INTRODUCTION

Anthropogenic activities have affected the global nitrogen (N) cycle substantially. Current estimates suggest that creation of reactive N has increased by 120% since 1970 due to agriculture and industry and the rate is still increasing dramatically (Galloway et al. 2008). Riverine export of total N increased globally by up to 30% between 1970 and 2000 (Seitzinger et al. 2010). Increased N loading in riverine systems can cause local eutrophication and can increase N fluxes to coastal systems. This loading adds to the problem of coastal eutrophication and, in extreme cases, can lead to hypoxic zones such as that in the Gulf of Mexico (Rabalais et al. 2001). The main biological process for removal of N as nitrate (NO₃⁻) from freshwater systems is the microbial process of denitrification (Seitzinger 1988). However, a competing process, dissimilatory nitrate reduction to ammonium (DNRA), retains N in the system in a bioavailable form (Tiedje et al. 1982). It is important to understand the processes that remove or transform NO₃⁻ in order to manage aquatic ecosystems properly and prevent potential problems such as harmful algal blooms (Davis & Koop 2006).

Respiratory denitrification (hereafter denitrification) is a dissimilatory process of facultatively anaerobic microbes in the absence of oxygen (O₂ < 10 µM, Tiedje 1988). NO₃⁻ is reduced to NO₂⁻, NO, N₂O and...
finally N₂ (Ye et al. 1995). The final reduction products, nitrous oxide (N₂O), a potent greenhouse gas (Ramaswamy et al. 2001), and dinitrogen gas (N₂), are lost from the system into the atmosphere (Dellwiche & Bryan 1976). In the presence of O₂, most denitrifying bacteria will switch to the physiologically preferred process of aerobic respiration at the expense of NO₃⁻ reduction. (Megonigal et al. 2004). Denitrification may be diminished by the presence of free sulfides, which can inhibit the enzymes responsible for the final 2 stages of the process (Burgin & Hamilton 2007).

DNRA is a microbial process that transforms NO₃⁻ to ammonium (NH₄⁺) via formation of NO₂⁻ in anaerobic or low O₂ environments. The final N form, NH₄⁺, is bioavailable and readily immobilized by microbes and plants, or transformed by nitrification (Bengtsson et al. 2003). There are 2 DNRA pathways: fermentative and chemolithoautotrophic. Fermentative DNRA microbes reduce NO₃⁻ to NO₂⁻ to produce ATP. The subsequent reduction of NO₂⁻ to NH₄⁺ is an electron sink that allows re-oxidation of NADH (Tiedje 1988). Chemolithoautotrophic DNRA is the transformation of NO₃⁻ to NH₄⁺, linked to oxidation of reduced sulfur (S) compounds. This sulfur-driven NO₃⁻ reduction leads to production of N₂ and N₂O via respiratory denitrification. However, because higher concentrations of free sulfides may inhibit the final steps of denitrification, (Brunet & Garcia-Gil 1996, Burgin & Hamilton 2007) reduction to NH₄⁺ via DNRA should dominate. The fermentative microbes are favored by non-sulfidic sediments with high C:N ratios, whereas the chemolithoautotrophic microbes prefer sediments where S oxidizers dominate and H₂S is present in appreciable concentrations (Burgin & Hamilton 2007). While most DNRA active microbes are anaerobes (Tiedje 1988), recent evidence suggests they can also tolerate low levels of O₂, while continuing to reduce NO₃⁻, especially at high C:N ratios (Fazzolari et al. 1998, Silver et al. 2001).

The main factors believed to govern the balance between denitrification and DNRA in freshwater sediments are the ambient O₂ concentration (Fazzolari et al. 1998, Silver et al. 2001), the C:N ratio (Tiedje 1988), and the presence of free sulfides (H₂S, S²⁻) or elemental S (Brunet & Garcia-Gil 1996, Burgin & Hamilton 2007). Other possible contributing factors include the presence of macrophytes (Nijburg & Laanbroek 1997a,b) and ambient temperature (Ogilvie et al. 1997, Scott et al. 2008, Nizzoli et al. 2010).

Spatial and temporal variations in the balance between denitrification and DNRA in freshwater ecosystems have been studied by relatively few researchers, and studies seldom quantify variation in both space (e.g. between different ecotypes) and time. Accordingly, we aimed to elucidate NO₃⁻ losses due to potential DNRA and potential denitrification, across a stream-lake interaction zone of a sub-alpine watershed. Our objective was to quantify the relative importance of DNRA compared to denitrification with changes in ecotype and season.

**MATERIALS AND METHODS**

**Sample sites**

The sampling area, Warm Springs Creek and Bull Trout Lake, is an oligotrophic stream-lake system in a sub-alpine watershed in the Sawtooth Mountains in Idaho, USA. Sediment cores and water samples were obtained from 7 sites (Fig. 1). We sampled in June...
2008, during snowmelt (runoff), close to peak discharge, measured at ~ 858 l s⁻¹ at Site 1 (K. J. Goodman pers. comm.). Samples were again taken at baseflow in August 2008, with a discharge of about 154 l s⁻¹ at Site 1 (K. J. Goodman pers. comm.). Peak discharge occurred on about the same date for all sites, as did baseflow.

Site 1 was located in-stream, approximately 1.5 km upstream from the lake (Fig. 1). Site 2 was in a lateral pool just downstream of Site 1 in the delta marsh, and contained abundant emergent plants on the outskirts of the pool. Site 3 was about 1 km upstream from the lake in an algae filled, stagnant side channel in the delta marsh. Site 4 was at the stream-lake interface at the head of the lake. Site 5 was located at about 3 m depth in the littoral zone of the lake where submerged macrophytes were plentiful. Site 6 was at the outflow stream-lake interface at the bottom of the lake. Site 7 was in-stream, approximately 100 m downstream of the lake. Sites 1 and 4 were categorized as the inflow stream ecotype. Sites 2 and 3 were categorized as the marsh ecotype. Sites 5 and 6 were taken as the lake ecotype. Site 6 was at the edge of the lake where the water temperature and sediment consistency indicated lake conditions. Site 7 was the outflow stream ecotype.

**Microcosms**

Four sample cores were obtained from each site on both dates. However only 3 cores were collected at Site 7 during runoff and none were collected for Site 3 at baseflow as it had dried out. Sediment from at least 15 cm below the water-sediment interface was extracted using a coring device. The cores were measured and the top 10 cm (6 cm for the lake samples) of sediment discarded. The rest of each sediment sample was then pushed out into a plastic bag and sealed and the core depth was recorded. Lake samples were taken using a Wildco® standard KB core sampler (Rickly Hydrological) at runoff and with hand deployed cores using SCUBA diving at baseflow. Water samples were also taken at each site.

On return to the lab the sediments were weighed out into Mason jars, topped off with sample water, sealed and shaken. After settling, the overlying water was sampled for ¹⁵N₂, ¹⁵N₂O, ¹⁵NH₄⁺, ¹⁴+¹⁵NH₄⁺ and ¹⁴+¹⁵NO₃⁻ and then the jars were topped off with the appropriate sample water again, sealed, shaken and stored in the dark for 24 h to assure anoxia. Duplicate samples were taken so that the O₂ levels could be checked for anoxia. We did not extract sorbed NH₄⁺ using KCl and therefore it is possible that our potential DNRA rates are underestimated.

Stable isotope tracer (0.4 ml and 0.8 ml to runoff and baseflow samples, respectively, of 50.32 mg l⁻¹ Na¹⁵NO₃-N solution, 99 atom %) and nutrient solutions (1.0 ml of 25 mg l⁻¹ KNO₃-N + 4 mg l⁻¹ KH₂PO₄-P + 1.5 g l⁻¹ Dextrose-C solution) were added with a syringe through a gas impermeable septa to each microcosm (sediment jar) at T₀. We calculate that addition of ¹⁵N tracer enriched the nitrate pool to 90 atom percent and 70 atom percent, at runoff and baseflow respectively. The addition of ¹⁵NO₃⁻-N increased the ¹⁴+¹⁵NO₃⁻-N mass in each microcosm on average from 2.1 µg to 47.2 µg at runoff and from 16.9 µg to 82.1 µg at baseflow. Because of both this increase in N and the addition of the nutrient solution we consider the rates we present here as potential rates. Microcosm septa were re-sealed with Aquaseal Urethane Repair Adhesive (McNett), incubated in the dark at 20°C for approximately 11 h and sampled once more for ¹⁵N₂, ¹⁵N₂O, ¹⁵NH₄⁺, ¹⁴+¹⁵NH₄⁺ and ¹⁴+¹⁵NO₃⁻.

**Chemistry**

All ¹⁴+¹⁵NO₃⁻ and ¹⁴+¹⁵NH₄⁺ samples were run on an Astoria Pacific flow injection analyzer using methods adapted from the phenolhypochlorite method (Solorzano 1969) for NH₄⁺ and the cadmium reduction method (Grasshoff 1976) for NO₃⁻. Dissolved organic carbon (DOC) samples were run on an OI Corporation model 700 TOC analyzer using the protocol outlined by Bernard (1984). ¹⁵N (N₂, N₂O and NH₄⁺) samples were run on a continuous flow Isotope Ratio Mass Spectrometer (IRMS) or on a Europa ANCA-SL elemental analyzer at the UC Davis and Marine Biological Laboratory stable isotope facilities, respectively.

Potential denitrification and DNRA rates were calculated as the change in ¹⁵N₂ and ¹⁵NH₄⁺ nitrogen mass, respectively, over time per gram of ash free dry mass (AFDM) of sediment (given as µgN gAFDM⁻¹ d⁻¹ and corrected for initial ambient ¹⁵NO₃⁻-N mass). Both microbial processes were also calculated as percent transformation of ¹⁵NO₃⁻-N mass per day (to ¹⁴NH₄⁺ mass for DNRA and ¹⁵N₂-N mass for denitrification) corrected for initial ambient ¹⁵NO₃⁻-N mass. ¹⁵N₂O production was measured but not attributed to either of these 2 processes. DNRA was also measured as a percentage of total dissimilatory NO₃⁻ removal, with the total being made up of denitrification plus DNRA plus N₂O production. Note that we measured
denitrification as production of $^{15}$N$_2$-N and our method did not distinguish between denitrification and anammox.

Percent organic matter was measured as the percentage of pre-dried sample burned off by the ashing process (sample heated to 450°C in muffle furnace for 2 h). AFDM was taken as the mass of the pre-dried sample remaining after ashing.

Statistical analysis

For pairwise comparisons of data groups we used the multiple response permutation procedure (MRPP) in the USGS statistical package Blossom (Cade & Richards 2005). This non-parametric analysis accommodates data with heterogeneous variances, non-normal distributions and small sample sizes. One-sample, single tailed $t$-tests (R statistical software, www.r-project.org) were used to evaluate whether the N transformations measured were significantly greater than zero.

RESULTS

Biogeochemistry

The lake and wetland ecotype sediments contained the most organic matter, 9.9 and 7.0% by mass, respectively. The inflow and outflow ecotypes only contained 0.4 and 1.3% organic matter, respectively. DOC was measured at Sites 1, 6 and 7 and then averaged to give total available C values (ambient + added DOC) of 2340 µg and 2040 µg per microcosm equivalent volume at runoff and baseflow, respectively. NH$_4^+$ and NO$_3^-$ were measured in microcosms from all sites, averaged, and combined to give total available N values (ambient + added DIN) of 51.0 µg and 87.9 µg per microcosm at runoff and baseflow, respectively.

Spatial trends

Potential rates of denitrification and DNRA varied spatially and temporally. The potential denitrification rate ranged from 0 to 0.14 ± 0.03 µgN gAFDM$^{-1}$ d$^{-1}$ over the entire study, while potential DNRA rates ranged from 0 to 0.0051 ± 0.0008 µgN gAFDM$^{-1}$ d$^{-1}$ (p < 0.050), measured at Site 6. Denitrification rate exceeded DNRA rate at Site 6 in June by an order of magnitude (p = 0.050). All other pairwise comparisons between denitrification and DNRA were not statistically significant (p > 0.050).

![Fig. 2. Potential mean (±SE) rates of denitrification and dissimilatory nitrate reduction to ammonium (DNRA) (µgN gAFDM$^{-1}$ d$^{-1}$) for each site, sampled at runoff and baseflow. Asterisks denote p < 0.050, with the exception of Baseflow, Site 1, p = 0.038, Site 2, p = 0.057, Site 5, p = 0.060](image-url)
The baseflow data set results show averages of the 2 microbial processes to be statistically different (p < 0.0001, Fig. 2), with the maximum rate of denitrification exceeding that of DNRA by nearly 3 orders of magnitude (p = 0.016, Fig. 2). Denitrification rate was highest at Site 1 (0.14 ± 0.03 µgN gAFDM⁻¹ d⁻¹), but means across sites were not significantly different (p > 0.050). DNRA rates ranged from 0.0002 ± 0.0001 µgN gAFDM⁻¹ d⁻¹ at Site 2 to 0.0006 ± 0.0002 µgN gAFDM⁻¹ d⁻¹ at Site 5, although means were not statistically different (p > 0.050).

The mean percent transformation of NO₃⁻N due to denitrification was lowest in the wetland ecotype (12.7 ± 4.4%, Fig. 3) and highest in the stream ecotypes (36.1 ± 8.0%, inflow stream, Fig 3). However, the only statistically significant difference between denitrification values was between the wetland and inflow ecotypes (p = 0.028), so there was no statistically significant spatial trend.

Percent NO₃⁻N transformation per day due to DNRA, averaged over both seasons, increased downstream from the wetland ecotype (0.5 ± 0.2%) to peak at the lake ecotype (3.6 ± 0.7%, Fig. 3). MRPP analysis showed the lake maximum to be significantly different to all other ecotypes (p < 0.050, with the exception of comparison to outflow, which was marginally significant, p = 0.086)

The rate of N₂O production was considerably lower than that of DNRA per ecotype (p < 0.001, Fig. 3), with the exception of the wetland ecotype, which had approximately equal transformations of N due to DNRA and N₂O production (wetland DNRA = 0.5 ± 0.2%, wetland N₂O = 0.5 ± 0.2%, p = 0.641).

We calculated DNRA as a percentage of total dissimilatory NO₃⁻ removal (with the total being defined as the sum of denitrification, DNRA and N₂O production) to evaluate the relative importance of this process as a NO₃⁻N removal pathway. Nitrogen transformations due to DNRA were greatest at the lake site (34.4 ± 21.9%, Fig. 4) and lowest at the inflow stream site (3.7 ± 2.8%, Fig. 4). Ecotypes were not significantly different to each other except for comparisons between the inflow and lake (p = 0.043) and between the inflow and outflow (p = 0.075, only marginal significance). DNRA seems to be a potentially more important pathway for NO₃⁻N removal in the lake than in any of the other ecotypes in our study.

**Temporal trends**

Transformation of N due to denitrification was potentially more important during baseflow (31.2 ± 4.9%) compared to runoff (19.9 ± 6.0%) when averaged across sites (p = 0.011, Fig. 5). In contrast, NO₃⁻N transformation due to DNRA was higher at runoff (2.9 ± 0.7%) than at baseflow (1.3 ± 0.4%, p = 0.027; Fig. 5). Similarly N₂O production was higher at runoff (0.2 ± 0.1%) than at baseflow (0.03 ± 0.02%, p = 0.037; Fig. 5).
DISCUSSION

Spatial patterns in NO$_3^-$ losses by dissimilatory pathways

The lake sediments were relatively productive in the littoral zone compared to the other ecotypes as confirmed by the calculated percent organic matter. The wetland and lake ecotype sediments contained considerably more organic matter than the inflow and outflow ecotype sediments. Additionally, the top 5 to 6 cm of each lake core collected at Site 5 was visibly green, and Site 6 samples were noted as smelling strongly of sulfides. Owing to high organic matter content, sediments from lake and wetland ecotypes were relatively highly reducing, as they all went anoxic within 30 min of being sealed in the dark, whereas microcosms from the other ecotypes took close to 11 h. Highly reducing sediments that contain free sulfides (S$_2^-$ or H$_2$S) can facilitate the chemolithoautotrophic DNRA process (Buresh & Patrick 1981, Burgin & Hamilton 2007), while at the same time free sulfides also inhibit the enzymes that sustain the final steps of the denitrification process (Brunet & Garcia-Gil 1996, Burgin & Hamilton 2007). Therefore the presence of highly reducing sediments and hence free sulfides may have suppressed denitrification in our samples while potentially enhancing the DNRA process.

High importance of DNRA to total dissimilatory NO$_3^-$ transformation in lake sediments also may be attributed to the presence of macrophytes. The presence of certain macrophytes in low nitrate sediments may greatly increase the proportion of DNRA to denitrification, possibly due to increased C availability from root exudates and elevated O$_2$ levels, (Nijburg & Laanbroek 1997b). Aerenchymatous plants release O$_2$ into the root zone when healthy (Nijburg et al. 1997), and this process in turn selects for DNRA over denitrification as DNRA is less inhibited by O$_2$ presence than denitrification, especially at high C:N ratios (Fazzolari et al. 1998). *Potamogeton praecox* and *Elodea canadensis* (identified as aerenchymatous macrophytes) were abundant in Bull Trout Lake and were present at Site 5. Macrophytes were not substantially present in the inflow and outflow stream ecotypes.

Temporal variation in NO$_3^-$ losses via dissimilatory pathways

The data in this study show that denitrification is potentially more important during baseflow than runoff, while the opposite is true for DNRA. A similar temporal trend was observed in a fringing marsh-aquifer ecotone where, seasonally, the denitrification:DNRA ratio was 25-fold lower at runoff (0.6) than at baseflow, suggesting that NO$_3^-$ removal was significantly higher during baseflow conditions. However water temperatures varied by about 2°C between seasons and were therefore unlikely to account for this trend (Tobias et al. 2001).

Denitrification and DNRA may be carried out by different competing species of microbes, with ambient conditions selecting for or against denitrifiers (Tiedje 1988, Meganijal et al. 2004). The relative changes in denitrification and DNRA from runoff to baseflow could be explained by this competition, which could be governed by a shift in the balance of available nutrients. Denitrification is generally favored by more C-limited conditions, and DNRA by sediments more enriched with available C, specifically with high C:N ratios, (Tiedje 1988, Omnes et al. 1996, Kelso et al. 1997). Fazzolari et al. (1998) measured DNRA at changing C:N ratios and found that in all but one case an
increase in C:N ratio correlated to an increase in NH$_4^+$ production via DNRA. Our nutrient data showed average dissolved C:N ratios (DOC:DIN) in our microcosms of 46 at runoff and 23 at baseflow. The higher ratio at runoff is expected in this system, due to increased DOC inputs with snowmelt from the watershed. B. McGlynn (pers. comm.) found C:N ratios of 35 at runoff and 22 at baseflow in the Warm Springs Creek/Bull Trout Lake system (average of 4 sites in the lake, inflow and outflow). Inputs to the inflow stream peaked at runoff in late May, when inflow DOC was measured at 2.81 mg l$^{-1}$, and stayed high through the first week of June. Baseflow average was measured as only 0.65 mg l$^{-1}$ (K. J. Goodman pers. comm.).

Temperature can influence the balance of denitrification and DNRA, and mounting evidence points towards a summer DNRA maximum. Ogilvie et al. (1997) reported that denitrifying bacteria were better than fermentative nitrate-ammonifiers at scavenging NO$_3^-$ at low temperatures (5°C) and vice versa at high temperatures (20°C). DNRA was only measured at Lake Waco wetlands in Texas during the summer months when temperatures averaged 28.6°C, as compared to a winter average of 8.4°C (Scott et al. 2008). Nizzoli et al. (2010) found that DNRA was appreciably higher in Lake Verde in summer samples (13°C) compared with the winter (5°C). However, modeled DNRA was favored in more extreme temperatures (<14°C and >17°C) whereas denitrifying microbes preferred a narrow range of 14 to 17°C (Kelly-Gerreyn et al. 2001). Although our microcosms were all incubated at 20°C, different ambient temperatures between seasons may have selected for different microbial populations at the time of sample collection.

**Sediment depths**

To obtain results from microbial communities controlled for O$_2$ concentration, we removed the top portion of sediment (6 to 10 cm) from each core. Highly oxygenated sediments (due to significant hyporheic flow in our lotic systems and a low density floc of episammic algae in the top 6 cm of loosely packed lake sediment) may have boosted the importance of DNRA relative to denitrification as the latter process is known to be inhibited by the presence of even low concentrations of O$_2$, whereas DNRA is more tolerant of oxygen (Fazzolari et al. 1998). Even though all of our microcosms were forced to be anoxic, sampling the oxygenated sediment could bias the microbial community composition in favor of O$_2$ tolerant microbes.

**N$_2$O**

N$_2$O production represented a small transformation of NO$_3^-$ compared to the processes of DNRA and denitrification. N$_2$O could be attributed to either DNRA or denitrification as it is believed to be an intermediate in both pathways (Tiedje 1988, Welsh et al. 2001, Burgin & Hamilton 2008).

Therefore, both DNRA and denitrification may be underestimated. However, because N$_2$O production was either not significantly different from zero, or negligible, this underestimation would be small relative to the measured rates of DNRA and denitrification. Thus, in this study N$_2$O production rates were only used to complete the calculation of total dissimilatory nitrate reduction.

**Anammox**

Anammox, the combination of NO$_2^-$ (from reduction of NO$_3^-$) and NH$_4^+$ to form N$_2$ gas under anaerobic conditions (Dalsgaard et al. 2005) has not been addressed in this study. This process is mainly of interest in marine systems, where it contributes up to 67% of total N$_2$ production in continental shelf sediments (Thamdrup & Dalsgaard 2002). In one freshwater system anammox accounted for 7 to 13% of the total production of N$_2$ but this was only measured in the water column (Schubert et al. 2006). Because we did not measure anammox in this study it is therefore possible that our denitrification figures are overestimated. However, anammox rates are believed to
be higher in eutrophic rather than oligotrophic sediment conditions (Megonigal et al. 2004) with relatively high NO$_3^-$ concentrations (Rysgaard et al. 2004) and low labile carbon concentrations (Jetten et al. 1998). It would, therefore, seem probable that this process would be minimal in our system.

**Cation exchange**

In our study, we used a simple mixing method versus the KCl extraction method (Morin & Morse 1999). Cation exchange in our sediments may have reached equilibrium in less than 2 h (Rosenfeld 1979), and so the exchange of NH$_4$ between the sediment surface and dissolved fraction should have been at equilibrium before the microcosm experiments started. It is possible that the $^{14}$NH$_4$ and $^{15}$NH$_4$ fractions could have interchanged during our microcosm experiments (Seitzinger et al. 1991, Gardner et al. 2006), and therefore DNRA may be underestimated due to this mechanism.

**Global comparisons**

Measured as percent of the total dissimilatory NO$_3^-$ removal at each ecotype, our DNRA results can be compared to global data as reviewed by Burdlin & Hamilton (2007). Our results range from 0 to 12% at the inflow stream ecotype to 6 to 99% at the lake ecotype and overlap with global freshwater data (Freshwater lakes: Nijburg & Laanbroek 1997b, Nizzoli et al. 2010; wetlands: Ambus et al. 1992, Scott et al. 2008; streams: Kelso et al. 1999, Omnes et al. 1996; Fig. 6). According to this small sample of global data, and data presented by Burdlin & Hamilton (2007), wetland and lake ecotypes in general have higher percent DNRA than stream ecotypes. The results of this study agree with this finding. However, in this study, the lake ecotype had by far the highest proportion of DNRA as a percentage of total dissimilatory nitrate removal, but was also most variable (34.42 ± 21.92 %, Figs. 4 & 6).

We infer that denitrification accounts for the main proportion of dissimilatory nitrate removal in each ecotype (Fig. 4). Optimal conditions for DNRA in freshwater sediments are still poorly defined. The results in this study show that DNRA varies spatially and temporally and has potential to rival denitrification in the sediments of some freshwater ecotypes, particularly those with high organic matter content.

**CONCLUSIONS**

DNRA was measured in each ecotype and season and, whilst not as prevalent as denitrification, was significant in this study. The lake ecotype was found to be the most favorable environment for DNRA, with a third of all dissimilatory nitrate reduction being attributed to it in our microcosms. DNRA was significantly higher during runoff compared to baseflow conditions, although temperature was kept constant between the 2 seasonal experiments and so did not contribute directly to the observed difference. We conclude that DNRA may be more important during runoff conditions compared to baseflow, with the opposite being true for denitrification.

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