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Abstract

Lakes are dynamic processors of nutrients and may hold an active role in modifying the water chemistry of stream systems. In this study, we examine the influence of lakes and an important terrestrial component—forest cover—on the nutrient levels of stream water in 11 Rocky Mountain (Idaho) watersheds. Water samples were collected from the inflow and outflow of lakes with varying amounts of upstream lakes and forested area during spring runoff and summer base flow. During base flow, mean total nitrogen concentrations at the inflow of final lakes were significantly related to relative upstream lake area, increasing from 34 to 103 µg N L^{-1} as upstream lake cover in the watersheds increased from 0% to 4%. Forest cover was not significantly correlated with total nitrogen concentrations exported from the watersheds. However, similar to other studies, inflow nitrate concentrations were negatively correlated with relative forest cover. At the scale of individual lakes, dissolved organic carbon and dissolved organic nitrogen increased, and nitrate was significantly reduced from inflows to outflows. The results indicate a potentially critical role of mountain lakes in governing nitrogen flux downstream, and suggest the role of lakes as nitrogen sinks or sources may reverse between spring runoff and summer base flow.

Introduction

Stream water chemistry at a given point in the watershed is the product of upstream aquatic and terrestrial factors. Biotic uptake in streams, lakes, and reservoirs can delay and modify the transport of nutrients (Kling et al., 2000; Tank et al., 2000). Due to the large volume of lakes, the occurrence of lentic environments along stream networks can greatly increase water residence times within the aquatic system. Increased water residence time slows nutrient transport and increases biotic processing, resulting in enhanced annual retention of nutrients (Saunders and Kalff, 2001). Lakes consequently can mute the seasonal flux of nitrate that occurs between spring runoff and summer base flow (Kaste et al., 2003) in snowmelt-dominated mountain watersheds. Biotic processes within lakes such as algal uptake, sedimentation, and benthic respiration convert nitrogen and phosphorous into forms different from the inflow streams, and these new forms may then be exported downstream. For example, lakes may serve as nitrate sinks (Kling et al., 2000; Musselman and Slauson, 2004) and export forms of suspended material and plankton that differ from the inflows (Hillbricht-Ilkowska, 1999). Lakes can be important sinks for dissolved inorganic nitrogen (DIN; nitrate + nitrite + ammonium) on a watershed scale as well. For example, in the Loch Vale Watershed of Rocky Mountain National Park, Colorado, lakes were a large sink for atmospheric N inputs and second only to tundra, which occupied more than 10 times the area of lakes (Baron and Campbell, 1997). Indeed, primary production in many lakes in the western United States is limited by nitrogen and/or phosphorous, and lakes effectively remove these nutrients from the water as it passes through (Stoddard, 1994).

Similarly, vegetated land cover of the watershed can be a driver of downstream water chemistry. High-elevation watersheds often have large areas composed of thin, sparsely vegetated soils, talus, and bare rock. The shallow soils and bedrock have a lower absorptive capacity for nutrients, which may prevent much of the long term assimilation of nitrogen and phosphorous that occurs in the forested regions of lower watersheds (Stottlemyer et al., 1997). Subsurface groundwater concentrations of DIN have been found to be higher in talus slopes and tundra than in forests in a high-elevation watershed (Campbell et al., 2000). Thus, combined with the mobility of nitrate in soil (Williams et al., 1996a), shallow soils may be unable to prevent nitrate from reaching water bodies downstream, and watersheds with sparse forest cover can be expected to export higher levels of nutrients.

Despite the vast biological activity within lakes and their subsequent potential to disrupt and transform the downstream transport of nutrients, there is a lack of research addressing the effects of natural lakes on downstream water chemistry. Existing research on stream water nutrient levels has focused largely on land cover characteristics (e.g. Campbell et al., 2000; Hood et al., 2003), soil and snow processes (e.g. Williams et al., 1996a; Campbell et al., 2000), hydrology (Lewis, 2002), or in-stream/hyporheic processes (e.g. Peterson et al., 2001) as the primary factors. Studies that do consider aquatic processes as determinants of stream chemistry rarely separate the roles of lakes and streams. The purpose of our study was to explore the effects that both lakes and forest cover have on downstream nutrient concentrations in snowmelt-dominated watersheds.

We hypothesized that lakes would be a significant driver of downstream nutrient dynamics in these systems, and that catchments with a greater proportion of lakes would exhibit nutrient concentrations dissimilar to those with few or no lakes. Our questions are relevant to issues of how watersheds will respond to increasing levels of atmospheric nitrogen deposition
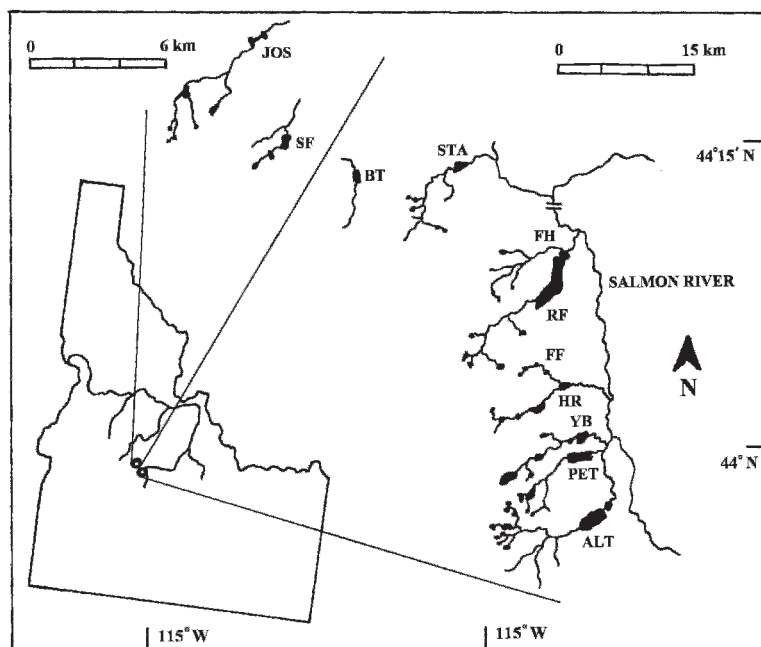
FIGURE 1. Location and relative orientation of the study watersheds in the Sawtooth Mountains of Idaho, USA. For lake abbreviations, see Table 1.

and soil saturation (Stoddard, 1994) and changes in vegetation structure that may accompany global climate change (Schmitz et al., 2003). Our results indicate that both aquatic and terrestrial processes influence stream water chemistry and that small differences in relative lake cover of a mountain watershed can have large implications for watershed nutrient fluxes.

Site Description

Eleven second- to third-order headwater watersheds in the Sawtooth Mountains and adjacent Frank Church–River of No Return Wilderness of central Idaho were sampled in this study (Fig. 1). The Sawtooth Mountains are comprised largely of granites, biotite-granodiorite, and glacial deposits from the Pleistocene (Fisher et al., 1992). The Sawtooth Range was sculpted by glaciers during the last glacial period, leaving behind a series of paternoster and moraine dammed lakes in many of the watersheds. The regional climate is cold and damp. Mean annual temperature and precipitation between 1948 and 2000 for nearby Lowman, Idaho, are 6.6 °C and 66.4 cm, respectively (Western Regional Climate Center, 2007). Precipitation occurs primarily as snow, and snowpack on 1 April comprises approximately 60% of the total annual sum (Steele et al., 1981). Precipitation for the three water years in our study (1992–1993, 2002–2003, and 2003–2004) were 113%, 79%, and 87% of the recorded average (Western Regional Climate Center, 2007). Nutrient levels of streams in these relatively pristine watersheds are low, and the lakes are oligotrophic (Budy et al., 1995).

The 11 study watersheds were selected on the following criteria: (1) presence of a significant lake at the base of the watershed (hereafter referred to as the final lake) with perennial inflows and outflows, (2) lack of recently burned regions within the contributing area, and (3) accessibility. One watershed lacked a final lake. Eight of the study watersheds are located on the eastern front of the Sawtooth Range and drain east to the nearby Salmon River. Two watersheds are located on the boundary of the Frank Church–River of No Return Wilderness and drain east to the Middle Fork of the Salmon River. One watershed is located on the western slope of the Sawtooth Range and drains to the north. Stream discharge of the study watersheds ranges from approxi-

mately 0.075 m^3 s^{-1} during base flow to greater than 2.0 m^3 s^{-1} during spring runoff.

Physical characteristics of the study watersheds vary widely (Table 1). The study watersheds have percentages of forested land cover ranging from 11% to 85% and various numbers and sizes of lakes above the final lake, ranging from 0% to 4% of total watershed area. Elevations of the final lakes range from 1981 to 2378 m, and vertical relief within the watersheds spans from approximately 500 to 1300 m from the elevation of the final lake to the highest point of the drainage. Forest cover within all study watersheds is composed almost exclusively of coniferous species, and includes *Pinus contorta* (lodgepole pine) and *Pseudotsuga menziesii* (Douglas fir) dominated communities in the lower and middle regions of the subalpine zone, and *Abies lasiocarpa* (subalpine fir) in the upper regions (Steele et al., 1981). Atmospheric nitrogen deposition in the region is low at 1.3 kg ha^{-1} yr^{-1} (National Atmospheric Deposition Program, Site ID 15). Previous studies have found primary production in many of the lakes to be co-limited by nitrogen and phosphorous (Wurtsbaugh et al., 1997), whereas stream periphyton are usually limited primarily by phosphorous (Marcarelli and Wurtsbaugh, 2006).

Methods

Water samples were collected in the late summers of 1993 and 2003 and springs of 1993 and 2004 to capture the seasonal variability of hydrologic flows and nutrient concentrations in stream water. Watersheds could not all be accessed in a single day, and sampling dates ranged from 22 May to 9 June and 17 to 21 August in 2003/2004. The average of weekly sampling from 15 May to 1 June and 14 August to 2 October were used for 1993. The summer sampling occurred during base flow conditions, while spring samples were collected approximately at peak runoff. Water samples were collected from only 6 of the 11 study watersheds in 1993.

Samples were collected approximately 20 m from the final lake on the inflow and outflow streams to ensure consistency. Water samples for total nutrient analysis were drawn beneath the stream surface with 60 mL polyethylene water bottles that had

TABLE 1

Landcover characteristics and lake area of the study watersheds.

Watershed	Watershed area (km^2)	Final lake cover (%)[a]	Lake cover above final (%)[a]	Forest cover (%)[a]	Inflow sampling location[b]
Alturas (ALT)	74.1	4.5	0.6	79	43°54′19″N, 114°52′36″W
Bull Trout (BT)	11.4	2.4	0.0	82	44°17′50″N, 115°15′10″W
Finger of Fate (FF)	2.9	1.3	2.3	11	44°01′36″N, 114°57′14″W
Fishhook (FH)	31.3	not present	1.0	58	44°08′34″N, 114°55′14″W
Hell Roaring (HR)	20.4	1.2	3.7	45	44°01′21″N, 114°56′24″W
Josephus (JOS)	10.3	0.3	1.5	85	44°32′50″N, 115°08′43″W
Pettit (PET)	26.9	6.1	2.2	62	43°58′49″N, 114°53′38″W
Redfish (RF)	110.9	5.3	1.3	47	44°05′56″N, 114°57′12″W
Seafoam (SF)	1.8	2.5	3.3	69	44°30′33″N, 115°07′16″W
Stanley (STA)	38.7	1.9	0.6	72	44°14′38″N, 115°04′03″W
Yellow Belly (YB)	29.7	2.7	2.9	65	44°00′10″N, 114°53′05″W

[a] Lake and forest cover is the percentage of area occupied by lakes and forest to the total area of the watershed upstream of the final lake.

[b] Sampling location given in NAD 83 datum.

been rinsed with 1N HCl, and then rinsed three times with deionized water. The bottles were then rinsed twice with stream water at the collection site. In 1993, the water was transported to a field laboratory and filtered through acid-washed and rinsed GF/C and Millipore filters (nominal pore size 0.45 μm). In 2003–2004, the water was filtered at the collection site using a rinsed 60 mL syringe and an ashed and rinsed GF/F filter (nominal pore size 0.7 μm), and stored in polyethylene bottles prepared similarly to those used for total nutrients. The samples were promptly frozen until analysis.

Water samples from 1993 were analyzed for total nitrogen (TN), nitrate (NO_3^-), and total phosphorous (TP). Water samples from 2003–2004 were analyzed for TN, total dissolved nitrogen (TDN), NO_3^-, TP, total dissolved phosphorous (TDP), phosphate (PO_4^{3-}), and dissolved organic carbon (DOC). Base flow 2003 samples were analyzed twice for TN and TP. The second analysis yielded similar results, so the average of the two replicates was taken to create a single data point for each watershed.

Total nitrogen for the 1993 samples was calculated as the sum of the total Kjeldahl nitrogen, nitrate, and nitrite (Gross and Wurtsbaugh, 1994). For all samples, total phosphorous and TDP concentrations were determined by persulfate digestion followed by colorimetric analysis using the molybdate-absorbic acid method (American Public Health Association, 1992). Persulfate digestion was used to determine TDN and TDP. Nitrate and PO_4^{3-} were measured on the 2003–2004 samples using a DIONEX ion chromatograph equipped with an AS14 anion column set. Detection limits for a 5 mL sample are 0.2 and 1.0 μg L^{-1} for NO_3^--N and PO_4^{3-}-P, respectively (Hedin et al., 1995; M. A. Baker, unpublished data). Dissolved organic nitrogen was determined by subtracting NO_3^--N from TDN. Ammonium concentrations are usually below levels of detection in the study watersheds and were not measured. Data from one of the study watersheds suggests ammonium constitutes less than 4% of TDN in the stream (B. Koch, unpublished data). Dissolved organic carbon was analyzed using the wet persulfate oxidation technique of Menzel and Vaccaro (1964) on an Oceanography International 700 TOC analyzer accurate to 0.2 mg C L^{-1}.

The areas of land cover of each watershed, including forest cover, bare rock/talus/tundra (alpine), upstream lake surface area, and contributing drainage area were determined by planimetry using 7.5-minute topographic maps produced by the U.S. Geological Survey. The date of survey for the topographic maps ranges from 1964 to 1990. Of the 11 watersheds, 8 are located in federally designated wilderness, and no major fires, logging, or development have occurred within the study watersheds for at least the past 30 years (Kari Grover-Wier and Liese Dean, U.S. Forest Service, personal communication). The forest cover, alpine, and upstream lake surface areas were then divided by the total watershed area to produce a proportional coverage of each land cover type. Stream water nutrient concentrations were then compared to the proportions of forest cover and upstream lake area. The area of the final lake was not included when analyzing relationships for inflow water chemistry, as it is not within the contributing area of the inflow stream. Backwards stepwise multiple linear regressions were used to explore significant relationships between the concentration of various nutrients in stream water and three land cover characteristics: relative lake area (% of watershed), forest cover (% of watershed), and watershed area (ha). The multiple linear regressions were conducted in SYSTAT, with minimum tolerance for cross-correlation set at 0.005, and an alpha of 0.075 necessary to enter the model. Relationships were considered significant for discussion in this study if the respective p values were less than or equal to 0.05. Differences between inflow and outflow nutrient concentrations for each final lake were tested with paired T-tests.

Results

NUTRIENT LEVELS

Nutrient concentrations were low in the study watersheds in 2003/2004 (Table 2). Inflow TN concentrations averaged 67 and 63 μg L^{-1} during spring runoff and base flow, respectively. In these relatively pristine watersheds, NO_3^--N averaged only 36% and 37% of the total amount of nitrogen in the inflows during the two seasons. Total phosphorous was also low, averaging 3.0 and 2.8 μg L^{-1} in the two flow periods, and TDP was usually below detection.

UPSTREAM LAKE EFFECTS

The effects of upstream lakes on inflow stream water nutrient concentrations varied widely among nutrients and seasons. Base flow concentrations of TN were up to three times higher for watersheds with extensive upstream lake development than watersheds without lakes (Fig. 2). Simple linear regressions showed that relative lake area explained 80% to 87% of the variation in base flow TN concentrations, and these relationships

TABLE 2

Final lake inflow nutrient concentrations for 11 small watersheds in the Sawtooth Mountains of Idaho. TN = total nitrogen, NO₃-N = nitrates, TP = total phosphorus, DON = dissolved organic nitrogen, DOC = dissolved organic carbon.

	Inflow nutrient concentration ($\mu g\ L^{-1}$)							
	TN				NO₃-N			
Watershed	Spring 1993	Baseflow 1993	Spring 2004	Baseflow 2003	Spring 1993	Baseflow 1993	Spring 2004	Baseflow 2003
ALT	148.3	57.7	44.2	33.9	11.7	12.2	15.3	7.7
BT			50.8	36.9			8.7	6.8
FF			71.5	72.8			47.2	40.5
FH	510.5	79.8	93.1	46.4	23.5	15.2	29.0	11.8
HR			60.1	102.8			20.9	40.6
JOS			52.7	39.6			8.6	7.8
PET	97.5	89.1	68.7	72.0	18.7	21.7	22.9	29.2
RF	122.7	89.4	73.0	59.1	31.0	44.8	39.1	55.5
SF			77.8	95.5			18.6	26.2
STA	61.8	61.8	52.1	60.7	16.0	12.9	16.1	11.9
YB	97.0	116.5	97.2	70.1	18.0	17.5	37.3	19.3

	TP				DON		DOC	
	Spring 1993	Baseflow 1993	Spring 2004	Baseflow 2003	Spring 2004	Baseflow 2003	Spring 2004	Baseflow 2003
ALT	18.3	6.1	2.4	2.7	31.8	26.4	1.2	0.6
BT			2.3	2.6	28.9	23.9	1.1	0.4
FF			1.3	2.3	25.1	38.0	1.0	0.5
FH	52.3	7.9	2.6	7.4	48.4	66.5	1.6	0.6
HR			1.2	5.1	27.4	33.2	0.9	0.4
JOS			4.3	1.8	40.3	15.1	1.4	0.5
PET	6.3	4.8	1.2	2.9	30.7	33.4	1.4	0.7
RF	8.3	5.6	2.1	1.1	31.1	21.6	1.3	0.6
SF			1.7	2.9	48.7	169.4	1.6	1.2
STA	23.3	5.2	4.8	2.2	39.6	29.0	1.1	0.4
YB	9.5	7.5	4.4	1.1	49.8	56.4	1.4	0.8

were highly significant (1993, $p = 0.007$; 2003, $p < 0.001$). Neither forest cover nor watershed area were significant variables in the multiple regressions of TN or TDN (Table 3). In contrast with the results from base flow, TN and TDN concentrations during spring runoff were not correlated to upstream lake proportion, forest proportion, or watershed area in either 1993 or 2004 (Table 3). No significant relationships were found between upstream lake area and DON, TP, or DOC in either season.
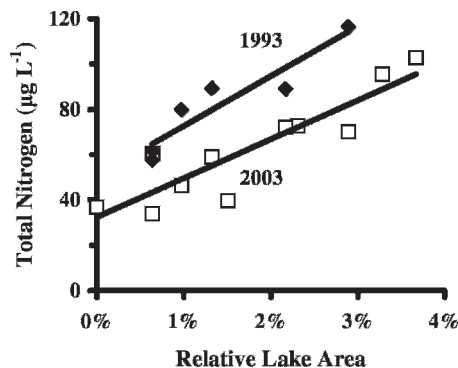

FIGURE 2. Total nitrogen concentrations in stream water vs. relative upstream lake area at the inflow of the final lakes for: 1993 base flow ($r^2 = 0.87$, $y = 2193.4x + 50.78$), and (b) 2003 base flow ($r^2 = 0.80$, $y = 1721.8x + 32.31$).

FOREST EFFECTS

The proportion of forest within a watershed had a strong negative effect on NO_3^--N concentrations in stream water in both 1993 and 2003–2004 (Fig. 3). Nitrate concentrations were approximately 3 to 7 times lower in heavily forested watersheds than those with sparse forest cover, and this effect was somewhat stronger during base flow than during runoff. In one case (2003 base flow) the multiple linear regression indicated that relative upstream lake area and watershed area had a significantly positive correlation with NO_3^--N concentrations, but their contribution was much smaller than that of relative forest area (Table 3). Forest cover, however, was not correlated with a reduction of TN in stream water (Table 3). The proportion of forest cover did not significantly affect inflow concentrations of any other nutrient tested in this study.

Concentrations of phosphorous were not significantly correlated with forest cover, lake abundance, or watershed area. However, phosphorous levels were below detection limits in over half of the watersheds, resulting in a paucity of data points and a lack of statistical power with which to test relationships.

EFFECTS OF FINAL LAKES

Comparisons of nutrient concentrations in the inflows and outflows of the final lakes showed that they were a sink for nitrate and a source for DOC (Fig. 4) and DON. Concentrations of NO_3^--N in the outflows of the final lakes were, on average, 28% and 12% of the respective inflow concentrations during spring runoff and base flow 2003–2004, and these differences were highly significant (paired T-tests; $p < 0.001$, 0.005, respectively). Dissolved organic nitrogen

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TABLE 3

Results of backwards stepwise multiple linear regression between stream water nutrient concentrations at lake inflows and the watershed characteristics above the final lake in the system.

Location	Period	Parameter	Regression coefficients[a]			p values	r^2, simple or multiple
			Lake proportion[b]	Forest proportion[b]	Watershed area		
Inflow	1993 baseflow	TN	21.5	—	—	0.007	0.870
Inflow	2003 baseflow	TN	17.0	—	—	0.000	0.803
Inflow	2004 spring	TN	8.5	—	—	0.072	0.288
Inflow	2003 baseflow	TDN	24.5	—	—	0.037	0.398
Inflow	1993 baseflow	NO_3-N	—	−0.92	—	0.038	0.699
Inflow	2003 baseflow	NO_3-N	6.0	−0.45	0.0024	0.051, 0.013, 0.026	0.826
Inflow	1993 spring	NO_3-N	—	−0.59	—	0.001	0.958
Inflow	2004 spring	NO_3-N	—	−0.36	—	0.012	0.481

[a] Only the results with an alpha less than 0.075 are included.

[b] Lake and forest proportion refer to the percentage of the watershed area (ha) covered by these features.

showed an opposite trend, with average outflow concentrations 41% and 129% higher than inflow concentrations for spring runoff and base flow, and these results were also significant ($p = 0.009, 0.050$). Outflow DOC concentrations were 82% higher than the inflow during base flow ($p = 0.001$), but there was no significant difference during spring runoff ($p = 0.59$). No pattern existed for TN between the inflows and outflows of the final lakes.

In contrast to the marked effects of individual lakes shown by the paired inflow and outflow sampling of the final lakes, most nutrient concentrations in the outflows of the final lakes were not significantly correlated to upstream lake cover, forest area, or watershed area for either season, though there were some exceptions. Outflow DOC concentrations were positively correlated to forest proportion during 2003 base flow ($r^2 = 0.56$, $p =$

0.045) and both forest proportion ($p < 0.001$) and watershed area ($p = 0.034$) during 2004 spring runoff (combined $r^2 = 0.9$). Spring outflow NO_3^--N concentrations were negatively correlated with forest proportion ($p = 0.004$) and watershed area ($p = 0.033$), and outflow TDN was negatively related to watershed area ($r^2 = 0.43$, $p = 0.04$) during 2004 spring runoff only.

Discussion

Relative upstream lake area and forest cover can have significant effects on the concentration, composition, and timing of stream nitrogen fluxes. Stream water chemistry at any given point in a watershed is the product of a myriad of upstream processes, but our results indicate that lake area and forest cover explain a considerable portion of the variance between watersheds in TN and NO_3^- exports in the relatively pristine watersheds of the Sawtooth Mountains.

Total nitrogen and TP concentrations were markedly higher in the 1993 samples than the 2003/2004 samples, particularly in spring. Spring 1993 sampling occurred on the steep ascending limb and peak of the hydrograph, whereas spring 2004 sampling occurred shortly after the peak of a hydrograph with a more shallow and gradual ascending limb. Because the spring nutrient pulse precedes peak discharge, the 1993 samples may have occurred near peak nutrient concentrations, while the nutrient pulse may have declined before the 2004 samples were collected. While wide interannual variability in nutrient concentrations may result from differences in hydrology and climate between years, the relative differences in nutrient concentrations among watersheds are driven by watershed land cover characteristics.

THE INFLUENCE OF LAKES ON NUTRIENT LEVELS

Percent lake cover was highly correlated with increased TN levels at the downstream end of study watersheds during base flow conditions. This is surprising, given that lakes are usually regarded as nutrient sinks (Saunders and Kalff, 2001). Sedimentation can remove a significant amount of nutrients, depending largely on water residence times (Windolf et al., 1996). Nitrogen may also be lost in lakes through denitrification (Axler and Reuter, 1996).

There may be several explanations for this result, such as water residence time and the transformation of inorganic nitrogen to less labile forms through lake biotic processes. Viewed at an annual period, nutrient budgets indicate that lakes are nitrogen sinks (Cooke et al., 1993; Jansson et al., 1994), but when viewed
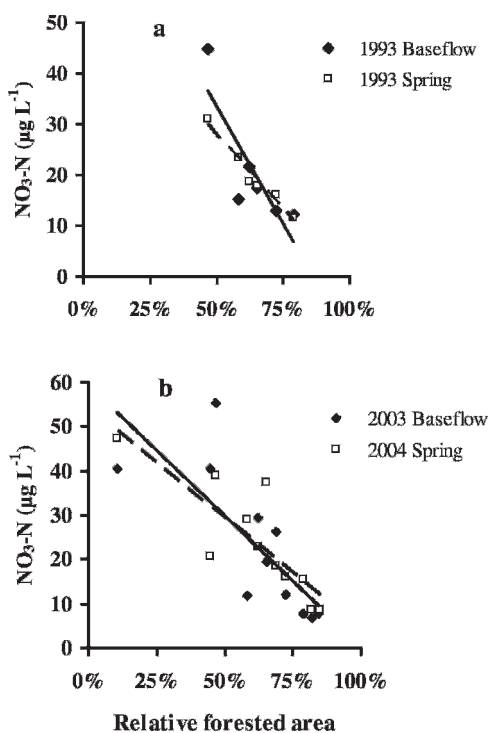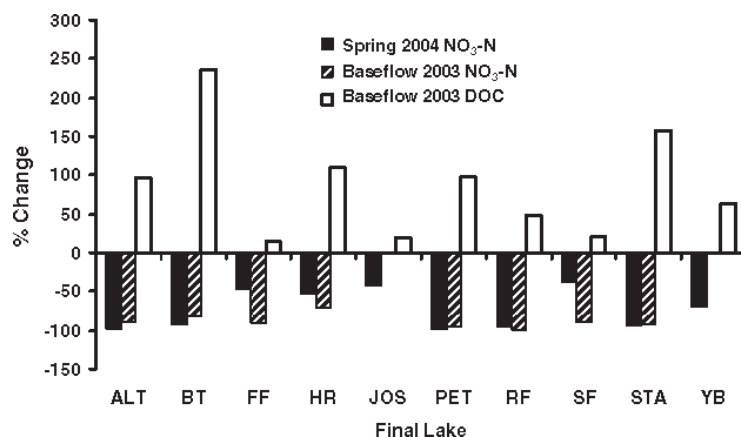

FIGURE 3. Concentrations of NO_3^--N in stream water vs. upstream forest cover at the inflow of the final lakes for (A) 1993 spring runoff ($r^2 = 0.96$, $y = -58.43x + 57.18$) and base flow ($r^2 = 0.71$, $y = -92.02x + 79.58$), and (B) 2004 spring runoff ($r^2 = 0.70$, $y = -49.75 + 54.49$) and 2003 base flow ($r^2 = 0.58$, $y = -59.06 + 59.59$).

FIGURE 4. Differences in concentration between final lake outflows and inflows for summer base flow 2003 and spring runoff 2004. Outflow NO_3^--N data are missing for JOS and YB during 2003. For lake abbreviations, see Table 1.

seasonally, lakes may both capture and attenuate the spring nutrient pulse and thus may be nitrogen sources during the base flow of late summer and fall. Wurtsbaugh et al. (2005) found that in one oligotrophic Sawtooth Mountain lake, TN concentrations in the spring were lower in the outflow than in the inflow, but late in the summer concentrations were higher in the outflow than in the inflow, possibly explaining why we found the positive relationship between TN and lake area to exist only during late season base flow. We hypothesize that lakes in our study watersheds may be acting as late-season nitrogen sources, collecting the pulse of nutrients that occurs on the ascending limb of the hydrograph and releasing those nutrients downstream later in the season. It is unlikely that nitrogen fixation within the lake is contributing significantly to this export. A study conducted on three of the final lakes used in this research indicates that within-lake nitrogen fixation provides an amount of nitrogen equivalent to only 2–4% of TN being supplied by the inflow streams during base flow (Marcarelli, 2006).

The downstream relationship between TN and relative lake area during base flow may be influenced by the higher proportional export of less labile N species by lakes. Biotic processes within lakes can convert NO_3^- to DON (Jansson, 1980) and particulate organic nitrogen (Ahlgren et al., 1994). The large volume of lakes provides an expansive environment for algal and bacterial production and excretions, as well as photobleaching of colored dissolved organic matter (Reche et al., 2001). While dissolved organic matter (DOM) produced in lakes is likely to be more labile than terrestrially derived DOM (Hood et al., 2003), the net outcome of in-lake production versus consumption of labile DOM (mediated by photobleaching) may result in either more or less labile material in lake outflows compared to inflows. Preliminary data suggest that for our study lakes, outflow DOM is less labile than inflow DOM. Despite the uncertainty in determining the relative bioavailability of DON exported from lakes, this DON is certainly less labile than NO_3^-. Consequently, although watersheds with lakes export considerable total nitrogen during base flow, much of this may pass through the streams and lakes and reach the watershed outlet. Our data supports this assertion. Nitrate, which comprises nearly all DIN in these streams, was always lower in outflow streams of the final lakes than inflow streams, and outflow DON concentrations were higher than inflow concentrations in 90% of the studied systems.

The final lakes in our study watersheds disrupted some of the upstream patterns in stream water nutrient concentrations. The strong correlations observed between watershed characteristics and TN and TDN concentrations at the inflows were not found at the final lake outflows. The final lakes greatly reduced the concentration of NO_3^--N and increased the concentration of DOC (Fig. 4) and DON in the outflows. Nitrate concentrations of the inflow streams were lowered by an average of 88%, so that outflow concentrations were frequently near our level of detection. The statistical significance of these relationships shown by the T-tests indicates that lakes can alter nutrients and act as major drivers of downstream nutrient transport. Additionally, in our study, the generally larger size of the final lakes than those upstream could increase this effect. For example, Alturas Lake at the terminal end of its watershed has a mean residence time of 1.8 years (Gross and Wurtsbaugh, 1994), whereas the lakes in the upper watershed are far smaller (Fig. 1; Table 1) and probably respond at much shorter time scales than does the final lake. Additional work to address the importance of lake size, position, and temporal scales is needed to resolve some of these issues.

The observed influence of lakes on stream water nitrogen is a departure from the current understanding of alpine nutrient cycling discussed in the literature. Stream water nutrient dynamics have often been viewed as just the product of terrestrial and hydrologic processes, yet the influence of lakes on downstream nitrogen transport and form in our study watersheds was substantial. Watershed-scale studies of nutrient processing and export should therefore approach lakes and reservoirs as dynamic processors of nutrients rather than passive transporters. The results suggest lakes and streams process and transport nitrogen in vastly different ways, emphasizing the need to study the roles of both lakes and streams when viewing nutrient cycling from a watershed scale.

The results of this study provide insight to the responses of ecosystems to increased anthropogenic nitrogen deposition and climate change. Changes in alpine climate have increased the precipitation and atmospheric NO_3^- deposition in the Rocky Mountains (Williams et al., 1996b), and nitrogen deposition has increased worldwide as the result of human activities (Galloway et al., 2004). Increased snow pack can result in the elevated release of solutes in meltwater, loading greater levels of NO_3^- and exacerbating episodic acidification in streams (Williams et al., 1996b). The results of our study suggest lakes may alter the manner in which such an increase in nitrogen is expressed downstream. Lakes may transform the labile inorganic forms of nitrogen from atmospheric deposition into less labile organic nitrogen, potentially slowing the eutrophication of downstream systems. Processing of NO_3^- into organic nitrogen in lakes also contributes biological acid neutralizing capacity (Schindler et al., 1986), which may reduce acidification downstream. The long water residence times of larger lakes may also mute the transmission of stream water acidified by the pulse of nitric acid in snowmelt. The acidified water may be diluted and released gradually throughout the year, as opposed to the periodic

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acidification events described in Williams et al. (1996b). Additionally, our results suggest that under the decreased seasonality of runoff patterns predicted for western North American mountains by global warming models (Dettinger and Cayan, 1995), lakes might have less influence in modifying the seasonal pulse of nutrients through watersheds.

THE INFLUENCE OF FOREST COVER ON NITROGEN EXPORT

The negative relationship between NO_3^--N concentrations in stream water and the extent of forest cover in the watershed is likely driven by the difference in biotic activity in forest soils compared to the sparser soils and exposed bedrock of the alpine areas. Stottlemyer et al. (1997) showed that forest soils have much higher biotic activity than alpine land cover. Runoff remains in contact with the thin soils and bedrock of alpine land cover for only short periods, which reduces biotic uptake (Stottlemyer et al., 1997; Sickman et al., 2002) and contact time with reactive soil material (Campbell et al., 1995), allowing more NO_3^- to be flushed to lower regions of the watershed. Given that NO_3^- deposition in the Sawtooth Mountains is low and the vast majority of all meltwater in the Rocky Mountains enters the soil matrix before reaching the stream (Stottlemyer et al., 1997), the significant decrease in NO_3^--N with increasing forest cover in our results was expected.

Global climate change and increased atmospheric nitrogen deposition may influence the importance of forests in ameliorating nitrogen export for mountain watersheds. Increasing forest cover and tree line altitude, as well as the increasing periods of biotic activity that accompany global warming (Williams et al., 1998) should allow forests to take up increasing proportions of nitrogen and export less nitrate (Stoddard, 1994).

Our results are consistent with other studies. Hood et al. (2003) recorded sharp declines in stream water NO_3^- concentrations directly downstream of the ecotone between alpine and subalpine regions of a Colorado watershed with high N-deposition rates, and detected lower NO_3^- levels in the more heavily forested control watershed. The authors, however, did not explicitly test the role of the chain of lakes within their study watershed, and these lakes may have contributed significantly to storing the spring nutrient pulse and delaying or reducing its occurrence downstream.

Although forest cover retained NO_3^-, our results suggest that it had less impact on the retention of total nitrogen, as there was not a significant correlation between percent forest cover and TN concentrations in either season. This has important implications for relatively pristine watersheds, where NO_3^- usually composes less than 25% of nitrogen export (Lewis, 2002). Because downstream systems will be impacted by both organic and inorganic nitrogen, it is crucial to understand how forests and other landscape features influence all components of the exported nitrogen.

The negative relationship between NO_3^--N and forest cover persisted during both spring runoff and summer base flow. Elevated levels of nitrate are expected during the initial stages of spring runoff, when incoming meltwater forces NO_3^--rich soil water into the stream, creating a spike in nutrient levels (Campbell et al., 1995; Williams et al., 1996a). Spring 2004 samples were collected in late May during the peak flow for the area, yet only half of the inflow NO_3^--N concentrations were higher than the base flow 2003 samples. Previous studies we have performed on Sawtooth Mountain watersheds have failed to reveal a significant spring nitrate pulse, so it is unclear whether the pulse was missed, or whether it does not exist in these watersheds. Others have found that DIN export from N-limited watersheds is expected to be small, even during the nutrient pulse of spring runoff (Stoddard, 1994; Williams et al., 2001).

Conclusions

The effect of land cover on stream chemistry is relatively well studied, and we found the expected negative relationship between forest cover and stream nitrate concentrations in our study area. Despite the capacity to alter nutrients, biotic activity, and long water residence time of lakes, the persisting effects of these water bodies on downstream stream water nutrient concentrations has been largely unexplored. Our results indicate that lakes may have an influence disproportionate to their relative size on a watershed scale. Lakes occupy a maximum of 4% of our study watersheds, yet are correlated with pervasive and dramatic increases in stream water TN concentrations during base flow. While our results are directly applicable only to mountain watersheds, the processes described may also apply to lowland watersheds and river-reservoir systems with seasonal runoff pulses and nutrient fluxes. Our results also suggest that a landscape perspective is useful for understanding how lakes influence nutrient transport from mountain watersheds. Although analyses of the inputs and outputs of individual lakes can provide insights on nutrient storage and processing (e.g. Musselman and Slauson, 2004), our whole-watershed analyses indicated how total lake area and forest cover may interact to influence the timing of nitrogen flux and the proportions of TDN and nitrate at the watershed outlet. Future studies will need to address complete annual (or longer) nutrient budgets to fully understand the fluxes and processes involved at landscape scales and to determine whether the relationships found in these small mountain watersheds are applicable to other, larger systems.

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