically different depending on the nature of the catchment areas being drained. In many freshwater systems, anthropogenic sources are responsible for significant inputs of DON that is transported downstream to estuarine and coastal waters (Seitzinger & Sanders 1997, 1999).

A study by Perakis & Hedin (2002) found that 70% of the TDN in streams and rivers of temperate South American forest regions that were pristine and free of human intervention consisted of DON. In contrast, DON comprised only 2% of the TDN in the running water of a forested area in NE USA. This dramatic difference was attributed to the impact of human activities that have doubled N input into the global terrestrial cycle within the last century. The consequences have been an atmosphere polluted with NH_4^+ and N oxides in heavily industrialized areas, increased atmospheric N deposition, acidified soils, streams and lakes, decreased biodiversity and impacted coastal ecosystems and fisheries (van Breemen 2002). Paradoxically, despite the low percentage of DON in the TDN of NE USA forest streams measured by Perakis & Hedin (2002), we note that Alberts & Takács (1999) estimated that DON accounts for 40 to 90% of the TDN in rivers of the SE USA.

The quantities and characteristics of DON in estuarine and marine coastal waters depend on riverine inputs. In coastal zones, terrestrial run-off is also an important factor and the amounts and availability of DON vary depending on the source. Approximately 25% of DON from 2 pastures and 20% of DON from a mixed hardwood forest in summer were utilized by freshwater bacteria in short-term bioassays (Wiegner & Seitzinger 2001). Seitzinger et al. (2002) found that storm water runoff from urban/suburban areas had a higher proportion of bioavailable DON ($59 \pm 11\%$) than that from agricultural pastureland ($30 \pm 14\%$) and forests ($23 \pm 19\%$). Only 8 to 15% of the bulk DON in a relatively pristine wetland in Sweden was potentially bioavailable to estuarine bacteria (Stepanuskas et al. 1999a,b).

In shallow freshwater, estuarine and coastal systems, sediments can be an important source of DON to the overlying water column (reviewed in Burdige & Zheng

1998). Sediment release was the major source of DON in meso-oligotrophic Castle Lake, California (Zehr et al. 1988) and in shallow Danish coastal waters. Lomstein et al. (1998) estimated that efflux of DON from sediment was about twice that of DIN. In another study of sediment-water C and N fluxes at Limfjord, Denmark, Middleboe et al. (1998) also found DON (urea, DFAA and DCAA) to be the dominant N form released from the sediments. These authors suggested that in many cases the estimates of DON flux were underestimated because rapid bacterial uptake of DON in the overlying water was not taken into account.

Although the importance of atmospheric DON inputs has now become evident both for freshwater and marine systems, few data are available to evaluate these inputs (Shaw et al. 1989, Cornell et al. 1995, 2001, Russell et al. 1998, Scudlark et al. 1998). Cornell et al. (1995) proposed that the atmospheric input of fixed N to the ocean is about twice that of previous estimates. At continental sites in North America, between 20 and 75% of the DON in atmospheric deposition has been reported to be bioavailable (Timperley et al. 1985, Peierls & Paerl 1997, Seitzinger & Sanders 1999), with urea as an important constituent. However, we note that the quantitative importance of urea in atmospheric deposition is under debate (Cornell et al. 1998). DON from rainwater stimulated growth of marine phytoplankton (Peierls & Paerl 1997) and of axenic cultures of freshwater algae (Timperley et al. 1985). One study in the NE USA demonstrated that a large percentage (45 to 75%) of the DON in rainwater was biologically available and stimulated the productivity of coastal marine bacteria and phytoplankton (Seitzinger & Sanders 1999).

Excretion by waterfowl is an additional exogenous source of DON that may be quite significant in some shallow and small freshwater environments (Manny et al. 1994). This is unlikely, however, to be of much importance in the pelagic ocean!

In the open ocean, autochthonous sources of DON dominate, especially for the more labile constituents of the pool. As noted previously, DON is excreted by living algae (e.g. Bronk & Ward 1999, Nagao & Miyazaki 2002) although the actual amounts of DON released are still controversial (Slawyk & Raimbault 1995, Pujopay et al. 1997, Flynn & Berry 1999, Nagao & Miyazaki 1999, Bronk & Ward 2000, Slawyk et al. 2000). DON is also released when algae lyse, due to viral infection (Bratbak et al. 1998) or by natural cell death (apoptosis), when grazers feed 'sloppily' (Dagg 1974, Jumars et al. 1989), or during zooplankton excretion (Lampert 1978, Riemann et al. 1986, Wiltshire & Lampert 1999, Rosenstock & Simon 2001). Protists may release DON compounds as a result of feeding on bacteria, pico-

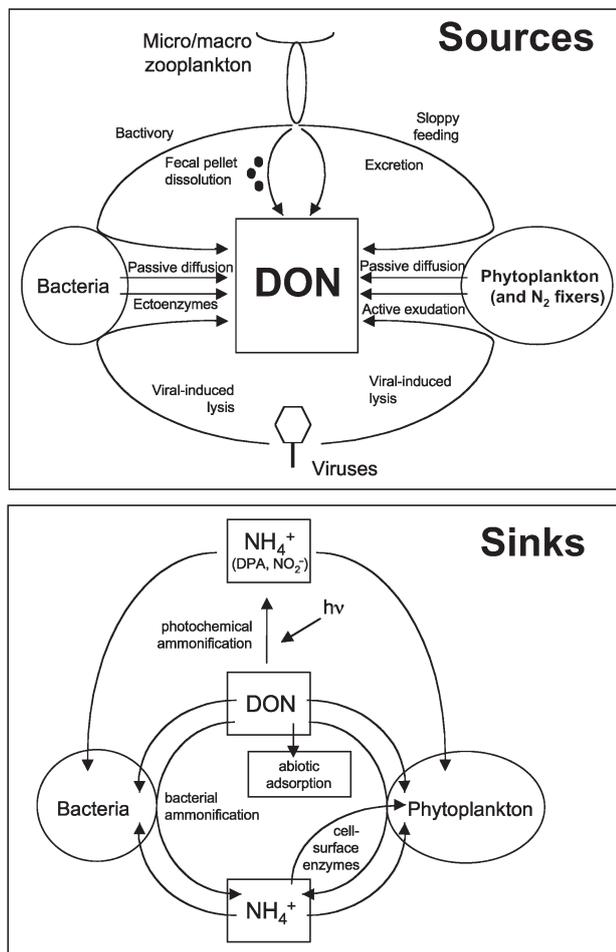


Fig. 3. Sources and sinks of dissolved organic nitrogen (DON) in aquatic systems. DPA stands for dissolved primary amines. Modified from Bronk (2002)

plankton or possibly when eaten (Antia et al. 1980, Berman et al. 1987, Hasagawa et al. 2000a,b, 2001, Nagata 2000). Zooplankton and higher trophic level animals may also contribute to DON. For example, in the sea, as contrasted to fresh water, the excretions of animals such as cetaceans, tunicates, teleost and cartilaginous fish may also add to the DON pool. The hydrolytic activity of bacteria and protists associated with macro- and micro-aggregates (Smith et al. 1992, Hoppe et al. 1993, Grossart & Simon 1998) and transparent proteinaceous particles (Long & Azam 1996, Berman & Viner-Mozzini 2001) that are numerous in both marine and freshwater environments may also release DON. Organic N contained within small bacteria and viruses that pass through the 0.45 or 0.2 μm pore-size filters generally used to obtain the 'dissolved' water fraction is likely an insignificant fraction of the total DON measured in most routine determinations.

SINKS FOR DON

The 4 main sinks for DON are bacterial uptake, phytoplankton uptake, photochemical decomposition and abiotic adsorption (Fig. 3).

Degradation as a result of bacterial activity probably accounts for the major flux of N out of the DON pool in most aquatic systems. Obviously some ON compounds are more labile than others. Many of the intermediate compounds formed (e.g. amino acids from hydrolysis of proteins and peptides, urea from purine breakdown) are taken up and utilized directly by bacteria and phytoplankton. Further breakdown will generate NH_4^+ , which is either assimilated directly by the microbiota or nitrified to NO_3^- . Berman et al. (1999) showed that NH_4^+ and urea were released from indigenous DON compounds in unamended, 1.0 μm filtered marine and freshwaters within several days, presumably as the result of bacterial metabolism.

The ability of some algal species to utilize DON sources such as amino acids and urea has long been known (Pintner & Provasoli 1963, North & Stephens 1967, Wheeler et al. 1973, Antia et al. 1975, Neilson & Larsson 1980). Most of these studies, however, used axenic batch cultures growing on high initial concentrations of ON substrates, thus the ability of organisms to exploit the much lower concentrations of these compounds encountered in the environment *in situ* is unclear. Nevertheless, it seems reasonable that the utilization of DON by different populations of bacteria and phytoplankton can vary considerably. Berman & Chava (1999) observed that different assemblages of dominant phytoplankton developed when they incubated Lake Kinneret water with various added ON sources. These authors suggested that the kind of ON

substrates available in any given environment could influence the species composition of the phytoplankton. Seitzinger & Sanders (1999) also noted that the community composition of phytoplankton differed in growth experiments with estuarine water enriched with rainwater DON (diatoms and or dinoflagellates dominant) or with NH_4^+ (small monads dominant). There is also some evidence that inputs of DON to estuarine and coastal waters stimulated the development of brown tide blooms of *Aureococcus anophagefferens* (Gobler & Sañudo-Wilhelmy 2001, Gobler et al. 2002). Axenic cultures of *A. anophagefferens* were able to hydrolyze a variety of DON compounds (peptides, chitobiose, acetamide and urea) indicating the ability of this organism to exploit these substrates (Berg et al. 2002).

It now appears that in many situations DON can be an important source of phytoplankton N nutrition in the natural environment. For example, Benner et al. (1997) estimated that 30 to 50% of daily phytoplankton N demand in the equatorial North Pacific could be supplied by remineralization of the DON pool. Brown tides off Long Island usually occur in drought years when NO_3^- inputs are reduced and DON concentrations are high relative to DIN (LaRoche et al. 1997). DON was found to be the major source of N for phytoplankton in the Gulf of Riga, Baltic Sea, and may be an important contributing factor to the eutrophication of these waters (Berg et al. 2001). Townsend & Thomas (2002) present data suggesting that DON provides some of the N requirement at the start of the winter-spring phytoplankton bloom on Georges Bank. In Lake Kinneret, a bloom of the cyanobacterium *Aphanizomenon ovalisporum* used the DON pool as its major N source (Berman 1997, 2001). Uptake rates and turnover times for total DON and for some of the major ON constituents in this pool, which have been reported from a variety of marine and freshwater locations, are given in Table 2.

Exposure of dissolved organic matter, in particular humic substances, to sunlight (especially in the UVA and UVB region) results in the photoproduction of biologically available N, including NH_4^+ , dissolved primary amines, and NO_2^- (Bushaw et al. 1996, Moran & Zepp 1997, Bushaw-Newton & Moran 1999, Kieber et al. 1999, reviewed in Bronk 2002). This process has been studied in humic-rich waters from many different locales including boreal ponds in Manitoba, swamps and an estuary in Georgia (Gao & Zepp 1998, Bushaw-Newton & Moran 1999), a Swedish (Jørgensen et al. 1998) and a Venezuelan lake (Gardner et al. 1998), a river and bayou in Louisiana (Wang et al. 2000) and in the Orinoco River plume (Morell & Corredor 2001). Photochemical release may account for considerable N flux from

DON in rivers, near-surface marine waters, and freshwater environments. For example, Bushaw et al. (1996) calculated that the additional input by photo-

chemical release from riverine DON into the SE USA coastal waters increased the available, terrestrially derived N by 20%. Although sunlight was effective in

Table 2. Uptake rates and turnover times of dissolved organic nitrogen (DON) compounds in marine (M) and freshwater (FW) systems. DFAA: dissolved free amino acids

Location	DON form	Uptake rate (nmol N l ⁻¹ h ⁻¹)	Turnover time (d)	Source
Gulf of Riga, Latvia (M)	DON	5.8–56.9		Jørgensen et al. (1999)
Eastern North Pacific (M)	DON	22.5–65.0		Cherrier et al. (1996)
Chesapeake Bay, mesohaline (FW-M)	DON	326.8 ± 111.8		Bronk & Glibert (1993)
Lake Kizaki, Japan (FW)	DON		1.4–21	Haga et al. (2001)
Castle Lake, CA (FW)	DON	54		Zehr et al. (1988)
Lake Kinneret, Israel (FW)	DON	10.9	~70	Berman (2001)
Akkeshi Bay, Japan (M)	DON	4.3–15.0		Hasagawa et al. (2001)
North Sea (M)	Urea	4.9 ± 5.6		Riegman & Noordeloos (1998)
North Sea (M)	Urea	0.3 ± 0.3		Riegman & Noordeloos (1998)
Straits of Georgia, Canada (M)	Urea	7.37 ± 25.6		Cochlan et al. (1991)
South Atlantic—oceanic (M)	Urea	0.5–2.6		Metzler et al. (1997)
South Atlantic—inshore (M)	Urea	21.9–55.9		Metzler et al. (1997)
North of Antarctic Peninsula (M)	Urea	0.5–1.0		Bury et al. (1995)
Bellingshausen Sea (M)	Urea	1.4–9.4		Waldron et al. (1995)
Chesapeake Bay plume (M)	Urea	7.5–660		Glibert et al. (1991)
Chesapeake Bay, mesohaline	Urea	142.3 ± 70.8		Bronk & Glibert (1993)
Chesapeake Bay (FW-M)	Urea	28–332		Lomas et al. (2002)
Shinnecock Bay, Long Island (M)	Urea	3.5–28.6		Berg et al. (1997)
Thames Estuary, UK (FW-M)	Urea	<0.1–7.0		Middelburg & Nieuwenhuize (2000)
Lake Dom Helvicio, Brazil (FW)	Urea	2.1–2.9	7.0–9.0	Mitamura et al. (1995)
Lake Jacare, Brazil (FW)	Urea	0.8–1.9	15–63	Mitamura et al. (1995)
Lake Carioca, Brazil (FW)	Urea	3.0–7.7	4.0–63	Mitamura et al. (1995)
Lake Biwa, Japan (surface) (FW)	Urea		0.6–430	Mitamura et al. (2000)
Lake Okeechobee (FW)	Urea	190 (10–270)		Gu et al. (1997)
<i>Pfiesteria piscicida</i> culture	Urea	2.0–7.9		Lewitus et al. (1999)
Delaware Bay	DFAA	15–600		Coffin (1989)
Gulf of Riga, Latvia (M)	DFAA	0.9–30.8		Jørgensen et al. (1999)
Central Arctic (M)	DFAA	1.3–4.2		Rich et al. (1997)
Chesapeake Bay plume (M)	DFAA	1.0–92.5		Glibert et al. (1991)
Shinnecock Bay, Long Island (M)	DFAA	0.6–7.1		Berg et al. (1997)
Long Island Sound (M)	DFAA	3.8–35.3		Fuhrman (1987)
Thames Estuary, UK (FW-M)	DFAA	6.0–150		Middelburg & Nieuwenhuize (2000)
Santa Rosa Sound, FL (M)	DFAA	39.4		Jørgensen et al. (1993)
Gulf of Mexico (M)	DFAA	5.03 ± 2.12		Jørgensen et al. (1994)
Santa Rosa Sound, FL (M)	DFAA	4.23 ± 0.26		Jørgensen et al. (1994)
Eleven Mile Creek, FL (FW-M)	DFAA	4.50 ± 1.32		Jørgensen et al. (1994)
Plüsee, Germany (FW)	DFAA (in light)	45 (11.7–198) ^a		Münster & Albrecht (1994)
Plüsee, Germany (FW)	DFAA (in dark)	33 (10.8–158) ^a		Münster & Albrecht (1994)
Lake Constance (FW)	DFAA		23.5 (0.9–115)	Rosenstock & Simon (1993)
Lake Constance (FW)	DFAA	<0.1–11.5 ^a	2.6–>50 ^b	Simon (1998)
Flax Pond, NY (FW)	DFAA	73.7		Jørgensen et al. (1993)
<i>Pfiesteria piscicida</i> culture	DFAA	950 ± 400		Lewitus et al. (1999)
Delaware Bay	DCAA	15–600		Coffin (1989)
Lake Constance (FW)	DCAA	<22–28.3	3.6–120	Rosenstock & Simon (1993)
Lake Constance (FW)	Protein		1.0 (<0.3–>3.0)	Rosenstock & Simon (2001)
Santa Rosa Sound, FL (M)	DNA	~8.7		Jørgensen et al. (1993)
Gulf of Mexico (M)	DNA	3.70 ± 0.53		Jørgensen et al. (1994), Kroer et al. (1994)
Santa Rosa Sound, FL (M)	DNA	4.50 ± 0.00		Jørgensen et al. (1994), Kroer et al. (1994)
Eleven Mile Creek, FL (FW-M)	DNA	101.2 ± 12.7		Jørgensen et al. (1994), Kroer et al. (1994)
Gulf of Trieste (M)	DNA		0.4	Turk et al. (1992)
Baltic Sea (M)	DNA		0.7	Turk et al. (1992)
Scripps Pier (M)	DNA		5.9	Turk et al. (1992)

^aRates as nmol C l⁻¹ h⁻¹

^bIncluding winter values

producing NH_4^+ from DON in samples from 2 tidal creeks and the Satilla River, Georgia, USA, this was not the case with surficial (<10 m depth) groundwater, suggesting that the ambient concentrations of NH_4^+ and the source of DON were both important factors in determining the impact of irradiation (Koopmans & Bronk 2002). However, sunlight has also been found to decrease NH_4^+ concentrations (Bertilsson et al. 1999, Wiegner & Seitzinger 2001) possibly as a result of interactions with the dissolved organic matter pool.

An often neglected 'sink' for components of the DON pool is their removal by adsorption to colloids (Schuster et al. 1998), sub-micron particles (Nagata & Kirchman 1996), very small particles such as transparent exopolymer particles (TEP; Alldredge et al. 1993) or Coomassie Blue proteinaceous particles (Long & Azam 1996). Significant quantities of ON compounds, such as amino acids and proteins, may be removed from solution by adsorption to particles, although they remain susceptible to exploitation by particle-associated bacteria and protists.

INDIVIDUAL ORGANIC N COMPOUNDS

The DON pool is a heterogeneous mixture of compounds that varies widely in space and time within the aquatic environment. The bulk of the ambient DON pool at any given time may consist of compounds that are relatively recalcitrant to biological, chemical or physical degradation, simply because the more labile and biologically available constituents are rapidly broken down and utilized (Gardner et al. 1996).

Below, we discuss some of the better-characterized constituents of the DON pool: urea, DFAA, DCAA and proteins, nucleic acids, amino sugars, and humic substances.

Urea

There has been some debate whether urea should be included as a component of the DON pool (Jørgensen et al. 1999, Capone 2000). We recommend that urea, the compound that had the distinction of being the accidental product of the 'first organic synthesis' by Wöhler in 1828, should be classified within the DON fraction for the sake of both consistency and continuity. Irrespective of semantics, urea is found ubiquitously in natural waters, sometimes in reasonably high concentrations, and is often a significant source of N and C for aquatic microbiota (see below).

Urea assays

Two methods have been used to determine urea concentrations in natural waters: (1) Complexation of urea with diacetyl monoxime to give an imidazolene that forms a red complex with thiosemicarbazide (Newell et al. 1967, Koroleff 1983, Mulvenna & Savidge 1992, Goeyens et al. 1998). (2) An enzymatic method based on hydrolysis of urea in the presence of added urease and subsequent determination of released NH_4^+ (McCarthy 1970). A study comparing these 2 techniques indicated that the enzymatic method tended to underestimate urea concentrations because urease activity was inhibited in some samples (Price & Harrison 1987).

Urea sources

Urea is produced by water column bacteria (Cho et al. 1996, Therkildsen et al. 1997), excreted by marine and freshwater teleost fish, cetaceans, cryptomonads, herbivorous marine and freshwater zooplankton, bivalve mollusks, freshwater crabs (Antia et al. 1991, Conover & Gustavson 1999, Wiltshire & Lampert 1999), protists (Johannes 1965), prawns (Chen & Cheng 1993), calanoid copepods (Miller & Glibert 1998) and likely by many other organisms. The degradation of purines and arginine through bacterial action can also give rise to urea (Antia et al. 1991, Berman et al. 1999), and urea may be released into the water column from sediments (Burdige & Zheng 1998, Thomsen & Jahmlich 1998). Rainfall, dust and atmospheric aerosols are further sources of urea (Timperley et al. 1985), although a recent study concluded that urea is not always a major DON constituent in wet deposition (Cornell et al. 1998).

Human-derived pollution and runoff from agricultural areas are important additional sources of urea in many lakes, reservoirs, estuaries and coastal waters. Urea accounts for ca. 40% of the total N fertilizer used globally (Matthews 1994). For example, long-term studies in Chesapeake Bay have found that external inputs of urea from the watershed are extremely significant in this estuarine system (Lomas et al. 2002).

The highest concentrations of urea in aquatic systems are frequently found at the surface of sediments. However, urea efflux from sediment only accounts for a minor fraction of sediment urea production (Lomstein et al. 1989, Therkildsen & Lomstein 1994), most of which is mediated by bacteria (Pedersen et al. 1993). Purines and pyrimidines, but not protein, were important substrates for urea generation in an anoxic coastal sediment (Therkildsen et al. 1996). This report would suggest that there is an as yet unknown metabolic

pathway of urea production from pyrimidines by bacteria in anaerobic sediments. Urea concentrations in Chesapeake Bay were generally higher but more variable in samples taken from ~1 m above the sediment than in surface samples (Lomas et al. 2002). High concentrations of urea (5.0 to 9.3 $\mu\text{M N}$) were also found in the surface films of lake and coastal waters (Saijo et al. 1974).

Although urea generally constitutes only a small percentage of DON in natural waters, it contributed from 60 to 80% of the N utilized during much of the year in the plume of Chesapeake Bay, and up to 50% in many other coastal regions (Harrison et al. 1985, Kokkinakis & Wheeler 1988, Glibert et al. 1991). We emphasize that the ambient concentrations of urea measured at any given time do not necessarily relate to the actual N flux passing through the urea pool.

Urea sinks

The potential importance of urea as a N source for phytoplankton in a variety of aquatic environments is well documented (McCarthy 1972, Horrigan & McCarthy 1981, Mitamura & Matsumoto 1981, McCarthy et al. 1982, Mitamura & Saijo 1986, Price & Harrison 1988, Mitamura et al. 1994, 1995, 2000, Glibert et al. 1995, Maguer et al. 1996, Bronk et al. 1998, Shaw et al. 1998, Berman & Chava 1999). Macrophytes, such as eel grass *Zostera capricorni* (Hansen et al. 2000), and benthic microbial mats (Rondell et al. 2000) can also use urea as a source of N. Although urea might be considered an 'ideal' N substrate, the relative preference index of McCarthy et al. (1977) indicates that the sequence of uptake rates *in situ* is usually $\text{NH}_4^+ > \text{urea} > \text{NO}_3^-$. Possibly the small size of the NH_4^+ ion facilitates its passage across cell membranes while a more energy-expensive, active transport system may be required to move urea into the cell (Price & Harrison 1988). Another reason for lower urea utilization may be the energetic costs of synthesizing urease needed to hydrolyze this substrate.

Some phytoplankton species show preferential growth with urea as the sole source of N, compared to growth on NH_4^+ , NO_3^- or other ON compounds (Berman & Chava 1999). There are also intriguing hints that urea may be a major N source for both marine and freshwater *Synechococcus* (Berman & Chava 1999, Collier et al. 1999, Mitamura et al. 2000, Sakamoto & Bryant 2001) as well as for other cyanobacteria. Preferential uptake by picophytoplankton of urea and NH_4^+ over NO_3^- was observed in Antarctic surface waters (Probyn 1985), in Lake Biwa (Mitamura & Saijo 1986, Mitamura et al. 2000), and in 3 Brazilian lakes (Mitamura et al. 1995), where turnover times for

urea ranged from 4 to 41 d during the dry season and 3 to 560 d during the wet season (Table 2).

Urea was a significant N source for phytoplankton in reservoirs of the Han River system in Korea and was decomposed more effectively by algae than by bacteria (Mitamura et al. 1989). Studies in estuarine and coastal systems have also found that N uptake from urea was predominantly by phytoplankton rather than by bacteria (Remsen et al. 1972, Savidge & Hutley 1977, Savidge & Johnston 1987, Cho & Azam 1995, Cho et al. 1996, Tamminen & Irmisch 1996, Lomas et al. 2002). In contrast, bacterial, rather than phytoplankton, uptake of urea predominated in Finnish coastal waters (Tamminen & Irmisch 1996), Danish estuarine and coastal waters (Jørgensen et al. 1999), and in the River Thames (Middelburg & Nieuwenhuize 2000).

Urea may have effects on phytoplankton in addition to serving as a direct source of N. Wiltshire & Lampert (1999) reported that urea excreted by the freshwater cladoceran *Daphnia* induced colony formation in the chlorophyte *Scenedesmus obliquus*.

Bacteria have long been known to mineralize urea, both in the ocean (Cho et al. 1996) and in lakes (Satoh et al. 1980). In Californian coastal waters, urea regeneration rates by bacteria were ~100-fold greater than for urea uptake (Cho et al. 1996). Temporal differences between production and uptake may account for some of the wide variability often shown in urea concentrations in natural waters (McCarthy 1972, McCarthy & Kamykowski 1972, Berman 1974). In contrast, other studies have found close coupling between urea production and uptake (Hansell & Goering 1989, Lomas et al. 2002).

Measurements of urea uptake by phytoplankton and bacteria have generally relied on the use of ^{15}N -tagged substrates. By using simultaneous additions of dual-labeled urea (^{15}N and ^{14}C), Hansell & Goering (1989) were able to correct for problems of isotope dilution and thus improve estimates of rates of urea production and uptake by natural phytoplankton in the Bering Sea. Their results indicate that urea is in a dynamic steady state, with rates of *in situ* urea production approximately equal to consumption. In another study using this technique, Bronk et al. (1998) found that not correcting for urea isotope dilution sometimes resulted in a substantial underestimate of urea uptake rates, and that urea regeneration was generally a small, but highly variable, source of N.

Recently Peers et al. (2000) showed that a constitutive urease activity was present in the marine diatoms *Thalassiosira pseudonana* and *T. weissflogii* regardless of N source. Urease activity in *T. weissflogii* was unaffected by iron limitation but sensitive to that of nickel (Milligan & Harrison 2000). Nickel is a constituent of

the active site of algal and cyanobacterial ureases, and has been shown to be an essential micronutrient for urea utilization by marine *Synechococcus* (Sakamoto & Bryant 2001) and by freshwater *Anabaena cylindrica* (Mackerass & Smith 1986).

Many species from all major phytoplankton taxa of freshwater and marine phytoplanktonic algae (Antia et al. 1991) and cyanobacteria (Berns et al. 1966) can use urea effectively as a source of N for growth. Some of these species have a somewhat notorious reputation as 'nuisance algae' and may cause toxic blooms. Potential uptake of urea by the brown tide chrysophyte, *Aureococcus anophagefferens*, was substantially greater than uptake of other N substrates including NH_4^+ , a mixture of amino acids, or NO_3^- (Berg et al. 1997). This ability to exploit urea may have contributed to the recent prevalence of *Aureococcus* blooms in NE USA coastal waters (Duzurica et al. 1989, Berg et al. 1997, LaRoche et al. 1997) although this may not always be the case (Gobler & Sañudo-Wilhelmy 2001).

Other toxic dinoflagellates that can utilize urea include *Gymnodinium breve* (Steidinger et al. 1998; now renamed *Karenia brevis*) and *Pfiesteria piscicida* (Lewitus et al. 1999). High levels of urea ($>1.5 \mu\text{M N}$) were found concomitantly with dinoflagellate blooms in commercial hybrid striped bass aquaculture ponds (Glibert & Terlizzi 1999), suggesting that urea specifically stimulated growth of *G. galatheanum*, *G. nelsonii*, *Prorocentrum minimum* and *Katodinium*. The high abundance of dinoflagellates may also have enhanced urea excretion by the fish in these ponds. A potentially toxic cyanobacterium, *Aphanizomenon ovalisporum*, isolated in non-axenic cultures from Lake Kinneret, grew optimally on urea as the sole N source. Mass balance determinations indicated that this organism utilized mostly DON as a direct or indirect source of N rather than N_2 fixation when it developed into a bloom in the lake in 1994 (Berman 1997, 2001).

We suggest that urea may be a more important source of N nutrition for aquatic microbiota in both freshwater and marine environments than has been generally appreciated. Further investigation of the role played by urea as a source of N nutrition in natural waters is certainly warranted.

DFAA, DCAA, and proteins

The importance of DFAA as sources of C, N and energy for both marine and freshwater heterotrophic bacteria has long been known (Williams et al. 1976, Zehr et al. 1985, Wheeler & Kirchman 1986). Release and uptake of amino acids tend to be closely linked (Fuhrman 1987) so that ambient concentrations of DFAA are usually very low and represent only a

small fraction of measured DON. Nevertheless, DFAA probably account for a substantial fraction of the N flux into and out of the DON pool. Although bacteria are still assumed to be the major clients for utilizing DFAA in aquatic environments, it is now apparent that many phytoplankton species can also use amino acids as N sources (Table 3), most probably by virtue of possessing cell surface amino-oxidases (Palenik & Morel 1990a,b, 1991, Pantoja & Lee 1994, Mulholland et al. 1998). These enzymes hydrolyze amino acids externally to NH_4^+ , which is then taken up by the cell.

The pool of DCAA compounds (containing proteins, oligopeptides, polypeptides, and humic-bound amino acids; Hubberten et al. 1995) often comprises the largest identifiable portion of DON pools. Three main components of the DCAA fraction have been proposed (Keil & Kirchman 1993): (1) a rapidly cycling (hours to days) protein, similar to that freshly extracted from phytoplankton; (2) a more recalcitrant, abiotically glucosylated protein that is very resistant to degradation; and (3) a pool of non-proteinaceous compounds, perhaps consisting of amino acids bound or adsorbed to humic substances or to small particles (Hubberten et al. 1994).

In the ocean, dissolved protein concentrations are low in surface waters, and increase below the euphotic zone (Bronk 2002). In some reports of dissolved protein determinations in German and Japanese lakes (Steinberg 1977, Hama & Handa 1980, 1983), between 55 and 74% of the proteins and polypeptides were <5 kDa. By contrast, most of the dissolved protein in the ocean appears to have a much higher MW. Some, as yet unquantified, portion of this pool consists of a ubiquitous, dissolved protein (MW 48kDa) that may be derived from porin-P, part of the phosphorus transport system in gram-negative bacterial cell walls (Tanoue 1995, Tanoue et al. 1995, 1996).

DFAA, DCAA, and protein assays

The most commonly used method for quantifying DFAA is based on pre-column derivatization with ortho-phthalaldehyde (OPA), followed by separation with HPLC (Lindroth & Mopper 1979, Mopper & Lindroth 1982). A flow injection method to determine the concentrations of primary amines in seawater gave results comparable to HPLC separation (Delmas et al. 1990, Petty et al. 1992). An alternate derivatization technique using 6-aminoquinolyl-N-hydroxysuccinimidyl carbamate that detected both primary and secondary amines was insensitive to amino acid concentrations below 200 nM (Jørgensen & Jensen 1997). These authors noted, however, that derivatization

procedures, such as with OPA, which tag only the primary amines, underestimate levels of DFAA and DCAA in natural waters.

Several approaches have been used to hydrolyze DCAA to DFAA. The original acid hydrolysis with 6N HCl required 20 h at 110°C (Parsons et al. 1984). A vapor phase hydrolysis method (Tsugita et al. 1987) was modified by Keil & Kirchman (1991a,b), who found that the modified technique gave up to 3-fold higher DCAA concentrations than the method of Parsons et al. (1984). The vapor phase technique, combined with microwave radiation, was used by Jørgensen & Jensen (1997) to achieve simultaneous hydrolysis of 20 samples in 20 min. In all cases, after hydrolysis of the DCAA, the total dissolved amino acids (i.e. DCAA plus

DFAA) in the sample were quantified by pre-column derivatization and separation by HPLC. The DCAA concentration was then obtained by subtracting DFAA, measured in the same, non-hydrolyzed water sample, from the concentration of DCAA plus DFAA.

Few studies have attempted to quantify or characterize dissolved proteins in natural waters. In order to isolate and identify a range of dissolved proteins in seawater from the Indian and Antarctic Oceans, Tanoue and colleagues (Tanoue 1995, Tanoue et al. 1995, 1996) used tangential-flow ultrafiltration, concentration and purification by precipitation with trichloroacetic acid and final separation with sodium dodecylsulphate-polyacrylamide gel electrophoresis (SDS-PAGE). Immunochemical methods were applied to further

characterize these dissolved proteins (Suzuki et al. 1997). Note that these methods are qualitative and do not provide concentrations of proteins *in situ*. The availability of new fluorescent tags such as Nano-orange (Molecular Probes) may lead to more sensitive and reliable methods for dissolved protein measurements.

Sources of DFAA, DCAA, and proteins

DFAA and DCAA are released from living phytoplankton directly (Mykkestad et al. 1989, Bronk & Glibert 1993a,b, Bronk et al. 1994), as well as by viral lysis or autolysis of senescent algae (Gardner et al. 1987, Sundh 1992, Agusti et al. 1998). Zooplankton generate these compounds through sloppy feeding, excretion and upon dissolution of their fecal material. Protists grazing on bacteria may also produce significant amounts of DCAA (Ferrer-Pagés et al. 1998, Rosenstock & Simon 2001). Release of DFAA and DCAA may occur from the solubilization of organic seston, of marine or lake snow particles, or transparent proteinaceous particles (Long & Azam 1996, Grossart & Simon 1998, Berman & Viner-Mozzini 2001).

The most detailed study of seasonal and vertical dynamics and turnover of DFAA and DCAA in freshwaters was made by Simon and colleagues (Simon 1998, Simon & Rosenstock 1992, Rosenstock & Simon 1993, 2001, Simon et al. 1998) in Lake Constance, Germany. Maximum DFAA release was in winter until the onset of the spring phytoplankton bloom.

Table 3. Freshwater and marine phytoplankton utilizing amino acids as nitrogen sources in axenic cultures. M: marine; FW: freshwater

Organism	System	Source
Chrysophyta		
<i>Cyclotella cryptica</i>	M	Liu & Hellebust (1974)
<i>Phaeodactylum tricornutum</i>	M	Flynn & Syrett (1986)
<i>Navicula incerte</i>	M	Landymore & Antia (1977)
<i>N. pavillardi</i>	M	Lewin & Hellebust (1975)
<i>Nitzschia angularis</i>	M	Lewin & Hellebust (1976)
<i>N. ovalis</i>	M	Lewin & Hellebust (1978)
<i>Skeletonema costatum</i> ^a	M	Fisher & Cowdell (1982)
<i>Asterionella japonica</i> ^a	M	Fisher & Cowdell (1982)
<i>Nitzschia closterium</i> ^a	M	Fisher & Cowdell (1982)
<i>Coscinodiscus</i> sp. ^a	M	Fisher & Cowdell (1982)
<i>Fragilaria</i> sp. ^a	M	Fisher & Cowdell (1982)
<i>Chaetoceros debile</i>	M	Poulet & Martin-Jezequel (1983)
<i>Melosira mediocris</i>	FW	Ming & Stephens (1985)
Haptophyta		
<i>Isochrysis galbana</i>	M	Landymore & Antia (1977)
<i>Prymnesium parvum</i>	M	Palenik et al. (1988)
<i>Emiliana huxleyi</i>	M	Palenik & Henson (1997)
Chlorophyta		
<i>Platymonas subcordiformis</i>	M	North & Stephens (1969)
<i>Chlorella vulgaris</i>	FW	Pettersen & Knutsen (1974)
<i>C. fusca</i>	FW	Richards & Thurston (1980)
<i>Chlamydomonas reinhardtii</i>	FW	Kirk & Kirk (1978a)
<i>Volvox carteri</i>	FW	Kirk & Kirk (1978b)
<i>Pandorina morum</i>	FW	Kirk & Kirk (1978c)
<i>Scenedesmus obliquus</i>	FW	Kirk & Kirk (1978c)
<i>Ankistrodesmus braunii</i>	FW	Kirk & Kirk (1978c)
<i>Tetraselmis subcordiformis</i>	M	Qafaiti & Stephens (1988)
<i>Pediastrum duplex</i>	FW	Berman et al. (1991)
<i>Scenedesmus</i> sp.	FW	Berman et al. (1991)
Cyanobacteria		
<i>Anabaena variabilis</i>	FW	Theil (1988)
<i>Anacystis nidulans</i>	FW	Lee-Kaden & Simonis (1982)
<i>Agmenellum quadruplicatum</i>	M	Kapp et al. (1975)
Pyrrophyta		
<i>Gymnodinium breve</i>	M	Baden & Mende (1979)
<i>Alexandrium fundyense</i>	M	John & Flynn (1999)

^aMay not have been bacteria-free cultures

DCAA and protein peaked during the spring and summer algal blooms. Protein accounted for 1 to 31% of DCAA (Rosenstock & Simon 2001). These authors also give a detailed analysis of the seasonal changes of the LMW and HMW fractions of the DCAA pool in this lake. The microplankton fraction (1 to 140 μm), especially phytoplankton and ciliates, was always the major source of DFAA and protein. A somewhat similar pattern was observed in 2 Swedish lakes where DFAA were preferentially released in spring, in contrast to more protein appearing during summer (Sundh 1992).

Sinks for DFAA, DCAA, and proteins

Much is known about the turnover of DFAA and their significance for growth of heterotrophic bacteria in both freshwater and marine environments (Gardner & Lee 1975, Williams et al. 1976, Jørgensen 1982, 1987, Gardner et al. 1987, 1998, Keil & Kirchman 1991a,b, Simon & Rosenstock 1992, Jørgensen et al. 1993, Middelboe et al. 1995). Recently Ouverney & Fuhrman (2000) reported the significant finding that marine Archaea are also capable of taking up amino acids at nanomolar levels.

Extensive dependence of marine heterotrophic bacteria on DFAA and DCAA has been documented in estuarine and coastal waters in Long Island Sound (Fuhrman 1987), Delaware Estuary (Coffin 1989, Middelboe et al. 1995), Chesapeake Bay (Fuhrman 1990), the Mississippi River plume (Cotner & Gardner 1993), as well as in pelagic waters (subarctic Pacific; Kirchman et al. 1989a,b, Keil & Kirchman 1991a,b). DFAA were used preferentially to DCAA unless the concentration of the former was very low (Keil & Kirchman 1991a,b). This may have been the situation in the extremely oligotrophic surface waters of the Northern Sargasso Sea, where protein was the dominant form of ON utilized for bacterial production (25 to 60%; Keil & Kirchman 1999). In locations where DFAA concentrations were high with rapid turnover, or when DFAA turnover exceeded bacterial N demand, high rates of NH_4^+ regeneration were often observed (Kirchman et al. 1989a,b, Keil & Kirchman 1991a,b, Cotner & Gardner 1993, Gardner et al. 1993).

In some environments, DCAA were of equal or even greater importance than DFAA for bacterioplankton growth (Coffin 1989, Coffin et al. 1993, Kroer et al. 1994, Rosenstock & Simon 2001). In Lake Constance, DCAA and DFAA supported 45 and 13% of bacterial biomass production, respectively (Rosenstock & Simon 2001), as an annual average. The sum of DFAA and protein supported 58% of bacterial C and 80% of bacterial N demands (Rosenstock & Simon 2001). There is 1 report of bacterial utilization of DCAA, mostly bound

to humic substances, in a Pennsylvania stream (Volk et al. 1997).

As shown in Table 3, many marine and freshwater algae can grow on amino acids as N sources (reviewed in Flynn & Butler 1986); additional earlier data are also given in Antia et al. (1975), Turner (1979), and Neilson & Larsson (1980). Care must be taken in extrapolating results from culture experiments to the real environment if unrealistically high concentrations of organic substrates were used. For example, although the toxic dinoflagellate *Alexandrium fundyense* could assimilate a wide range of amino acids, with uptake being greatest during the exponential phase (Ogata et al. 1996), this organism was incapable of using amino acids for growth (John & Flynn 1999). Nevertheless, the discovery of cell surface amino-oxidases in many phytoplankton species (Palenik & Morel 1990a,b, Pantoja & Lee 1994) suggests that amino acids can indeed serve as N sources for algae in aquatic systems (Mulholland et al. 1998).

There is a dearth of information on the fate of dissolved protein in natural waters. Some proteins are undoubtedly degraded enzymatically to peptides and DFAA (Hollibaugh & Azam 1983, Pantoja & Lee 1999a,b), and some are transformed to recalcitrant organic forms (Keil & Kirchman 1994). Curiously, there is 1 report of heterotrophic flagellates using dissolved proteins (ferritin, casein, albumin, and concavalin A) as a direct source of nutrition (Tranvik et al. 1993). We have no idea how widespread or important this process might be, but this observation raises the interesting possibility that members of the planktonic community, other than bacteria and phytoplankton, can use proteins and other constituents of the DON pool.

Nucleic acids and their breakdown products

Nucleic acids, and degradation products such as nucleotides, purines and pyrimidines, are relatively neglected constituents of DON pools. Dissolved DNA and RNA (dDNA and dRNA) are part of the general pool of HMW DON, and would be expected to result from cell lysis, sloppy zooplankton feeding, and protistan grazing (Weinbauer & Peduzzi 1995a,b, Ishii et al. 1998, Kawabata et al. 1998). In a 2-stage chemostat experiment, Turk et al. (1992) showed that nanoflagellates grazing on bacteria released dDNA. Pioneering studies of dDNA and particulate DNA dynamics in marine and freshwater environments were published by Paul et al. (1988, 1989) and others (Beebee 1991, De Flaun et al. 1987, Karl & Bailiff 1989).

Reported concentrations of dDNA in marine and freshwaters range from several to $\sim 100 \mu\text{g N l}^{-1}$ (Paul et al. 1987, Bailiff & Karl 1991, Ishii et al. 1998). How-

ever, in a recent study, Siuda & Chrost (2000) pointed out some difficulties in quantifying the concentrations of dDNA. A considerable, but not easily defined, part of total dDNA may be adsorbed on particles or colloids and substantial proportions of measured dDNA may actually derive from viral DNA that has passed through 0.45 or 0.2 μm filters (Beebee 1991, Weinbauer & Peduzzi 1995b).

D-DNA assays

Four analytical methods have been used to quantify ambient concentrations of dDNA in natural waters: (1) Staining with Hoechst dye (De Flaun et al. 1986). (2) Precipitation with CTAB (cetyltrimethyl-ammonium bromide) followed by fluorometric detection after staining with DAPI (4,6 diamidino 2 phenylindole; Karl & Bailiff 1989, Siuda & Güde 1996a). (3) Measuring the decrease in DAPI fluorescence upon enzymatic hydrolysis of dDNA by DNase (Siuda & Chrost 2000). This method is believed to obviate overestimates (from 27 to 54%) of actual DNA concentrations as given by the CTAB technique and to give a more appropriate measure of 'available' dDNA. (4) Detection with ethidium bromide (Sakano & Kamatani 1992).

D-DNA sinks

Paul et al. (1989) were the first to measure *in situ* dDNA turnover using ^3H -DNA in oligotrophic and eutrophic subtropical Florida lakes. The turnover rates were rapid (~ 10 h) in both systems. Similarly rapid turnover times for dDNA were reported in Lake Constance (Siuda & Güde 1996a). Slower rates were found for the hydrolysis of plasmid DNA added to river and marine waters (Alvarez et al. 1996) or to epilimnetic waters in Lake Biwa, Japan (Matsui et al. 2001). In the latter case, the dDNA rapidly lost its transformation ability and was completely hydrolyzed after 170 h. This observation was consistent with earlier results (Paul et al. 1988) showing that DNA gene sequences from added DNA were not assimilated by estuarine bacteria. By contrast, in the hypolimnion of Lake Biwa, exogenous dDNA was not perceptibly degraded, and seeded plasmid DNA did not lose its transformation efficiency even after 170 h (Matsui et al. 2001). This result raises the possibility that dDNA may be stable in hypolimnetic lakes or deep marine waters for a relatively long time (weeks or more), and thus may remain capable of causing genetic transformation. It is therefore feasible that recombinant DNA from genetically modified microorganisms, released intentionally or unintentionally, might retain its transformation

potency for extended periods in hypolimnetic or deep aquatic environments.

In studies with seawater bacterial cultures, Jørgensen et al. (1993) found that dDNA could supply up to 5 and 10% of the bacterial C and N requirement, respectively, in batch cultures of marine bacteria. However, most studies have focused on dDNA (C:N:P ratio, 10:4:1) in marine and freshwaters as a potential source of phosphorus rather than N nutrition (Siuda & Güde 1996b). Degradation of dDNA was rapid in a P-limited region of the Adriatic Sea, but much slower in an N-limited region of the Californian Bight (Turk et al. 1992).

The incorporation of dDNA by natural bacteria in estuarine microcosms was also studied by Jørgensen & Jacobsen (1996). When no nutrients were added, dDNA supplied 6, 8 and 46% of bacterial C, N and P requirements, respectively. Tests of uptake preference by the bacterioplankton for DNA of different sizes (100, 250 and 569 bp) showed that the smallest fragments were the most readily utilized.

With 2 exceptions (Koenings & Hooper 1973, Sakano & Kamatani 1992), there do not appear to be any studies of dRNA in natural waters.

Nucleotides and derivatives

The dissolved nucleotide that has received the most research attention has been ATP (Azam & Hodson 1977). Bjørkman & Karl (2001), using a new method to measure dissolved ATP and GTP (guanosine tri-phosphate), reported concentrations of 70 ng l^{-3} in summer and ~ 30 ng l^{-3} in winter of dissolved ATP in the 0 to 100 m layer of the oligotrophic North Pacific Ocean (Stn Aloha). Although active cycling of nucleotides and their purine bases probably occurs, this process may be more important in providing P rather than N to the microplankton.

Purines and pyrimidines and their derivatives are also potentially significant DON compounds. Purines, such as guanine and hypoxanthine, are rapidly degraded to yield urea and/or NH_4^+ that can be easily used by phytoplankton and bacteria (Antia et al. 1980, 1991, Berman et al. 1999). Pyrimidines are also degraded but seem to be less effectively taken up by microbiota than purines (Antia et al. 1991). No data concerning the rates of cycling of these compounds in aquatic systems are available, but this pathway of N flux may be important in some environments (Antia et al. 1980).

Hypoxanthine, guanine, uric acid and their derivatives (e.g. allantoinic acid) can support microalgal growth N requirements for many algal taxa (Droop 1961, Guillard & Ryther 1962, Guillard 1963, Antia & Chorney

1968, Kapp et al. 1975, Oliveira & Huynh 1990, Lisa et al. 1995, Berman & Chava 1999). One source for these purines may be excretion from ciliates (Antia et al. 1980). Cytoplasmic inclusions composed mainly of hypoxanthine and guanine were isolated from the marine hymenostome ciliate *Parauronema acutum* (Soldo et al. 1978). Guanine, hypoxanthine, adenine and dihydro-uracil were excreted from freshwater ciliates, such as species of *Paramecium* (Soldo & Van Wagtendonk 1961). Berman et al. (1987) observed the release of ATP in 'reconstituted' seawater cultures containing bacteria, pico-phytoplankton and heterotrophic flagellates. We are not aware of any more recent studies that have investigated the release of purines or related ON compounds from protists in aquatic environments.

Amino sugars

There have been few studies of dissolved amino sugars in aquatic environments. Amino sugars may be produced as breakdown products of bacterial, cyanobacterial and algal cell walls, chitin, and microbial and fish mucus (Blackwell et al. 1967, Sutherland 1985, Nakagawa et al. 1988, Bertocchi et al. 1990, Decho 1990). Amino sugars have been found in lakes (Göcke 1970, Steinberg 1977, Bunte & Simon 1999), reservoirs (Hejzlar 1989), and rivers (Ittekkot et al. 1982, Chudoba et al. 1986). In contrast to freshwater, amino sugars in marine systems cannot be detected by ion-exchange HPLC and the pulsed amperometric method used for dissolved monosaccharides (Mopper et al. 1992) because they are selectively removed in the desalting step prior to HPLC (M. Simon pers. comm.). However, McCarthy et al. (1998) determined amino sugars in marine HMW DON using thermal desorption-mass spectrometry and pyrolysis.

The reported concentrations of amino sugars (predominantly glucosamine and N-acetyl-glucosamine) range from about 10 to 100 $\mu\text{g l}^{-1}$, somewhat lower but in the same order of magnitude as levels of amino acids. Nedoma et al. (1994), using a modification of the method of Barnes (1984), reported concentrations of dissolved amino sugars ranging from ~20 to 1200 $\mu\text{g l}^{-1}$ in 2 mountain lakes, 2 reservoirs, 2 river backwaters and 2 highly eutrophic fishponds. Approximately 42% of the dissolved amino sugars in the Rimov Reservoir, Czech Republic, consisted of N-acetyl-glucosamine and glucosamine (Hejzlar 1989). Other amino sugars identified were 2-amino-2-deoxygalacturonic acid and fucosamine, probably originating from bacterial cell walls. Using autoradiography, Nedoma et al. (1994) showed that microorganisms (bacteria, cyanobacteria and diatoms), capable of taking up N-acetylglucosamine, were present in all the water bodies studied. Overall, the in-

ference from this work is that glucosamine and N-acetylglucosamine could be important bacterial substrates for organic C and N in some aquatic environments. Early studies by Antia & Chorney (1968) and Berland et al. (1976) showed that many species of marine algae could use glucosamine for N nutrition. Several non-axenic freshwater algal cultures also grew successfully on this compound as a sole N source (Berman & Chava 1999).

Humic substances

Variable, but often substantial, proportions of DON are comprised of poorly characterized humic substances falling into 2 operationally defined categories: humic acids, insoluble at $\text{pH} < 2.0$ and obtained by retention on XAD-8 resin, and fulvic acids, separated with XAD-4 resin (Aiken 1985, 1988). Schnitzer (1985) identified 2 types of nitrogenous humic components: (1) a major fraction consisting of LMW N compounds (such as amino acids, purines, pyrimidines) loosely held by, or adsorbed to, the humic core structure, and (2) an N fraction that is integral to the humic molecule itself (Lytle & Perdue 1981). Presumably only the first humic component is actively involved in short-term N flux. Most humic compounds in freshwater and coastal environments are of terrestrial origin, but some of them in pelagic oceans and large lakes may be derived from organic matter produced autochthonously.

Not much is known about the potential of humic substances to serve as a source of N for planktonic microbiota, although it now appears that they may be somewhat less refractory than previously believed (Amon & Benner 1994, Moran & Hodson 1994a,b, Gardner et al. 1996). Humic bound DCAA has been shown to be at least partially available to bacteria (Hubberten et al. 1994, 1995, Volk et al. 1997, Amon et al. 2001). Some attention has been focused on the potential impact of these compounds on phytoplankton development in coastal waters. Increasing amounts or different types of humic compounds derived from human activities may have caused eutrophication and the proliferation of toxic dinoflagellates in these waters. The N bound to humic substances may be directly available to some algal groups, such as dinoflagellates (Granéli et al. 1985, Carlsson & Granéli 1993, Carlsson et al. 1993). When humic material, isolated from a river, was added to a phytoplankton assemblage from a Swedish fjord, both bacterial and algal production were stimulated (Carlsson et al. 1993). In this instance, the bacteria used both C and N from the humic compounds directly for growth; subsequently, the phytoplankton exploited the regenerated DON and NH_4^+ . As yet, these studies have been limited to estuarine and coastal waters in the Baltic Sea and the Atlantic coast of the USA.

UTILIZATION OF MULTIPLE N SOURCES

A somewhat neglected topic is the simultaneous uptake and utilization of mixtures of N substrates (organic or inorganic/organic) by phytoplankton (Antia et al. 1991). With some exceptions (Pintner & Provasoli 1963, Pettersen 1975, Flynn & Wright 1986, Collos 1987), few studies have examined how algae or bacteria respond to multiple ON sources, although this situation corresponds more closely to real life environments than experiments with uptake of only a single ON source. The inhibitory effects of NH_4^+ on urea and DFAA uptake have been extensively documented but, as yet, little is known about the interplay of various DON sources that are used by phytoplankton in environments with limited DIN availability. Ricketts (1988) studied the separate and combined uptake and assimilation of NH_4^+ , NO_3^- , urea, and glycine in the marine prasinophyte, *Tetraselmis strata*, and concluded that this organism maintained a relatively constant rate of total N-assimilation, irrespective of the mixture of utilizable N-sources. In eutrophic Lake Okeechobee, Florida, Gu et al. (1997) analyzed total N utilization by a summer cyanobacterial bloom and found that 53% of the uptake was from NH_4^+ , 19% was from NO_3^- , 16% was from urea, and 12% was by N_2 fixation. The growth of a bloom of *Aphanizomenon ovalisporum* in Lake Kinneret used DON and DIN in a ratio of ~4:1 for N supply, with only a minor amount of the N requirement derived from N_2 fixation (Berman 1997, 2001). A similar situation was reported in Glebokie Lake, Poland, where cyanobacterial growth was mainly supported by DON with only a small proportion contributed by N_2 fixation (Krupka 1989). Presumably the higher energetic costs involved in fixing N_2 compared to using reduced N in organic compounds will dispose azotrophic cyanobacteria to exploit suitable DON sources preferentially if these are available.

There have been several studies of the use of multiple N sources by marine bacteria (Middelboe et al. 1995, Jørgensen et al. 1999). Tupas & Koike (1990) examined the differential uptake of NH_4^+ and DON (mostly DCAA) by natural bacterial assemblages in seawater cultures that were enriched with dissolved substances released by the mussel *Mytilus edulis*. Even when large amounts of DON were utilized, NH_4^+ continued to be taken up and incorporated into the bacterial cells. Simultaneous assimilation and regeneration of NH_4^+ occurred, contradicting the idea that NH_4^+ utilization occurs in natural bacterial populations only when ON is limiting. Middelboe et al. (1995) found that bacterial populations in batch cultures from the Delaware Bay Estuary derived very different proportions of their N requirements from DFAA, DCAA and NH_4^+ depending on whether they were C- or N-

limited, or in the exponential growth phase. In Santa Rosa Sound, DFAA were the dominant N source for bacteria, followed by DCAA and then NH_4^+ (Jørgensen et al. 1999).

In Lake Constance, Simon & Rosenstock (1992) and Rosenstock & Simon (1993) followed the simultaneous bacterial uptake of NH_4^+ , DFAA and DCAA and found distinct seasonal patterns. As noted by Simon & Rosenstock (1992), when studying the bacterial use of multiple N substrates it is important to consider the availability of NH_4^+ and carbohydrates versus amino acids and, in addition, the molar percent of available DFAA and DCAA relative to the amino acid requirements for protein synthesis. DFAA and DCAA are taken up without any NH_4^+ regeneration if the molar percent composition of the amino acid pool is similar to the amino acid requirements for protein synthesis. When 1 or a few amino acids are assimilated in excess, they are deaminated to release NH_4^+ . Simon (1991) and Simon & Rosenstock (1992) used the mole percent composition of the bacterial intracellular amino acid pools and the intracellular isotope dilution of individual DFAAs to estimate the relative importance of NH_4^+ and DFAA in bacterial N uptake.

A particularly interesting and ecologically significant case of uptake of multiple N sources is that of *Trichodesmium* (reviewed in Mulholland & Capone 2000). This azotrophic marine cyanobacterium is quantitatively the most important fixer of N_2 in the pelagic ocean. Cells of *Trichodesmium* are usually found as spherical aggregates (puffs) or fusiform bundles (tufts), each containing several hundred multicellular filaments (trichomes). Not all cells within filaments or colonies contain nitrogenase, the enzyme required for fixing N_2 . Most of the active N_2 fixation occurs during the few hours around midday and only in some parts of the trichome (Berman-Frank et al. 2001). Recently it has become evident that in the ocean, trichomes and colonies of *Trichodesmium* simultaneously fix N_2 and take up combined N, including forms of DON (NH_4^+ , NO_3^- , urea, and amino acids; Mulholland & Capone 2000). In cultures, *Trichodesmium* cells grown on urea were reported to be devoid of nitrogenase (Ohki et al. 1992), but this was not the case under all growth conditions (Mulholland et al. 1999).

Trichodesmium colonies that are actively fixing N_2 also release DON and NH_4^+ (Capone et al. 1994, Glibert & Bronk 1994, Mulholland et al. 1999). It has been suggested that N, primarily in the form of amino acids, is released by actively growing cells and that the released DON is utilized by those *Trichodesmium* cells that lack nitrogenase, possibly through the mediation of cell surface amino-oxidases.

The details of N cycling within *Trichodesmium* colonies in the ocean are presently the focus of

intense research. This process is obviously complex and certainly involves other organisms usually associated with *Trichodesmium* colonies, such as harpacticoid copepod grazers (O'Neil et al. 1996, O'Neil 1998). Some, perhaps considerable, part of the DON uptake attributed to *Trichodesmium* may be due to associated heterotrophic bacteria. Nevertheless, it seems clear that in their natural environment, *Trichodesmium* are simultaneously using a variety of N sources, including DON.

In general, situations where multiple sources of N are utilized concomitantly may well be the rule rather than the exception and may reflect the micro-heterogeneity (patchiness) of aquatic systems. Undoubtedly the use of multiple nutrient sources by aquatic microorganisms is a topic deserving more extensive research attention.

CONCLUSION

As we have documented, there has been considerable progress in our understanding of various aspects of aquatic DON over the last decade. Nevertheless, there are still few studies that have quantified the amounts of N flux into, and out of, the DON pool relative to the other major N pools in any specific lake, estuary or marine system. Although it seems clear that components of DON pools such as urea or amino acids may sometimes be 'major players' in N flux, we still lack a general evaluation of the quantitative or qualitative importance of DON cycling in freshwater and marine ecosystems.

In this review we have attempted to summarize the current 'state of the science' in respect to aquatic DON. Our take-home message is simple. The DON fraction in natural waters is by no means inert. DON should not be neglected either as a source or as a sink for N. Many biotic and abiotic processes generate DON in both marine and freshwater systems. The DON pool acts as a source of N nutrition for many microorganisms, and in so doing may affect the species composition of the ambient microbial assemblage. There is still a need for a greater appreciation and understanding of the potential role of DON as a dynamic participant in aquatic ecosystems, especially in freshwater environments.

Acknowledgments. We are grateful to Ms. R. Hershkowitz and Ms. A. Jensen for secretarial help. We also thank a quartet of reviewers for constructive comments and criticism. This work was supported by National Science Foundation grant OCE-0095940 to D.A.B. This paper is a contribution of Israel Oceanographic and Limnological Research and is VIMS Contribution 2535 from the Virginia Institute of Marine Science, College of William and Mary.

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