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THE LINK BETWEEN BIOGEOCHEMICAL NITROGEN CYCLING AND INTERTIDAL GREEN MACROALGAE IN DUBLIN BAY

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ABSTRACT

Biogeochemical nitrogen cycling plays a critical role in the nutrient dynamics of intertidal zones. High denitrification rates in intertidal sediments, together with a lack of comparable nitrogen fixation rates, are considered to be causal factors in the nitrogen limitation of these systems. In addition, inorganic nitrogen efflux from the sediment can make a significant contribution to the nutrient requirements of primary producers, particularly where sediments receive high inputs of organic matter in the incoming tide. In the intertidal zones of Irish coastal systems, sediment ammonium efflux has been found to contribute up to 850 µmol NH_4^+ m^{-2} h^{-1} to the overlying water. The rate of ammonium release is highly dependent on the quality and quantity of sediment organic nitrogen and on temperature. It has been proposed that this source of nitrogen is linked to temporal and spatial patterns in the occurrence of intertidal green macroalgae in Dublin Bay. This paper reviews the literature on the occurrence of green macroalgae in the intertidal areas of the bay and provides an overview of a series of studies that have investigated this relationship.

INTRODUCTION

Although intertidal sediments and the overlying water column can be viewed as two separate systems, they are linked though fluxes of both organic and inorganic nutrients. When tidal waters cover the sediment, particulate organic matter may be deposited onto the sediment surface, recharging the sediment organic matter pool. Following mineralisation of this organic matter by the sediment bacterial and faunal populations, inorganic nutrients may diffuse upwards into the water column. Inorganic nutrients may also diffuse downwards from the water column into the sediment to be used by the sediment biota.

While nutrient cycling occurs in both phases, processes within the sediment occur at rates that are several orders of magnitude higher than those in the water column. This reflects, in particular, the high numbers of bacteria found in surface coastal sediments, with typical numbers in the order of 4×10^9 cm^{-3} (Zobell and Feltham 1943; Fenchel 1992).

Biogeochemical nitrogen cycling plays a critical role in the nutrient dynamics of intertidal zones. High denitrification rates in intertidal sediments, together with a lack of comparable nitrogen fixation rates, are considered to be causal factors in the nitrogen limitation of these systems (Billen and Lancelot 1988; Howarth 1988; Seitzinger 1988). In addition, inorganic nitrogen efflux from the sediment can make a significant contribution to the nutrient requirements of primary producers. The role of sediment bacterial mineralisation in explaining patterns in intertidal productivity was recognized by Zobell and Feltham as early as 1943 when they stated that 'detailed observations of the numbers and kinds of bacteria in localised areas may help to explain presence or absence of flora and fauna' (Zobell and Feltham 1943). Ammonium efflux from sediments has since been consistently identified as an important source of nitrogen for phytoplankton productivity (Klump and Martens 1983; Billen and Lancelot 1988). Maximum ammonium release rates are usually recorded at sites which have significant organic nitrogen inputs, with highest rates at temperate sites occuring in summer in response to seasonal temperature rise (Raine and Patching 1980; Klump and Martens 1983; Pomroy *et al.* 1983; Jeffrey *et al.* 1992; Forja *et al.* 1994; Jennings 1996; Jennings and Jeffrey 1998).

However, in addition to seasonal and diurnal cycles, temperature in intertidal sediments is influenced by the semi-diurnal lunar tidal cycle. This dictates the duration of exposure of intertidal flats to solar radiation and is reflected in a unique 14.76-day cycle with highest summer temperatures occurring when low tide and midday coincide (Vugts and Zimmerman 1975; de Wilde and Berghuis 1979; Pinckney and Zingmark 1991). High uptake of ammonium by sediment microalgae has been reported following exposure to daylight during low tide, decreasing the amount released from the sediment during the subsequent immersion period (Pinckney and Zingmark 1991; Rysgaard *et al.* 1995). Extended periods of exposure to solar radiation at low tide may also induce cracking in the sediment surface and increase oxygen diffusion. This can lead to high nitrification rates of mineralised ammonium and further reduce the efflux of inorganic nitrogen to the water column during the next tidal cycle (Laima *et al.* 2002).

In Ireland, sediment inorganic nitrogen efflux rates have been measured at only a few sites. These include Roskeeda Bay in Galway (Raine and Patching 1980), the Shannon estuary (Brennan 1991; Brennan and Wilson 1993) and Dublin Bay (Jeffrey *et al.* 1992; Brennan *et al.* 1994; Jeffrey *et al.* 1995; Jennings 1996; Jennings and Jeffrey 1998). Low ammonium release rates were recorded at the two western sites. The highest rates (up to 850 mmol NH_4^+ m^{-2} h^{-1}) have been recorded in parts of Dublin Bay at sites impacted by moderate levels of organic pollution.

Investigations in Dublin Bay have indicated that nitrogen released from the sediment can play an important role in explaining seasonal and spatial patterns in the occurrence of green macroalgal mats (Jeffrey *et al.* 1992, 1995; Brennan *et al.* 1994; Jennings 1996,

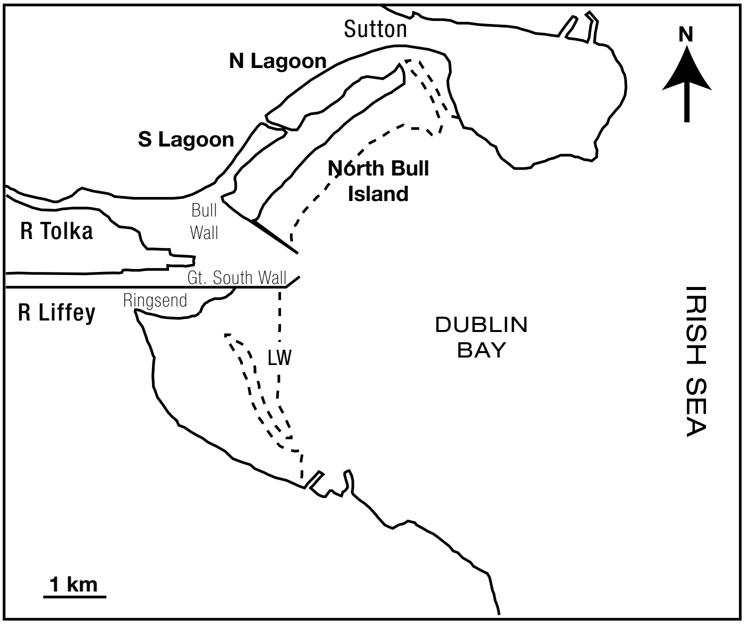

Figure 1. Map of Dublin Bay

Jennings and Jeffery 1998). This paper reviews the literature on the occurrence of green macroalgae in the intertidal areas of Dublin Bay. It also provides an overview of the series of studies that investigated the hypothesis proposed by Jeffrey *et al.* (1992). This hypothesis linked the occurrence of green macroalgae in the bay to the release of ammonium from the sediments following the mineralisation of sedimented sewage particulates.

DUBLIN BAY

Dublin Bay is a large shallow bay on the east coast of Ireland with an extensive intertidal zone that encompasses approximately one third of its area (53° 21' N, 6° 13' W) (Figure 1). The entire perimeter of the bay is urbanised and the inner section of the port has been particularly modified by human activity. These modifications included the building of the Great South Wall and the Bull Wall in the late eighteenth and nineteenth centuries to increase the effect of tidal scouring and deepen the shipping channel (Flood 1977). The River Liffey flows into the area between these two walls. The only other major freshwater input is from the River Tolka, which flows into the bay to the north of the River Liffey.

Much of the sediment in the bay consists of well-sorted, fine, clean sands (Harris 1977). These originate from glacial debris that was deposited as sandbanks in the Irish Sea at the end of the last Ice Age and are brought into the bay on each tide. One of the main features of Dublin Bay is a large island, North Bull Island, which runs parallel to the northern shore. The island is relatively young and its growth was accelerated by the building of the Great South Wall and the Bull Wall (Figure 1). The area between the island and the coast consists of two shallow lagoons, the North Lagoon and the South Lagoon, which are separated by a causeway built in the 1960s. While the sediments in the outer bay consist almost exclusively of sand, those in the intertidal areas and in the lagoon areas behind North Bull Island have a higher percentage of smaller silt and clay size particles, which have originated mainly from river discharge (Harris 1977; ERU 1992).

North Bull Island and its intertidal areas are recognised as the most important section of Dublin Bay in terms of environmental and conservation value. The island, which is now owned and managed by Dublin City Council, received international recognition in 1988 when it was designated a UNESCO Biosphere Reserve. It is also a registered site under the Ramsar Convention and a Special Protection Area under Section 4 of the EC Birds Directive 79/409/EEC. In addition, in 1988, the island and the adjacent lagoons were designated as National Nature Reserves, while in 1995 a Special Amenity Order was adopted for the island by Dublin Corporation (now Dublin City Council).

The main sewage treatment plant for the city is situated at Ringsend, at the mouth of the Liffey. Until the treatment facility was upgraded, the sewage received only primary treatment, which included screening, grit separation and primary sedimentation (ERU 1992). Although the bay has relatively good dispersion and flushing characteristics, particulate material from the treatment plant tends to be moved towards and deposited in the northern sections of the inner bay (Mansfield 1992). This deposition of organic wastes from the Liffey mouth in the intertidal area behind Bull Island was noted as early as 1804 (Flood 1977). These wastes were described at the time as soft ooze from the sewers of the city and were said to be covered with a green slime.

Off-shore nutrient concentrations and productivity in Dublin Bay are usually low (ERU 1992; EPA 2001). However, the consensus of studies of the ecology of the bay has been that, although it is largely unaffected by pollution, organic contamination resulting from sewage discharge has affected some areas, particularly in the northern section (Jeffrey *et al.* 1978, 1985, 1992; Brennan *et al.* 1994, 1998; EPA 2001). Excessive levels of total coliforms were reported in the waters in the Bull lagoons during the Dublin Bay Water Quality Management Plan (DBWQMP) study in the late 1980s confirming that sewage discharge was reaching the intertidal area behind Bull Island (Mansfield 1992). The DBWQMP study also reported that, while the outer intertidal areas of the bay were relatively pristine, the lagoons behind North Bull Island were considered moderately polluted and the Tolka Estuary heavily polluted (Jeffrey *et al.* 1992).

DUBLIN BAY ALGAL STUDIES

Some of the earliest literature on the algal ecology of the bay arose from studies initiated during the redevelopment of the port in the nineteenth century. Bailey (1886) noted the occurrence of green algae on the foreshores of Dublin Bay, stating that ‘the seaweed consists mainly of the Chlorosperma appearing as a verdent green on all the sloblands’. The link between the occurrence of large quantities of green algae and excess nutrients arising from sewage discharge to the bay was referred to by Letts and Adeney

(1907) who demonstrated the capacity of *Ulva* and *Enteromorpha* growing in the intertidal area to utilise 'ammonium salts and nitrate' in the tidal waters. This study reported that the main species of green algae occurring in the channels beside the developing North Bull Island were the green algal species, *Ulva* and *Enteromorpha*.

The first comprehensive study of the ecology of North Bull Island was published in 1977 (Jeffrey 1977). This included a history of the development of the island, together with detailed accounts of the flora and fauna and of its various habitats. The distribution of green algae in areas surrounding the island was detailed by Pitkin (1977). The study noted that green algae, mostly of the order Ulvales, were almost ubiquitous in the intertidal area from the Tolka Estuary to Sutton Creek. Species of *Enteromorpha* were found to be particularly common, while other filamentous algae, such as *Cladophora* and *Chaetomorpha,* were also recorded (Pitkin 1977). Measurements along the northern shoreline showed that the highest biomass occurred in the South Lagoon. In contrast, algal mats occurred less frequently in the North Lagoon. The whole of the South Lagoon was described as being covered by large areas of lush green, while the area north of the causeway had noticeably less growth (Pitkin 1977). A subsequent study, undertaken a decade later, also recorded large quantities of algal biomass in the South Lagoon, with biomass measurements comparable to the highest values in the literature (Walsh 1988).

The studies of algal growth and distribution which were undertaken as part of the DBWQMP investigations still recorded *Enteromorpha* as being the dominant species in the lagoons (Jeffrey *et al.* 1992). The scoping study for these investigations identified the occurrence of large quantities of green algae in the intertidal zone, and the odours released when the algae decomposed, as areas of particular public concern. The highest green algal biomass in the entire bay was again recorded in the South Lagoon. High biomass values were also recorded in some outer areas of the Tolka Estuary and in the inner areas of the North Lagoon. However, the heavily polluted soft muds of the main Tolka Estuary had little algal cover.

The study found that biomass had increased in both the North and South Lagoons since Pitkin's initial study of the algal biomass in the 1970s. Pitkin (1977) recorded a maximum biomass measurement of 120g DW.m^{-2} in the South Lagoon. The values recorded during the DBWQMP study were frequently over 200g DW.m^{-2} with some values of 400–500g DW.m^{-2} (Jeffrey *et al.* 1992). Khan (1998) reported that the species distribution in the lagoons in the mid 1990s was similar to that reported by Pitkin in 1977 and was characteristic of eutrophic intertidal areas. Biomass measurements indicated that growth in the late 1990s was approaching optimal levels, with a maximum biomass at one site in the South Lagoon of 501g DW m^{-2} and some individual measurements ranging up to 833g DW.m^{-2} (Khan 1998).

The DBWQMP study noted that the distribution of algae in the bay was relatively consistent from year to year (Jeffrey *et al.* 1992). However, the timing of peak biomass varied. This variation was not related to differences in temperature. Based on the observations in the DBWQMP and other studies, a hypothesis was formulated to explain the temporal and spatial patterns of algal biomass accumulation in the intertidal areas of the bay (Jeffrey *et al.* 1992, 1995). This stated that mineralisation of sedimented sewage particulates provided a major source of nitrogen for macroalgae. The spatial and temporal patterns of algal growth could be explained by variation in the availability of nitrogen from this source. However, the temperature regime in any year would play a key role in temporal patterns. When higher than normal temperatures occurred in the early summer, sediment organic nitrogen would be utilised at a faster rate. This would lead to a cessation in the supply of inorganic nitrogen to the algae and subsequent nitrogen limitation of algal production. This hypothesis was investigated in a series of subsequent studies (Brennan *et al.* 1994; Jeffrey *et al.* 1995; Jennings 1996; Jennings and Jeffrey 1998; Khan 1998)

INVESTIGATION OF THE HYPOTHESIS RELATING ALGAL GROWTHS TO A SEDIMENT NITROGEN SOURCE

A study of particulate nutrient inputs to Dublin Bay in 1992/1993 included the first measurements of the particulate component of the river and sewage effluent nutrient loads (Brennan *et al.* 1994). The results confirmed that the sewage treatment plant was the main contributor of particulate nitrogen to Dublin Bay (Brennan *et al.* 1994). Tidal cycle water column studies carried out also indicated that the South Lagoon received a much greater quantity of both particulate and dissolved nutrients than the North Lagoon, reflecting its closer proximity to both the main rivers and the sewage treatment plant (Brennan *et al.* 1994, 1998; Jeffrey *et al.* 1995).

Measurements of sediment inorganic nitrogen efflux, using sediment-water incubations, were carried out in conjunction with the particulate nutrient input study (Jennings 1996). These demonstrated that a substantial quantity of ammonium was released from some intertidal sediments in Dublin Bay and that both seasonal and spatial variation occurred in these release rates (Jeffrey *et al.* 1995; Jennings 1996; Jennings and Jeffrey 1998). The highest rates were measured in the South Lagoon at sites where high algal biomass measurements had been recorded. The rates were at the higher end of the ranges reported in other literature and were significantly related to monthly temperature. However, other nearby sites had consistently low release rates. Little or no algal biomass occurred at these sites. High rates were also recorded in some sites in the heavily polluted Tolka estuary but these sites had little or no algal biomass (Brennan *et al.* 1994, 1998). This was attributed to the anoxic nature of the sediments and to high water column turbidity.

A positive relationship was noted in the particulate input study between high rates of sediment ammonium efflux and the occurrence of algal biomass at sites in the North Bull Island lagoons (Brennan *et al.* 1994). Sediment ammonium release was calculated to account for an increase of *c.* 70% in the availability of inorganic nitrogen in the water column of the South Lagoon in late summer (Jennings 1996). This contribution was an order of magnitude higher than that from any other source within the lagoon. An estimate of the quantity of inorganic nitrogen released at sites with green macroalgal mats was equivalent to 96–98% of the nitrogen content of the biomass that accumulated in that season. The total amount of nitrogen estimated to have been released by the sediments in the South Lagoon was three times that in peak algal biomass. While Khan (1998) illustrated the importance of light intensity and temperature as limiting factors for

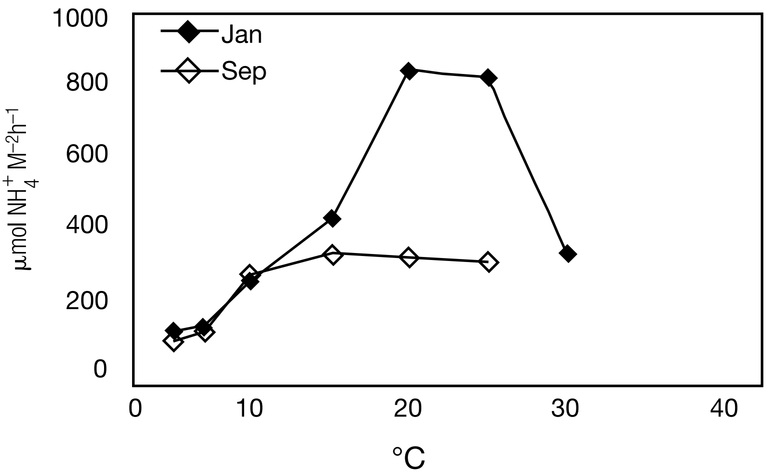

Figure 2. Sediment ammonium release rates (µmol $NH_4^+.m^{-2}.h^{-1}$) from Dublin Bay sediments incubated at a range of temperatures (5°C–30°C) in January and September (after Jeffrey *et al.* 1995).

macroalgal growth in the bay in spring, these results indicated that sediment nitrogen release could play a role in the patterns of macroalgal biomass over the summer, as proposed by Jeffrey *et al.* (1992). This nitrogen source would be of particular importance when water column inorganic nitrogen concentrations in the bay become depleted as often occurs in late summer (Jeffrey *et al.* 1992; Brennan *et al.* 1994; EPA 2001).

Sediment ammonium efflux rates from cores collected in the lagoons during the winter and incubated at a range of temperatures were found to be highly correlated with temperature, with an apparent optimum temperature of 200°C (Figure 2) (Jeffrey *et al.* 1995; Jennings, 1996). However, in autumn a significantly lowered temperature dependence was observed (Jeffrey *et al.* 1995; Jennings 1996). This appeared to confirm the proposal in the hypothesis that the availability of nitrogen *via* sediment release might be decreased in the late-summer/autumn and indicated that factors other than temperature contributed to the observed seasonal patterns. In addition, this lowered response was found to have a significant inverse relationship with the occurrence of high sediment temperatures in the preceding period, possibly as a result of changes in the sediment organic nitrogen pool following high rates of bacterial decomposition (Jennings 1996).

Experimental addition of particulate material, extracted from sea water in the North Bull lagoons, to sediment cores resulted in an immediate response in nitrogen efflux rates, confirming that these particulates represented a labile organic nitrogen source to the sediment (Jeffrey *et al.* 1995; Jennings 1996). Investigation of the sediment organic nitrogen pool indicated that ammonium efflux was also significantly dependent on the C:N ratio of the sediment (Jennings 1996; Jennings and Jeffrey 1998). The relationship with sediment C:N ratio was negatively exponential, with highest release rates occurring at sites with lowest ratios. This relationship reflects the fact that bacteria have a high nitrogen requirement and will only excrete nitrogen when the C:N ratio of the substrate is lower than their own (*c.* 6:1) (Goldman *et al.* 1987).

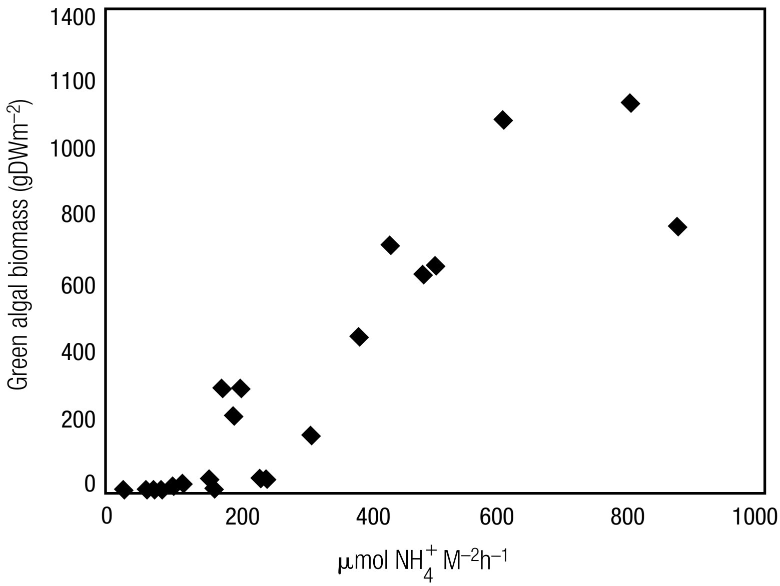

Figure 3. Sediment ammonium release rates (µmol $NH_4^+.m^{-2}.h^{-1}$) at an incubation temperature of 200°C measured in the February/March 1998 at 35 sites in the intertidal area of Dublin Bay plotted against green algal biomass (g $DW.m^{-2}$) measured in July 1998.

Sites in the bay with high ammonium efflux rates also had higher concentrations of hydrolysable protein in surface sediments. The measurement of hydrolysable protein estimates the fraction of the organic nitrogen pool that is easily decomposed by sediment bacteria (Mayer *et al.* 1986). Protein is the main form of nitrogen contained in sewage particulates. The high labile protein concentrations recorded at these sites indicated that they were subject to high deposition rates of particulates from the water column, most probably from sewage treatment. A further investigation into sediment organic matter characteristics at sites throughout the bay in 1997–8 confirmed a highly significant positive relationship between ammonium efflux and the concentration of hydrolysable protein in the sediment (Jennings 1999).

SEDIMENT NITROGEN EFFLUX AND MACROALGAL BIOMASS

During the 1997/1998 study an experiment was carried out to investigate the relationship between sediment inorganic nitrogen efflux and the occurrence of green macroalgae at 35 sites throughout the bay. These sites included the North Bull lagoons, the intertidal areas off North Bull Island, the Tolka estuary and the south bay. Sediment-water incubations were carried out at a temperature of 200°C, the apparent optimum temperature for ammonium release, on one core from each site, in the period February/ March 1998. These measurements were considered to be representative of the potential for nitrogen release from the sediment prior to the commencement of macroalgal growth. Macroalgal biomass was measured at these sites in July of that year.

The results indicated a positive relationship between the amount of nitrogen released from the sediment in the early spring and the accumulation of green macroalgal biomass at those sites later in the growing season (Figure 3). The relationship between nitrogen availability and green macroalgal biomass was generally linear above *c*. 200 μmol NH_4^+.m^{-2}.h^{-1} but appeared to plateau at 600 μmol NH_4^+.m^{-2}.h^{-1}. It was considered from field observations that some of the algal biomass recorded at sites with higher weights may have represented stranded material. While this experiment does not prove a direct coupling between macroalgal growth and sediment ammonium efflux, it adds further weight to the hypothesis that the availability of a sediment nitrogen source can be important in sustaining green macroalgal productivity.

SUMMARY

The series of studies initiated to investigate the hypothesis of Jeffrey *et al.* (1992) confirmed that biogeochemical cycling plays a key role in the supply of inorganic nitrogen to macroalgae in the bay. The input of organic matter from sewage treatment was shown to represent the main source of organic nitrogen in Dublin Bay. It was also shown that the South Lagoon area, in particular, received high concentrations of this material. High efflux rates of ammonium were measured from sediments in those areas that consistently had high green algal biomass in summer months. Other areas with little or no algal biomass had low sediment nitrogen efflux rates. The highest algal biomass was recorded at sites with the greatest stores of labile organic nitrogen as measured by hydrolysable protein content and measurements of sediment nitrogen efflux in the spring. While light and temperature are the main factors controlling algal biomass production in the early season, a dependence on a sediment nitrogen source as the growth season continues may contribute to eventual nitrogen limitation if sediment efflux rates decrease. The quantity of nitrogen released from sediments is related to the supply of labile organic matter and thus is highly sensitive to anthropogenic inputs. The dependence of macroalgae on a sediment nitrogen source may help explain patterns in the distribution of primary producers at other sites, particularly those with significant inputs of labile organic nitrogen.

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