

Potential Denitrification Activity in the Landscape of a Western Alaska Drainage Basin

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ABSTRACT

We examined denitrification potentials in six of the major landscape structure (riparian soils of both meandering and braided streams, peat lands, coniferous flats, alder slopes, and groundwater seeps) of the Lake Nerka catchment in southwest Alaska. We found significant potential denitrifying activity in all the soils of the main landscape patch types of the Lake Nerka catchment. The lowest potential denitrifying activity was measured in the peat lands. A highly significant relationship was found between soil organic matter and potential denitrification activity in three landforms—coniferous flats, groundwater seeps, and riparian soils of meandering streams. These three landscape structures also had the highest denitrifying potential. The finer soils of

riparian zones along spawning streams, which corresponded to meandering streams, showed a significantly higher potential denitrification activity than the coarse riparian soils along nonspawning streams. These nonspawning streams corresponded to braided streams, where finer sediments were not as prevalent. Therefore, if this high potential denitrification measured in riparian soils of spawning streams is combined with large inputs of nitrate to anaerobic sites, it can result in ¹⁵N signatures that mimic that of the marine-derived nitrogen provided by Pacific salmon in these Alaskan ecosystems.

Key words: Landscape; Denitrification; Alaska; Riparian zone; Salmon.

INTRODUCTION

The role of Pacific salmon (*Oncorhynchus* spp.) in transferring nutrients from marine to freshwater environments has received considerable attention in the last decade (Willson and others 1998; Bilby and others 2001; Naiman and others 2002). The five species of Pacific salmon that perform this function are anadromous, semiparous, and often spawn in large numbers. More than 95% of the body mass of salmon is accumulated from the marine environment (Groot and Margolis 1991). This material is transported and deposited in freshwater habitats,

providing an important nutrient subsidy to freshwater and riparian ecosystems.

The biological significance of this nutrient subsidy has long been recognized for sockeye salmon (*O. nerka*) rearing lakes (Juday and others 1932; Stockner and Issac 1996). However, recent quantitative evidence suggests that marine-derived nutrients also have a positive effect on the plants and animals of streams and riparian zones. In the last decade, the application of stable isotope analyses has enabled direct quantification of marine-derived nitrogen (N) and carbon (C) in streams and riparian zones (Kline and others 1990; Bilby and others 1996b; Ben-David and others 1998; Helfield and Naiman 2001). Salmon are enriched with the heavier isotopic forms of nitrogen (¹⁵N) and carbon (¹³C) relative to other sources. As a result, the proportion of N and C of marine origin found in

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aquatic organisms, riparian vegetation, benthic organic matter, or dissolved in water can be estimated. The apparent ecosystem consequences of the additional nutrients are increased aquatic invertebrate densities (Wipfli and others 1998), higher fish growth rates (Bilby and others 1998), and greater riparian tree growth (Helfield and Naiman 2001).

Salmon carcasses are not, however, the only potential sources of a strong ^{15}N signal. The lighter isotope often reacts more rapidly in biogeochemical cycles than the heavy one; therefore, processes involved in the N cycle can also affect the ratio between the light and the heavy isotopes in environmental N pools. Among these processes, microbial denitrification, a sequence of respiration processes that transform nitrate (NO_3) into gaseous forms of N such as NO , N_2O , and N_2 (Knowles 1981), significantly alters the N isotope ratio. In cases of large constant inputs of nitrate at the denitrifying sites, the lighter isotopes are lost to the atmosphere, while the remaining nitrate becomes enriched in the heavier N isotope (Mariotti and others 1982; Bohlke and Denver 1995; Mengis and others 1999). Furthermore, denitrification can be an important ecological process in riparian zones (Haycock and others 1997). Hence, the strong ^{15}N signal found in riparian vegetation along salmon spawning streams could be caused by denitrification as well as the marine derived N from salmon.

Many salmon spawning streams differ geomorphologically from those not used for spawning (Groot and Margolis 1991). Each salmon species selects substrate sizes appropriate to its reproductive requirements. Nevertheless, most streams used for spawning are meandering with well-developed, fine-textured riparian soils. In contrast, streams that are not used for spawning are often braided or on bedrock with either limited riparian soil development or with coarse sediments.

We hypothesized that the difference in riparian soil along spawning and nonspawning streams results in higher denitrification potentials in the fine-textured soils of spawning streams. If this hypothesis is true, the ^{15}N signal could be significantly altered under constant input of nitrate and could give a false interpretation of the importance of salmon in delivering marine-derived N to streams and riparian vegetation. Our specific objectives were to measure potential denitrification activity in riparian soils of spawning and nonspawning streams and to compare those rates with those associated with other main landscape features (alder slopes, coniferous flats, peat lands, and groundwater seeps). These measurements will assist in devel-

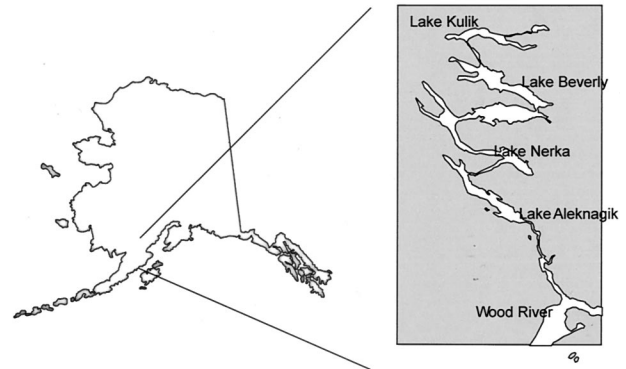


Figure 1. Map of the study area in southwest Alaska, USA.

oping a broader ecosystem context within which the relative importance of denitrification potential can be assessed.

STUDY SITES

The study sites are located within the Wood River Lakes system of southwest Alaska, USA. The University of Washington's Fisheries Research Institute initiated studies of populations of sockeye salmon (*Oncorhynchus nerka*) in 1946 within the Wood River Lakes system, and it has maintained field camps since that time (Rogers and Rogers 1998b). The Wood River system ($59^{\circ}20'\text{N}$ lat., $158^{\circ}40'\text{W}$ long.) is a series of five interconnected lakes (425 km^2) formed by Pleistocene glaciations (Manley and others 2001) that drain into Bristol Bay (Figure 1). Bristol Bay supports the world's largest commercial sockeye salmon fishery.

Lake Nerka is the largest (201 km^2) of the lakes in the Wood River Lakes system and is located within the Wood-Tikchik State Park. The lake is oligotrophic and covered with ice from December through May (Rogers and Rogers 1998a). Annual precipitation averages 51–89 cm per year (Hartman and Johnson 1984). Annual stream discharge is lowest in the winter months (December–March), then peaks with snowmelt in June, and declines through the summer, with a secondary peak in early fall corresponding to increased rain and decreased vegetative transpiration (US Geological Survey gauging station data for Elva Creek and Grant River). Lake Nerka's primary inlet is the Agulukpak River, which drains the upstream lakes; the primary outlet is the Agulowak River, which drains into Lake Aleknagik. Approximately 60 additional surface water streams enter Lake Nerka, along with innumerable lakeside seeps at the base of mountain slopes.

The Lake Nerka catchment is characterized by mountainous terrain (up to 800 m) along its western shores and flat muskeg (that is, peat lands) at its eastern end. The surrounding vegetation is a boreal forest association of white spruce (*Picea glauca*) interspersed with balsam poplar (*Populus balsamifera*) and willow (*Salix* sp.) along riparian zones, moist tundra communities at low elevations, and extensive stands of green alder (*Alnus crispa*) at higher elevations (Helfield and Naiman 2001). Within this landscape setting, we identified six primary patch types that are characterized by their distinct topography, vegetation, and hydrologic characteristics. These patch types are the riparian zones of (a) salmon spawning streams (MR) and (b) nonspawning streams (BR), (c) peat lands (or muskeg) (PL) comprised of a nearly continuous mat of *Sphagnum* mosses with woody species (for example, *Betula glandulosa*, *B. nana*, *Ledum decumbens*, *Vaccinium vitis-idaea*, *V. uliginosum*, and *Empetrum nigrum*) and tussock-forming sedges (for example, *Eriophorum vaginatum*), (d) steep alder slopes (AS) covered with *Alnus crispa*, (e) conifer flats (CF) located at the base of mountain slopes and covered with white spruce, (f) and groundwater seeps (GS) of a few squares meter that are fed by upslope subsurface flows and located at slope break zones and surrounded by alder stands (*Alnus crispa*).

MATERIALS AND METHODS

In each landform type, three noncontiguous sites were selected within the Lake Nerka catchment area. At each site, nine stations were sampled, yielding 27 different soil samples for each landform. Except for the PL sites, where the upper 10 cm of dead sphagnum were sampled, the upper 10 cm of soil were sampled after the litter and roots were manually discarded. The upper 10 cm is the most biologically active zone (for example, the zone of maximum root and organic matter concentration) and is subject to the mechanical processes of erosion and deposition on an annual basis.

A subsample from each station was dried at 60°C to determine fresh and dry mass and percent soil moisture. Nitrogen concentrations were determined on soil samples that were dried at 50–60°C for 72 h and ground to a fine powder via a two-step process using a coffee grinder and then a Wig-L-Bug (a dental grinder distributed by Dentsply-Rinn). Total organic N was measured on a Carlo Erba CHN analyzer at the University of Washington's oceanography marine chemistry laboratory.

Denitrification enzyme activity was measured in the laboratory using slurries of four subsamples

from each sampling station mixed with deionized water. Samples were incubated anaerobically in 125-ml gastight flasks for 8 h in the dark at the average soil temperature during the growing season (10°C). Samples were made anoxic by alternatively vacuuming with an electric pump and flushing with oxygen-free N₂ for 15 min under shaking conditions. Acetone-free acetylene was added to bring the sample's atmosphere concentration to 10 kPa (10% V/V) acetylene and 90 kPa N (Yoshinari and Knowles 1976). Then 5-ml headspace samples were extracted after having been shaken for 5 min; the samples were stored in evacuated collection tubes (Venoject; Terumo Scientific, NJ, USA) after 4 and 8 h of incubation. Gas samples were analyzed via gas chromatography (GC Chrompack CP 9001, Walnut Creek, CA, USA) equipped with an electron capture detector (ECD 63Ni) and Porapak Q columns.

Four different amendments were performed; all of them were rendered anaerobic by replacing the air space with pure N. The first subsample had only deionized water added (DEA_{ana}); the second was amended with water and nitrate (DEA_n 10 µg NO₃-N g⁻¹, soil fresh weight basis), the third with water and glucose (DEA_c 4 mg C g⁻¹, soil fresh weight basis), and the fourth (DEA_{c+n}) with both nitrate (10 µg NO₃-N g⁻¹, soil fresh weight basis) and glucose (4 mg C g⁻¹, soil fresh weight basis). Amendments of nitrate and glucose were made in excess. This procedure provides a potential rate of denitrification activity under nonlimiting factors (Smith and Tiedje 1979), which can be used as an index of denitrifying population density. Although absolute rates are not very informative per se, the relative rates within soil profiles and among sites are useful for comparing denitrifying population abundance. Moreover, comparing rates within unamended soil slurries with slurries to which combinations of nitrate and C have been added reveals which factors limit denitrification.

Potential denitrification rates were expressed on an area basis for the upper 10 cm of soil or sediment (that is, mg N per m² d⁻¹) because soil bulk densities varied widely among sites, making it difficult to compare results based on soil dry weight. Statistical analyses were performed using Mini-Tab software (Minitab, Canyon Lake, TX, USA). The minimum significance level was $P < 0.05$.

RESULTS

Average soil organic C and N concentrations varied widely among patch types. Significantly higher values were associated with AS and CF soils (Table 1).

Table 1. Average Soil Characteristics of the Study Sites and Potential Denitrification (DEA_{c+n})

	Landform	Carbon ($g\ m^{-2}$)	Nitrogen ($g\ m^{-2}$)	C:N (mass basis)	DEA_{c+n} ($mg\ N\ m^{-2}\ d^{-1}$)
PL	Peat land	42 (2.6)	2.0 (0.1)	21.5 (0.5)	2.6 (0.5)
AS	Alder slope	71 (4.6)	4.7 (0.3)	15.2 (0.2)	5.8 (0.5)
BR	Nonspawning stream	26 (3.8)	2.2 (0.3)	11.5 (0.4)	3.3 (0.5)
MR	Spawning stream	39 (2.2)	2.8 (0.1)	14.0 (0.3)	11.4 (0.6)
GS	Groundwater seep	59 (2.4)	4.0 (0.2)	14.8 (0.2)	14.6 (1.0)
CF	Coniferous flat	79 (4.1)	5.6 (0.3)	14.1 (0.2)	18.1 (1.9)

Values given are the average of 27 samples, with SEM in parentheses.

However the C:N ratio was not significantly different among patch types, except in PL, which had a high C:N ratio (t -test; $P < 0.001$).

DEA_{c+n} represents the maximum potential denitrification activity against which the other modalities can be compared. The highest rate of DEA_{c+n} ($18.1\ mg\ N\ m^{-2}\ d^{-1}$) was measured in the CF soils and was significantly greater (t -test, $P < 0.01$) than the rates measured in all the other sites (Table 1). The lowest rates ($2.4\ mg\ N\ m^{-2}\ d^{-1}$), measured in PL, were not significantly different from the AS and BR rates, but all three sites had significantly lower rates than the MR, GS, and CF soils. DEA_{c+n} rates were significantly higher ($P < 0.01$) in the riparian soils of the spawning streams (MR) than in the riparian soils of nonspawning streams (BR) (11.4 and $3.3\ mg\ N\ m^{-2}\ d^{-1}$, respectively).

The rates of potential denitrification activity with nitrate and glucose amendments (DEA_{c+n}) were significantly higher than other treatments for the MR, GS, and CF locations. Denitrification response under anaerobiosis alone (DEA_{ana}) was significantly lower than other treatments (Figure 2). It should be considered as the baseline modality. Carbon plus nitrate amendments (DEA_{c+n}) significantly increased the potential denitrification activity in the sites. Moreover, most of the other amendments increased the potential denitrification activity, although not always significantly.

Rates of potential denitrification activity with nitrate (DEA_n), with glucose (DEA_c), and with nitrate and glucose (DEA_{c+n}) responded differently for the six landforms types (Figure 2). In PL locations, despite the low rates measured, maximum potential denitrification activity occurred with nitrate addition (DEA_n). In the AS soils, glucose addition produced rates of potential denitrification activity close to the maximum obtained under both C and nitrate addition. In riparian soils of the nonspawning streams (BR), only the DEA_{c+n} treatment produced potential denitrification activity significantly higher

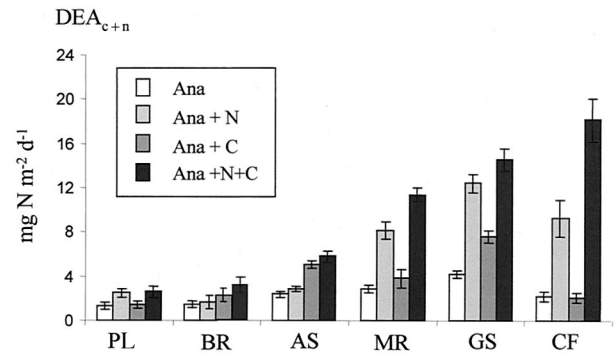


Figure 2. Denitrification potential rates in the soils of the six different landforms (PL, peat land; BR, nonspawning stream; AS, alder slope; MR, spawning stream; GS, groundwater seep; CF, coniferous flat) under various incubation treatments. Ana, anaerobiosis; Ana + N, anaerobiosis plus nitrate; Ana + C, anaerobiosis plus glucose; Ana + N + C, anaerobiosis plus nitrate and glucose. The error bars indicate the SEM.

than DEA_{ana} ($P < 0.05$). In MR and GS soils, nitrate addition alone (DEA_n) triggered soil denitrification activity at rates that were not significantly different from the maximum potential (that is, DEA_{c+n}). Similarly the response with nitrate addition (DEA_n) was high for the CF even though its activity was significantly lower than DEA_{c+n} .

The overall relation between soil C and N was complicated, as was the maximum denitrification potential. There was no statistical relationship between the soil organic C:N ratio and the maximum potential denitrification activity (Figure 3), although the maximum denitrification potential was measured in soils with a C:N ratio around 15, and very low rates were measured in soils with a C:N ratio above 18. Soil organic C was positively correlated to maximum potential denitrification activity in CF, GS, and MR soils (Figures 4 and 5) with a similar relationship:

Soil C was not correlated with maximum poten-

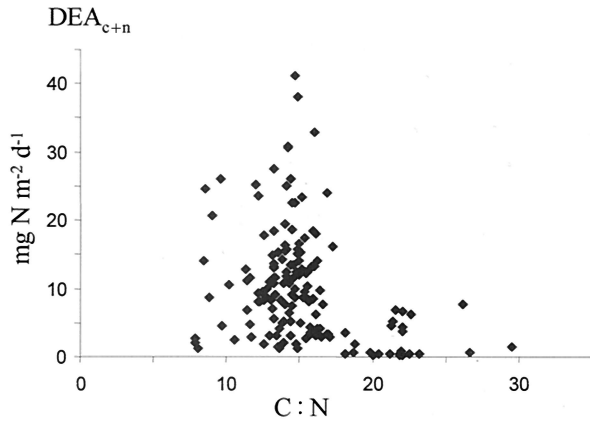


Figure 3. Relationship between soil organic carbon–nitrogen (C:N) ratio and potential denitrification activity (DEA_{c+n}).

tial denitrification activity in BR, AS, and PL soils (Figure 4). A similar pattern, not presented here, was found between soil organic N and DEA_{c+n} .

DISCUSSION

Denitrifying enzyme activity assays (DEA_{c+n}) force the metabolism of denitrifying bacteria under non-limiting conditions—that is, anaerobiosis, nitrate and C supply—for a short period of time to avoid the population increase (Smith and Tiedje 1979). Therefore, they can be used to determine the maximum denitrification capacity of a soil and to provide an indirect evaluation of the denitrifying community present.

We found significant rates of potential denitrification activity in all the soils of the main landforms of the Lake Nerka catchment (Table 1). The lowest potential denitrifying activity was measured in the PL. Nitrate was the dominant factor limiting denitrification in these sites (Figure 2). Peat lands are usually water-saturated, a condition that limits oxygen penetration and promotes the establishment of anaerobic conditions. This in turn prevents in situ organic N nitrification and nitrate production. Moreover, peat lands may not be as tightly connected hydraulically as the other landforms to groundwater flows from the surrounding catchment. Hydraulic isolation would reduce allochthonous nitrate inputs, such as groundwater transfers of nitrate leached from alder thickets upslope.

Low denitrification potential rates were measured in the riparian zones of the nonspawning streams (BR) (Figure 2 and Table 1). These rates were significantly lower than those measured in the riparian soils of the salmon spawning streams. The

potential denitrification rates measured in the alluvial soils of the salmon spawning streams were within the range of those measured in other riparian soils of more temperate climates in southern France (Pinay and others 1993, 2000) and in poorly drained soils of riparian forests of the northeastern United States (Groffman and others 1992a). We observed that in the Lake Nerka catchment the nonspawning streams (BR) tend to be braided channels with steeper channel slopes, coarser alluvial gravels, and coarser riparian soils. It has been demonstrated elsewhere that meandering channels have more gentle slopes, with a finer and more homogeneous riparian soil grain size, than braided channels (Richards 1982). Soil texture is a landscape-scale factor that has a significant effect on denitrification activity (Groffman and others 1992b; Pinay and others 2000), nutrient content (Johnston and others 2001), and organic matter distribution (Hassink 1994). For instance, Pinay and others (2000) found that below a threshold of 65% of silt and clay in alluvial soils, no significant denitrification was measured; above that threshold, denitrification activity increased linearly with the percentage of silt and clay. In braided nonsalmon spawning streams, most of the sediments are composed of coarse and fine sand, with small, isolated patches of fine sediment in zones protected from scouring. Hence, the low average DEA_{c+n} measured in the BR soils suggests that denitrification activity in nonsalmon riparian soils is of minor importance in the N cycle of those streams. In contrast, the high rates of denitrification potential measured in meandering salmon spawning stream soils suggest that denitrification is an important process in the N cycling of these riparian soils and could substantially alter the soil $\Delta^{15}\text{N}$ if a constant supply of nitrate is available.

The geomorphic context of the streams could be considered as the main landscape-scale factor resulting in high $\Delta^{15}\text{N}$ in salmon spawning stream ecosystems, both directly, by providing the spawning conditions to salmon (riverbed slope and sediment grain size), and indirectly, by producing fine-sediment deposits that have a high denitrification potential.

Potential denitrifying activity increased in spawning stream soils in response to added N and again to added N and C (Figure 2). Spawning salmon contain both large amounts of organic N and labile organic C that are broken down to inorganic N and dissolved organic matter during decomposition. Ammonium and nitrate concentrations increase during spawning runs (Rice and Bailey 1980; Bilby and others 1996a; Minikawa and Gara 1999), and decomposing carcasses release organic C that is rap-

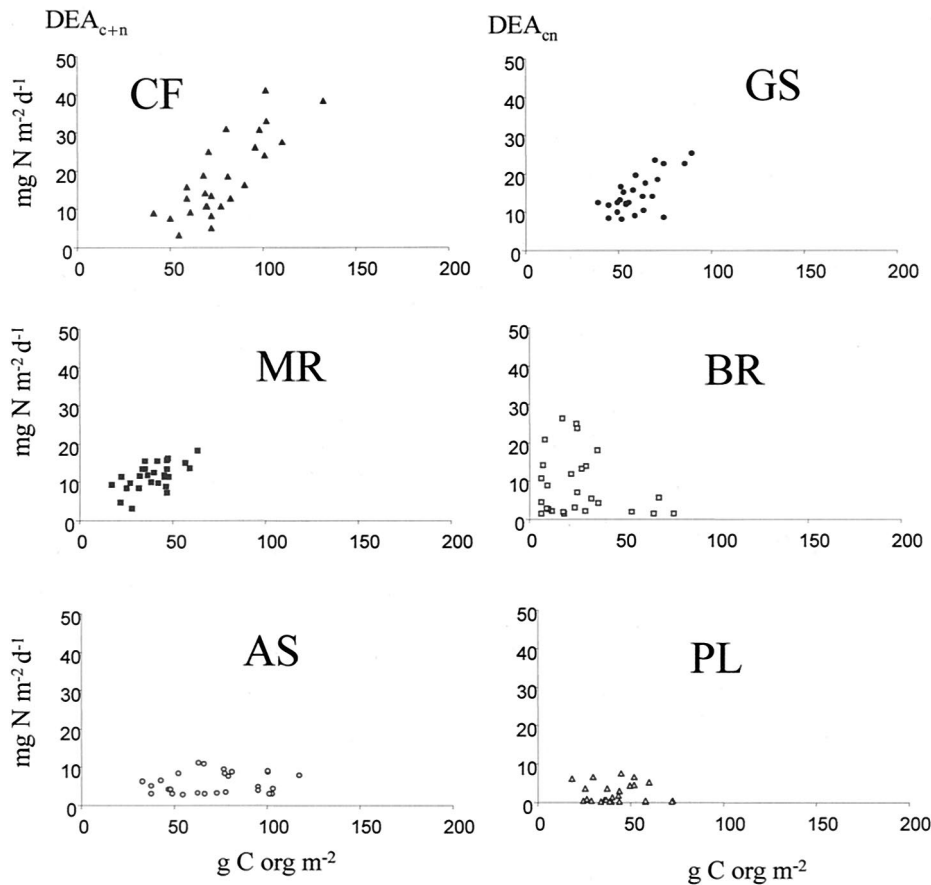


Figure 4. Relationship between concentration of soil organic carbon (C_{org}) in the six different (CF, coniferous flat; MR, spawning stream; AS, alder slope; GS, groundwater seep; BR, nonspawning stream; PL, peat land) landforms and potential denitrification activity (DEA_{c+n}).

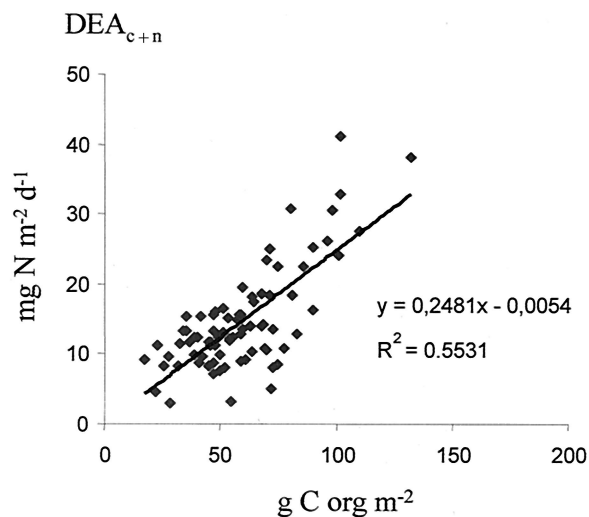


Figure 5. Correlation between concentration of soil organic carbon (C_{org}) and potential denitrification activity (DEA_{c+n}) for the riparian zones of the spawning streams (MR), groundwater seeps (GS), and coniferous flats (CF).

idly taken up by sediment communities (Bilby and others 1996a). The combination of high denitrification potential within spawning stream riparian soils

and increased availability of labile C and inorganic N may further increase the realized differences in denitrification potentials between salmon and non-salmon streams, thereby creating a systematic bias toward increased ^{15}N within spawning streams. However, more research is needed to determine whether there is a constant input of nitrate at the denitrifying sites to significantly affect the ^{15}N signal. Therefore, our research cannot determine to what extent the higher $\Delta^{15}N$ measured in spawning streams is due to microbial denitrification, but it is clear that the contribution of N cycling could be significant and it has not been adequately addressed in mixing model approaches.

We did not find any significant relationship between the soil organic C:N ratio and potential denitrification activity (Figure 3). However, above a C:N of 18, very low potential denitrification was measured. These high C:N values were mostly measured in the PL sites, where the main vegetation cover has a high C:N ratio and its decomposition is limited by constant waterlogged conditions. Therefore, the lack of easily available organic C and low nitrification, which limits nitrate availability, probably inhibit the maintenance of a large, active deni-

trifying bacteria community (Urban and others 1988).

A highly significant relationship (Figure 5) was found between soil organic matter and potential denitrification activity in three of the landforms, CF, GS and MR. These three landscape structures also contained the highest potential denitrification activity (Figure 2 and Table 1). Moreover, the potential denitrifying activity of these communities was triggered by anaerobiosis and nitrate amendment (Figure 2), confirming that nitrate was a factor limiting denitrification. Because of their location and physical structure, these sites receive and retain dissolved or particulate nutrients and organic matter. Coniferous flats, positioned at the bottom of steep mountain slopes, receive both surface and subsurface flow from the alder-dominated slopes. Groundwater seeps (GS) are the surface expression of subsurface flow from upslope, and like conifer flats, they tend to occur at slope breaks at the base of alder-covered mountain slopes. Riparian zones along meandering streams (MR) are preferential zones of alluvial sediment deposition during floods. We did not evaluate the denitrifying community density in the present study. However, we can expect from the high rates of potential denitrification measured in these three types of landscape structures that large communities of denitrifying bacteria can thrive on the mineralization of allochthonous organic matter with a low C:N ratio (Table 1) and the nitrate inputs from watershed slopes.

CONCLUSION

We have shown that different landforms presented significantly different denitrification potentials within the Lake Nerka system. However, the highest denitrification potential was measured in landscape structures that represent depositional zones for dissolved and particulate C and nutrients. According to our hypothesis, geomorphic differences between salmon spawning streams and non-spawning streams in the Lake Nerka system lead to systematic differences in potential denitrifying activity within their riparian soils. The finer soils of riparian zones along meandering spawning streams had a larger potential denitrifying activity than those in nonspawning streams. Indeed, the braided character of nonspawning streams in this region prohibits retention of fine sediments except in isolated areas. This high denitrification potential in riparian soils of spawning streams could contribute to the observed increases in $\Delta^{15}\text{N}$ in the riparian zones of spawning stream if a constant nitrate supply is available. Therefore, it is important to deter-

mine the relative influence of marine-derived ^{15}N and microbial denitrification on observed isotope signatures in riparian vegetation. In this region, maximum nitrate discharge probably occurs during the late-spring snowmelt, when vegetation uptake is still low. An analysis of the seasonal fluxes of N and their delta ^{15}N within and in between these landscapes would allow a comprehensive evaluation of the significance of denitrification in the annual biogeochemical cycle of N in these subarctic landscapes.

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REFERENCES

- Ben-David M, Hanley TA, Schell SM. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* 83:47–55.
- Bilby RE, Fransen BR, Bisson PA. 1996a. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can J Fish Aquat Sci* 53:164–73.
- Bilby RE, Fransen BR, Bisson PA. 1996b. Response of juvenile coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can J Fish Aquat Sci* 53:161–4.
- Bilby RE, Fransen BR, Bisson PA, Walter JK. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and Steelhead (*O. mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Can J Fish Aquat Sci* 55: 1909–18.
- Bilby RE, Fransen BR, Walker JK, Cederholm CJ, Scarlett WJ. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* 26:6–14.
- Bohlke JK, Denver JM. 1995. Combined use of groundwater dating, chemical and isotopic analyses to resolve the history and fate of nitrate contamination in two agricultural watersheds, Atlantic Coastal Plain, Maryland. *Water Resources Res* 31:2319–39.
- Groffman PM, Gold AJ, Simmons RC. 1992a. Nitrate dynamics in riparian forests: microbial studies. *J Environ Qual* 21:666–71.
- Groffman PM, Tiedje JM, Mokma DL, Simkins S. 1992b. Regional scale analysis of denitrification in north temperate forest soils. *Landscape Ecol* 7:45–53.
- Groot C, Margolis L. 1991. Pacific salmon life histories. Vancouver: University of British Columbia.
- Hartman CW, Johnson PR. 1984. Environmental atlas of Alaska. Fairbanks: University of Alaska.
- Hassink J. 1994. Effects of soil texture and grassland management on soil organic C and N and rates of C and N mineralization. *Soil Biol Biochem* 26:1221–31.
- Haycock NE, Burt TP, Goulding KWT, Pinay G. 1997. Buffer

- zones: their processes and potential in water protection. Harpenden (UK): Quest Environmental.
- Helfield JM, Naiman RJ (2001) Effects of salmon-derived nitrogen on riparian forest growth and implications for stream habitat. *Ecology* 82:2403–2409.
- Johnston CA, Bridgman SD, Schubauer-Breigan JP. 2001. Nutrient dynamics in relation to geomorphology of riverine wetlands. *Soil Sci Soc Am J* 65:557–77.
- Juday C, Rich WH, Kemmerer GI, Mean A. 1932. Limnological studies of Karluk Lake, Alaska 1926–1930. *Bull US Bur Fish* 47:407–36.
- Kline TCJ, Goering JJ, Mathisen PH, Poe PH, Parker PL. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. ^{15}N and ^{13}C evidence in Sashin Creek, southeastern Alaska. *Can J Fish Aquat Sci* 47:136–44.
- Knowles R. 1981. Denitrification. In: McLaren AD, Peterson GH, editors. *Soil biochemistry*. London: E Arnold. p 480.
- Manley WF, Kaufman DS, Briner JP. 2001. Pleistocene glacial history of the southern Ahklun Mountains, southwestern Alaska: soil development, morphometric, and radiocarbon constraints. *Quat Sci Rev* 20:353–70.
- Mariotti A, Mariotti F, Champigny M, Amarger N, Moysé A. 1982. Nitrogen isotope fractionation associated with nitrate reductase activity and uptake of NO_3^- by pearl millet. *Plant Physiol* 69:880–4.
- Mengis M, Schiff SL, Harris M, English MC, Aravena R, Elgood RJ, MacLean A. 1999. Multiple geochemical and isotopic approaches for assessing ground water NO_3^- elimination in a riparian zone. *Ground Water* 37:448–57.
- Minikawa N, Gara RI. 1999. Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. *J Freshwat Ecol* 14:327–35.
- Naiman RJ, Bilby RE, Schindler DE, Helfield JM (2002) Pacific salmon, nutrient and the dynamics of freshwater ecosystems. *Ecosystems* 5:399–417.
- Pinay G, Black VJ, Planty-Tabacchi AM, Gumiero B, Décamps H. 2000. Geomorphic control of denitrification in large river floodplain soils. *Biogeochemistry* 30:9–29.
- Pinay G, Roques L, Fabre A. 1993. Spatial and temporal patterns of denitrification in a riparian forest. *J Appl Ecol* 30:581–91.
- Rice SD, Bailey JE. 1980. Ammonia concentrations in pink salmon (*Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska. *Fish Bull* 78: 809–11.
- Richards K. 1982. Rivers: form and process in alluvial channels. London: Methuen. 358 p.
- Rogers DE, Rogers BJ. 1998a. Limnology in the Wood River lakes. Seattle: University of Washington.
- Rogers DE, Rogers BJ. 1998b. Spawning ground surveys in the Wood River lakes. Seattle: University of Washington.
- Smith MS, Tiedje JM. 1979. Phases of denitrification following oxygen depletion in soil. *Soil Biol Biochem* 11:261–7.
- Stockner JG, Issac EAM. 1996. British Columbia lake enrichment programme: two decades of habitat enhancement for sockeye salmon. *Regul Rivers* 12:547–61.
- Urban NR, Eisenreich SJ, Bayley SE. 1988. The relative importance of denitrification and nitrate assimilation in bogs. *Limnol Oceanogr* 33:1611–7.
- Willson MF, Gende SM, Marston BH. 1998. Fishes and the forest: expanding perspectives on fish–wildlife interactions. *BioScience* 48:455–62.
- Wipfli MS, Hudson J, Caouette J. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macro-invertebrates in southeastern Alaska, U.S.A. *Can J Fish Aquat Sci* 55:1503–11.
- Yoshinari T, Knowles R. 1976. Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. *Biochem Biophys Res Comm* 69:705–10.