ABSTRACT

$^{15}$N Tracer and Modeling Analyses of Nutrient Transport Through Lakes in a Subalpine Watershed

by

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Lakes have historically been overlooked as important nutrient processors within their watersheds. In general ecologists have focused on streams as zones of uptake and transformation, while viewing lakes as simple nutrient traps. However, recent research has highlighted the large influence that lakes may have on water chemistry within their watersheds. Within the field of limnology, researchers have traditionally focused on the pelagic zone for in-lake production. Further research in shallow lakes has highlighted the role benthic production within the littoral zone plays in the lake ecosystem. The greater influence of lakes is highlighted when comparing watersheds containing lakes with watersheds composed of solely stream channels. To assess the influence that lakes have on water chemistry and nutrient transport, both field and modeling analyses were performed for Bull Trout Lake, Idaho. In 2008 a large field sampling effort was conducted along with a $^{15}$N tracer experiment to characterize the limnology of Bull Trout Lake (Idaho) and nitrogen uptake and transport through the lake. Following the
termination of the field season a multi-lake ecosystem model was developed with the use of a one-dimensional lake water quality model. Results from both experiments demonstrated the role of Bull Trout Lake as a nutrient processor and source within its watershed and further suggested the added influence additional lakes might have on water chemistry. The outcomes of the tracer study indicated that pelagic primary producers have the first opportunity to assimilate nitrogen delivered by the inflow stream; however, nutrients incorporated into plants within the littoral zone are held on to longer. Further the tracer experiment demonstrated the small role that large organisms have in ecosystem nutrient dynamics. The multi-lake model demonstrated the effect of BTL as a nutrient source within the watershed and indicated that although multiple lakes in sequence may have additive effects, most of this influence is expressed in the first two lakes of a series. Our research provides examples of valuable tools in limnological research. While whole-lake tracer studies have rarely been performed, they are extremely effective in understanding ecosystems. Additionally, even though lake models may be simplifications of natural systems, they can provide an efficient means of understanding lake functioning and testing hypotheses.

109 pages

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TABLE OF CONTENTS
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Page</th>
<th>Section</th>
</tr>
</thead>
<tbody>
<tr>
<td>iii</td>
<td>ABSTRACT</td>
</tr>
<tr>
<td>v</td>
<td>ACKNOWLEDGMENTS</td>
</tr>
<tr>
<td>vii</td>
<td>LIST OF TABLES</td>
</tr>
<tr>
<td>viii</td>
<td>LIST OF FIGURES</td>
</tr>
<tr>
<td>1</td>
<td>CHAPTER I. INTRODUCTION</td>
</tr>
<tr>
<td>5</td>
<td>References</td>
</tr>
<tr>
<td>8</td>
<td>CHAPTER II. NITROGEN PARTITIONING AND TRANSPORT THROUGH SUBALPINE LAKE MEASURED WITH $^{15}$N</td>
</tr>
<tr>
<td>11</td>
<td>Study Site</td>
</tr>
<tr>
<td>13</td>
<td>Methods</td>
</tr>
<tr>
<td>21</td>
<td>Results</td>
</tr>
<tr>
<td>27</td>
<td>Discussion</td>
</tr>
<tr>
<td>36</td>
<td>References</td>
</tr>
<tr>
<td>49</td>
<td>CHAPTER III. ARE SUB-ALPINE LAKES NUTRIENT SINKS? MODELING OF BULL TROUT AND ADDITIONAL LAKES</td>
</tr>
<tr>
<td>52</td>
<td>Study Site</td>
</tr>
<tr>
<td>53</td>
<td>Methods</td>
</tr>
<tr>
<td>60</td>
<td>Results</td>
</tr>
<tr>
<td>65</td>
<td>Discussion</td>
</tr>
<tr>
<td>72</td>
<td>Conclusion</td>
</tr>
<tr>
<td>73</td>
<td>References</td>
</tr>
<tr>
<td>88</td>
<td>CHAPTER IV. CONCLUSION</td>
</tr>
<tr>
<td>90</td>
<td>APPENDICES</td>
</tr>
<tr>
<td>91</td>
<td>A. Enrichment of Bull Trout Lake Ecosystem Compartments</td>
</tr>
<tr>
<td>94</td>
<td>B. Mass of Tracer in Bull Trout Lake Ecosystem Compartments</td>
</tr>
<tr>
<td>97</td>
<td>C. Hypsometry of Bull Trout Lake</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Mass of macronutrient flux into and out of each lake</td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
</tr>
<tr>
<td>1</td>
<td>Location of Bull Trout Lake</td>
</tr>
<tr>
<td>2</td>
<td>Temperature and Chlorophyll Profiles of Bull Trout Lake</td>
</tr>
<tr>
<td>3</td>
<td>Hydrograph, Residence time and Br⁻ Concentrations</td>
</tr>
<tr>
<td>4</td>
<td>Map of Bull Trout Lake and Sampling Locations</td>
</tr>
<tr>
<td>5</td>
<td>Loss of Br⁻ and ¹⁵N Tracers from Bull Trout Lake</td>
</tr>
<tr>
<td>6</td>
<td>Enrichment of Ecosystem Compartments with ¹⁵N Tracer</td>
</tr>
<tr>
<td>7</td>
<td>Enrichment of Bull Trout Lake Seston by Depth</td>
</tr>
<tr>
<td>8</td>
<td>Mass Balance for ¹⁵N Tracer on 30-June-2008</td>
</tr>
<tr>
<td>9</td>
<td>Mass Balance for ¹⁵N Tracer Throughout the Summer of 2008</td>
</tr>
<tr>
<td>10</td>
<td>Location of Bull Trout Lake</td>
</tr>
<tr>
<td>11</td>
<td>Bull Trout Lake Hydrograph</td>
</tr>
<tr>
<td>12</td>
<td>Graphical Depiction of the BTL Lake Model</td>
</tr>
<tr>
<td>13</td>
<td>Seasonal Temperature and Nitrogen Concentrations in Bull Trout Lake and The BTL Lake Model</td>
</tr>
<tr>
<td>14</td>
<td>Seasonal Ammonia, Chlorophyll a and Phosphorus Concentrations in Bull Trout Lake and The BTL Lake Model</td>
</tr>
<tr>
<td>15</td>
<td>Seasonal Phosphorus and Carbon Concentrations in Bull Trout Lake and The BTL Lake Model</td>
</tr>
<tr>
<td>16</td>
<td>Predicted Temperature and Concentrations of POC and DOC for Lakes 1-4 and Spring Creek</td>
</tr>
<tr>
<td>17</td>
<td>Predicted Concentrations of Nitrogen for Lakes 1-4 and Spring Creek</td>
</tr>
</tbody>
</table>
18 Predicted Concentrations of Phosphorus and Chlorophyll a for Lakes 1-4 and Spring Creek

19 Change in Nitrogen, Carbon, and Phosphorus Concentrations From Inflow to Outflow
CHAPTER I
INTRODUCTION

Traditional perspectives in aquatic ecology have largely overlooked lakes within the watershed scale. Lakes have traditionally been viewed as discrete entities within watersheds, ecologically disjointed from the rivers and streams they connect. Some have viewed lakes as a simple, one-dimensional discontinuity within a stream network (Ward & Stanford 1983; Arp and Baker 2007), and much of the focus in aquatic ecology has been on water quality transformations in streams, not lakes. Some watershed-scale studies have assumed lakes to be unimportant in affecting nutrient transport through landscapes, but others have suggested that lakes can significantly decrease or alter the timing of nutrient export (Baron and Campbell 1997; Brown et al. 2008). It has been argued that lakes may be extremely important within their watersheds, influencing the downstream transport of nutrients, water, and sediments (Brown et al. 2008).

Water chemistry may be influenced by a multitude of landscape variables within watersheds, and researchers have begun to explore the effect of the physical characteristics of watersheds on downstream nutrient concentrations. Focusing specifically on lakes, studies have correlated variation in water chemistry within lakes with physical variables within their watersheds. In some cases nutrient concentrations may be largely influenced by the geology and land cover of the catchment, among other variables (Johnson et al. 1997; Swanson et al. 1998). The parent geologic material (Duarte and Kalff 1989), percent of forest cover (Hood et al. 2003), and the amount of lake area (Brown et al. 2008) relative to stream area are all factors that can dramatically
influence nutrient concentrations and nutrient flow within watersheds. Given the influence that lakes can have on nutrient transport, the percent of lake cover in addition to the size and location of lakes within watersheds have the potential to significantly influence nutrient processes at the watershed scale (Kratz et al. 1997; Riera et al. 2000). Along with landscape position come many other variables, which influence flow paths and therefore the speed at which water travels as runoff. The size and location of lakes (which determine hydraulic residence time), and the proportion of the watershed that contributes runoff that passes through a given lake, are highly influential in determining the proportion of runoff in the watershed that is subject to the influence of the lake (Jones 2010). Collectively, the number, size and position of lakes in a watershed may all be important in addition to the location of lakes in determining downstream water chemistry.

Within the study of lakes, limnologists have historically separated the pelagic and littoral zones of lakes and have considered pelagic photoautotrophs to be the foundation of lake food webs (Reynolds 2008). This reflects a “pelagic-centric” view of lakes that has traditionally dominated the field of limnology (Vadeboncoeur et al. 2002; Vander Zanden et al. 2006). Lakes have been viewed as vertical systems, with an emphasis on hydraulic transport processes between the pelagic zone and deep hypolimnion and profundal sediments. Under this perspective, fluxes (sedimentation, eddy diffusion, fall turnover) are considered largely responsible for controlling nutrient concentrations and therefore primary production. This generally depicts lakes as large, deep bodies of water; however, many lakes (such as those in the Sawtooth Mountains) are relatively small and shallow with extensive littoral zones. Other than a few publications (Wetzel and Allen 1972; Wetzel and Hough 1973) the role of the littoral zone plays nutrient uptake and
spiraling has largely been neglected; however, in recent years the importance of the littoral zone has been re-emphasized (Axler and Reuter 1996; Vander Zanden et al. 2006).

The existence of an extensive littoral zone creates a situation where a significant portion of lake sediments are in contact with epilimnetic waters, creating opportunity for nutrient exchange and increased production and nutrient cycling. In some cases periphyton may out-compete phytoplankton for nutrients (Axler and Reuter 1996), which may end up slowing the flow of these nutrients out of the lake through recycling or retention in the benthic zone. Numerous studies have illuminated the importance of the littoral zone in nutrient uptake and lake productivity (Fee et al. 1979; Vadeboncoeur et al. 2003). The relative importance of the littoral zone likely depends on the proportion of littoral to pelagic habitats in a given lake and the pathway by which nutrients are delivered into the lake.

There are different mechanisms involved in recycling nutrients back to the base of the food web. An extensive littoral zone may facilitate faster nutrient cycling as nutrients regenerated within littoral sediments are already within the warmer, epilimnetic photic zone. Also, shallow littoral zones may provide ideal habitat for juvenile fishes and macroinvertebrates. In systems where spring nutrient inputs are lost via sedimentation to oxic profundal sediments, fish may be important in re-delivering these nutrients back into the epilimnion and pelagic zone (Sereda et al. 2008). Additionally, submergent macrophytes can be critical links between nutrients buried within the sediments and the water column (Barko 1991). Otherwise, nutrients may become trapped within the
hypolimnion of stratified oligotrophic lakes during the growing season, when they are most needed in primary production.

Whereas cycling of nutrients from littoral sediments into the water column may be crucial to growth of primary and secondary producers in winter months, nutrients delivered from the upper watershed into the epilimnion may be most important to lake ecosystems during the summer. The majority of external nutrient inputs to lakes are delivered in the spring; however, recycling within the lake may allow these nutrients to fuel productivity throughout the year. Predatory macroinvertebrates and fish may continue to accumulate nutrients delivered during spring runoff well into the fall and re-release these nutrients back into the lower food web (Vanni 2002).

Traditional perspectives on lakes have depicted the systems as net nutrient sinks (Jansson 1979; Persson and Broberg 1985). Nutrient pulses delivered by the inflow streams are slowed down when they reach the lake, assimilated and maintained within the lotic biota, and/or sedimented down to the hypolimnion or sediments where they may be “lost” from the food web. However, certain attributes of lakes may cause them to serve as sources of certain nutrient species within their watersheds. For example, nitrogen fixation and internal nutrient loading both can serve as fluxes of nutrients into a lake in addition to what is delivered by the inflow.

In particular, sub-alpine oligotrophic lakes may be expected to behave as nutrient sinks. In high elevation watersheds, streams carry the majority of nutrients during high flow periods and therefore nutrients may be transported through the streams without adequate time for uptake by stream biota. However, once these flows reach downstream lakes, velocities are slowed dramatically and contact time between biota and organisms...
increases. The effects of a single lake within a watershed may be compounded by the presence of other lakes downstream by exacerbating or negating the effects of the first lake. Paternoster lakes are a common occurrence in glaciated watersheds such as those in the Sawtooth Mountains, and therefore understanding the effects of lakes in sequence is highly relevant. This research aims to further our understanding of in-lake nutrient processing and the role that lakes play in landscape limnology within their watersheds.

In this project I conducted multiple studies utilizing stable isotope analysis (SIA) and a one-dimensional lake model. While SIA nitrogen tracer studies have been done in aquatic ecosystems, the majority have been completed in streams (Mulholland et al. 2000; Hall et al. 2009) and estuaries (Tobias et al. 2003; Drake at al. 2009), and the application to lakes has largely been unexplored. Within the realm of lake modeling, the majority of models have been written and utilized to characterize a single lake system. While these studies often have water quality and management implications for the surrounding watershed, none have attempted to link successive models to simulate a multi-lake watershed. I connected a series of Bull Trout Lake models to simulate the cumulative effect of multiple lakes in sequence on downstream water quality. Our research provides new applications of established methods in limnology to examine important questions in limnology and landscape limnology.

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CHAPTER II

NITROGEN PARTITIONING AND TRANSPORT THROUGH A LAKE IN A SUBALPINE WATERSHED (IDAHO) MEASURED WITH A $^{15}$N TRACER

Introduction

Lakes have traditionally been viewed as discrete entities within watersheds, ecologically disjointed from the rivers and streams they connect. Some have viewed lakes as a simple, one-dimensional discontinuity within a stream network that may or may not influence downstream stream reaches (Ward & Stanford 1983; Arp and Baker 2007). Certain watershed-scale studies have assumed lakes to be unimportant in affecting nutrient transport, but others have suggested that lakes can significantly decrease or alter the timing of nutrient export (Baron & Campbell 1997; Brown et al. 2008). Further, it has been suggested that lakes may be extremely important within their watersheds, influencing the downstream transport of nutrients, water, and sediments (Brown et al. 2008). Although the effect of lakes in altering water chemistry has been increasingly recognized, the pathways by which nutrients are taken up and transformed within lakes perhaps have been over-simplified.

Within the study of lakes, limnologists have historically overlooked the littoral zone in lakes and have considered pelagic photoautotrophs to be the foundation of the lake food web, ushering in nutrients (Reynolds 2008). This reflects a “pelagic-centric”
view of lakes that has traditionally dominated the field of limnology (Vadeboncoeur et al. 2002; Vander Zanden et al. 2006). Lakes have also been viewed primarily with regard to processes influencing the vertical structure of the ecosystem, with an emphasis on hydraulic transport processes between the epilimnion and deep hypolimnion and profundal sediments. Under this perspective, vertical fluxes (sedimentation, eddy diffusion, fall turnover) are considered largely responsible for controlling nutrient concentrations and therefore plankton production. This attitude reflects a general depiction of lakes as large, deep bodies of water; however, the majority of lakes found throughout landscapes are relatively small and shallow, with extensive littoral zones. Other than a few studies (Wetzel and Allen 1972; Wetzel and Hough 1973) the role of the littoral zone in nutrient uptake and spiraling had largely been neglected; however, in recent years the importance of the littoral zone has been re-emphasized (Axler and Reuter 1996; Vander Zanden et al. 2006). Growing evidence suggests that benthic primary production and the littoral zone should be incorporated into our depiction of lake ecosystems.

The presence of an extensive littoral zone creates a situation where a significant portion of lake sediments are in contact with epilimnetic waters, creating opportunity for nutrient uptake, exchange, and increased production and cycling. In some cases periphyton may out-compete phytoplankton for nutrients (Axler and Reuter 1996), which may end up slowing the flow of these nutrients out of the lake through recycling or retention in the benthic zone. Certain studies have illuminated the importance of the littoral zone in nutrient uptake and lake productivity (e.g., Wetzel and Allen 1972; Fee 1979; Vadeboncoeur et al. 2003). The relative importance of the littoral zone likely
depends on the proportion of littoral to pelagic habitats in a given lake and the pathway by which nutrients are delivered into the lake.

Even during the spring when hydraulic residence times are low in lakes, the transport of watershed-derived nutrients may be slowed down significantly due to uptake and other interactions with lake biota. Depending on the turnover time of different organisms, these nutrients may remain bound up or they may quickly become re-available for uptake or export out of the system. There are different mechanisms involved in recycling nutrients, making them available for autotrophs. An extensive littoral zone may facilitate faster nutrient cycling as nutrients regenerated within littoral sediments are already within the warmer, epilimnetic photic zone. Whereas in deeper lakes, nutrients that sediment out of the water column may be largely lost to the hypolimnion. Submergent macrophytes growing in littoral sediments can be critical links between nutrients buried within the sediments and the water column (Barko 1991). These macrophytes are capable of mining buried nutrients that may otherwise be lost from the lake food web. Additionally, macrophytes and other benthic primary producers may be particularly important in recycling nutrients from multiple sources including the water column, other benthic plants, and the sediments (Dong et al. 2000; Tobias et al. 2003). The greatest flux of external nutrient inputs to sub-alpine lakes in snowmelt-dominated systems is delivered in the spring; however, recycling within the lake may allow these nutrients to fuel productivity throughout the year.

Stable isotope analysis (SIA) has become a commonly used tool in ecosystem studies to examine food-web relationships and energy flow pathways (Vander Zanden et al. 1997, 1999). There are two general ways in which stable isotopes are utilized in
ecological studies: one is through natural abundance stable isotope sampling to determine trophic relationships within food webs, and the other is as a tracer used to follow nutrient flow pathways with additions of heavy stable isotopes ($^{15}$N, $^{13}$C) of commonly occurring elements. The relatively new technique of performing tracer-level stable isotope studies in natural ecosystems has helped to better describe the flow of nutrients and quantify the importance of certain pathways under natural conditions (e.g. Hall et al. 2009; Tobias et al. 2003). In this research I utilized a tracer ($^{15}$N) to describe nitrogen flow through Bull Trout Lake, a sub-alpine oligotrophic system in central Idaho.

**Study Site**

Bull Trout Lake is a 0.30 km$^2$ subalpine lake located adjacent to the Sawtooth National Recreation Area within the Boise National Forest in central Idaho (Fig. 1). The lake sits at 2118 m and is part of the headwaters of the South Fork of the Payette River (44º 17’ 58” N, 115º 15’ 16” W). The watershed is relatively pristine with limited recreational land use and low wet atmospheric N-deposition (~1.0 kg ha$^{-1}$ yr$^{-2}$; NADP 2001). The physical hydrology of the watershed has been studied extensively (see Arp et al. 2006). The watershed above BTL drains an area of 11.7 km$^2$ composed of biotite-granodiorite, and glacial deposits (Kiilsgaard et al. 2003) with a maximum elevation of 2550 m. The stream hydrographs are dominated by spring snowmelt, and the area is typically snow covered from mid-November to late-May or early-June. The outflow, Warm Springs Creek (WSC), is a small, slow-moving stream that originates as a shallow marsh connecting to the epilimnetic shelf at the north end of the lake.
Bull Trout Lake’s watershed is 99.9% vegetated with upland areas dominated by lodgepole pine (*Pinus contorta*) and riparian areas dominated by willows (*Salix* sp.), sedges (*Carex* sp.) and grasses (Arp et al. 2006). The lake is dimictic and the epilimnion thickness varies from approximately 2 m in early June to 11 m in September (Figure 2a). The lake is oligotrophic with an average epilimnetic summer chlorophyll concentration of 1.1 µg L\(^{-1}\) and a maximum around 4 µg L\(^{-1}\), within a deep chlorophyll layer in the metalimnion (Fig. 2b). Bull Trout Lake watershed has low nutrient concentrations and primary production in lakes in this region are generally co-limited by N and phosphorus (P) availability (Wurtsbaugh et al. 1997). Summer epilimnetic total phosphorous (TP) and total nitrogen (TN) concentrations average 4.3 and 85 µg L\(^{-1}\), respectively, and epilimnetic NO\(_3\)-N concentrations range from near 20-30 µg L\(^{-1}\) during spring runoff to <3 µg L\(^{-1}\) by late June (M. Baker, unpublished data). The maximum lake depth is 15 m with a mean depth of 4.3 m.

The littoral zone between 1.5 and 9 m is dominated by submerged macrophytes, which accounts for approximately 63% of the lake’s benthic area. Flocculent sediments are present at depths < 1.5 m and > 9 m, and are also interspersed between patches of macrophytes. There is essentially no rocky substrate and little sand. A large portion of the water column and benthic sediments are in the photic zone (Appendix C), which varies from 9 m depth in spring to 12 m in late summer (Wurtsbaugh, unpublished data). During the study the zooplankton community was dominated by rotifers with mean densities of 7.0 L\(^{-1}\). Crustacean zooplankton, dominated by *Bosmina* sp., averaged only 0.2 L\(^{-1}\) throughout most of the summer, but rose to 4.2 L\(^{-1}\) in mid-September (D. Lamarra and W. Wurtsbaugh, unpublished data). Bull Trout Lake supports a population of brook
trout (*Salvelinus fontinalis*) and is stocked through the summer with catchable (15-20 cm) rainbow trout (*O. mykiss*). Low numbers of kokanee salmon (*O. nerka*) are also present.

**Methods**

*Tracer Additions* - To further our understanding of nitrogen dynamics on a landscape scale by tracking nitrogen flow, two tracer injections were coordinated in Spring Creek; one at the top of the watershed and another approximately 50 m above the junction of Spring Creek and BTL. Preliminary experimentation in the headwaters indicated that a large portion of nitrogen is removed before it reaches the lake (Baker and McGlynn, unpublished data), and therefore the second injection 50 m above the lake was done to ensure adequate tracer delivery to the lake. The tracers were added for 10 days from 21–30 June, during the descending limb of peak spring flows (Fig. 3a). This period was chosen because most nutrients are transported during spring runoff, but when flows had subsided sufficiently so that a companion study could be done in the creek. Each day during the tracer addition we continuously pumped in a solution containing 20 g of \(^{15}\text{NO}_3^-\)N (99% atom enriched) along with 6.5 kg of a sodium bromide (NaBr). The entire mass of tracers added 50 m above the lake were assumed to enter the lake. The mass of Br\(^-\), \(^{15}\text{NO}_3^-\) and \(^{15}\text{N}\) in seston that reached the lake from the addition in the upper watershed was measured by sampling stream water near the lake on 14 different dates from 21 June to 4 October. Stream discharges (Q) were measured weekly using a flow meter and top-setting wading rod (Flo-mate 2000, Marsh-McBirney Inc., Frederick MD), and stream stage was measured hourly with capacitance rods (Tru-Track, Inc.,
Christchurch, New Zealand) from April 2007 through October 2008. Stream samples of isotopic enrichment were taken above the lake injection point in the inflow stream every 10-60 minutes on days 0 and 9, in addition to daily sampling throughout the injection period. Further details on the stream injection will be reported by Baker et al. (unpublished). A total of 86 g of $^{15}$NO$_3$-N and 5 g of seston $^{15}$N were estimated to have entered the lake from the stream injection during the addition. By the end of the season it was estimated that 110 g of $^{15}$N as NO$_3^-$ and 12 g as seston entered into the lake from the stream injection. Laboratory measurement protocols for Br$^-$ and $^{15}$N are described below.

*Lake Collections* - Isotope samples were taken prior (to obtain background del $^{15}$N values), during, and subsequent to the tracer injection -5, 0, 3, 8, 15, 30, 51, and 115 days after the start of the injection (day 0) for each of the ecosystem compartments. Ecosystem “compartments” sampled included dissolved $^{15}$NO$_3^-$, seston (phytoplankton + bacteria + detritus in the water column), zooplankton, epiphytes (attached algae growing on macrophyte hosts), macrophytes, sediments, fish, and benthic invertebrates (Ephemeroptera, Odonata, Amphipoda). Fluxes of $^{15}$N were measured as sedimentation and as dissolved $^{15}$NO$_3^-$ and seston in the stream outflow. All samples were stored promptly on ice while transported to the lab, dried (at 60°C) and encapsulated in the laboratory in preparation for analysis at the UC Davis Stable Isotope Facility (SIF). Results from the SIF included mass of N and the atom ratio ($^{15}$N/$^{14}$N) of each sample.

Seston and bromide were sampled with a peristaltic pump at 0.5, 3, 6, 9, and 12 m depths and at four different stations (Fig. 4) through vinyl tubing. The depths at each station were 15 m (Stations 1 and 2), 10.5 m (Station 3) and 4.5 m (Station 4). Bottles were acid washed and triple rinsed with sample water before they were filled and
subsequently stored on ice. Within 5 hours of collection samples were filtered in the laboratory through 80-µm mesh to remove zooplankton and onto 25-mm Gelman A/E filters (1.0 µm pore size) until clogged. The volume of water filtered was recorded and filters were dried at 60°C before encapsulation. A small sample of filtered water from each seston sample was frozen in a plastic vial for Br⁻ analysis. Water samples for DON and NO₃⁻ were analyzed using methods from Sigman et al. (1997). Water samples were spiked with NO₃-N and concentrated to 0.1 L by boiling before Devarda’s alloy catalyzed conversion of NO₃⁻ to NH₄⁺ during a 48-hr incubation. ¹⁵N-NH₄ was collected on an acidified filter, which was sent to the UC Davis SIF.

Bromide, ¹⁵NO₃⁻ and seston were sampled in the outflow stream at the same frequency as lake water by dipping sample containers into the thalweg. Discharge measurements are described above and samples were processed and analyzed with the same protocols as lake samples. Bromide samples were run on a Dionex ion chromatograph that uses a solid-state column medium to separate compounds by polarity. Anions are detected by a conductivity detector, which displays peaks with retention times and peak heights in µS (relative to known standards).

Zooplankton were sampled in vertical tows with a 24-cm diameter, 80-µm mesh net at each of the four stations. Quantitative tows were made at each station from 1 m above the lake bottom to the surface. The sample volume was recorded and a one-organism thick layer was filtered onto a 25-mm Gelman GF/D filter (2.5 µm pore size) and oven-dried for subsequent isotopic analysis.

Sedimentation out of the water column was measured near the four different sampling stations with traps that were 0.60 m long, 3.81 cm (diameter) polyvinyl chloride
pipes (capped on the bottom side) with floatation collars positioned with the entrance 1.5 m above the bottom of the lake. Traps were deployed at depths of 13.5 (Stations 1 & 2), 9 (Station 3), and 3 m (Station 4). To compare net and gross sedimentation, duplicate traps of two different treatments were deployed at each station. Traps measuring gross sedimentation were first filled with chilled, non-chlorinated tap water (to limit the entry of lake water (with seston) during deployment and then 50 ml of a high-density formalin preservative (2% formaldehyde and 5 g/L NaCl) was injected with a long tube to the bottom of the traps to stop organic particle decomposition. Traps measuring net sedimentation were also filled with chilled, non-chlorinated tap water before being deployed. After a 2-day deployment, sedimentation traps were slowly raised to the surface where the contents were transferred into storage bottles prior to filtration onto 25-mm Gelman A/E (1.0 µm pore size) until clogged.

Epiphyte and sediment core samples were taken along four different transects from the “corners” of the lake into the center (Fig. 4). These transects provided four spatial replicates for epiphyte and sediment $^{15}$N. Epiphytes were sampled at 3, 6, and 9 m along each transect by SCUBA divers who engulfed entire plants of designated species in a 41-cm tall, 11-cm diameter cylindrical plastic sample container (3.9 L volume). To minimize turbulence and the loss of loosely attached materials on the plants, the top cap was modified with 323-µm mesh to allow water through as the container was placed over the plant. A solid cap was fitted back onto the bottom of the container once the macrophyte was cut at the sediment surface. After the diver returned the sample to the boat the mesh cap was replaced with a solid lid, and the sample was vigorously shaken for one minute to dislodge attached epiphytic algae and sedimantated particles from the
macrophyte host. Macrophytes were then removed from the sample, the volume of the epiphyte solution was recorded and the samples were stored on ice until laboratory processing. In the laboratory macrophytes were dried to constant weight and epiphyte solutions were filtered onto 25-mm Gelman A/E filters (1.0 µm pore size) until clogged, and the volume of water filtered was recorded.

In addition to sampling epiphytes, SCUBA divers estimated percent cover of each macrophyte genus (and bare sediments) at 1.5-m depth increments along each of the four transects. A rectangular quadrant divided into a grid was used by two different divers to estimate percent cover. The mean coefficient of variation between the two divers for these observations was 22%, indicating moderate error in our estimates. One section (4%) of the quadrant was harvested entirely, dried, and weighed to obtain a standard weight of plant material per area at each transect and depth. These estimates were used to estimate whole-lake macrophyte and epiphyte biomass.

In an effort to measure the $^{15}$N uptake by bare sediments (not covered by macrophytes), cores were taken with a Wildco® 4.8-cm diameter gravity corer at lake depths of 0.5, 1, 3, 6, 9 and 12 m along each of the four transects. In the lab, the first 4 cm of the upper part of the core were sectioned into two separate 2 cm slices, placed into sample cups and dried in an oven at 60°C until the weight was constant. Once dried, these samples were homogenized and ground into a powder with a mortar and pestle prior to encapsulation for isotopic analysis.

Brook trout (18 – 23.5 cm FL) muscle plugs were collected from anglers, dried and then ground into a powder before encapsulation. A muscle plug was removed from behind the dorsal fin of the fish, dried and then ground into a powder before
encapsulation. An estimate of fish biomass in BTL was obtained from assessments of similar Idaho ecosystems by Reiman (1992) and Gross et al. (1998), utilizing chlorophyll-biomass relationships ($y=2.2x^{1.3}$; $r^2=0.63$). This yielded an estimated fish biomass of 2.2-5.5 kg ha$^{-1}$ (we used the mean) based on chl concentration of 1-2 µg L$^{-1}$.

Aquatic insects were sampled at three different stations along the western edge of the littoral zone with dip nets. Insects of the same order were dried and ground into a powder for encapsulation. We assumed a biomass estimate for alpine lakes/oligotrophic temperate lakes (0.4 – 1 g dry wt m$^{-2}$) reported by Le Cren and Lowe-McConnell (1980).

**Tracer Mass Balance** - A mass-balance was constructed for $^{15}$N in BTL for the extent of our sampling program (summer 2008). The $^{15}$N mass-balance summarizes $^{15}$N uptake and transfer from the $^{15}$NO$_3^{-}$ delivered by the inflow (Spring Creek) to bacteria and primary producers, primary and secondary consumers, sedimentation out of the water column, or export out of the system (through the outflow). This $^{15}$N inventory assessed $^{15}$N uptake, storage, and loss in each of the ecosystem compartments throughout the growing season and compared this storage to the total $^{15}$N that entered the lake. Uptake of the $^{15}$N tracer was assessed by change in the atom ratio of samples above background, which is depicted by $\delta^{15}$N and calculated by:

$$\delta^{15}N = \left[\frac{(R_{sample} - R_{background})}{R_{standard}} - 1\right] \times 1000$$

where $\delta^{15}$N is expressed per thousand (‰), $R_{sample}$, $R_{background}$ and $R_{standard}$ are the $^{15}$N/$^{14}$N ratios of the sample, background samples and standard (‰ =0), respectively. Isotopic samples were analyzed with a Europa Scientific ANCA 2020 mass spectrometer linked with a CN analyzer at the University of California Davis SIF.
The $^{15}$N content in each sample was determined by the isotopic enrichment of the sample, the isotopic enrichment of samples taken prior to the tracer addition, and the mass of N in the sample according to:

$$N_x = N_i \ast R_{\text{sample}} - R_{\text{background}}$$

where $N_x$ is the mass of tracer $^{15}$N in the sample, $N_i$ is the mass of nitrogen in the sample, $R_{\text{sample}}$ is the atom ratio of the sample, and $R_{\text{background}}$ is the atom ratio of the background (taken prior to the $^{15}$N injection).

The total mass of tracer $^{15}$N in each ecosystem compartment was calculated from the product of the mass of $^{15}$N tracer in the samples and the total volume (or area) of the given compartment. A hypsographic curve for BTL was used to estimate volumes and areas of different strata. Stocks of $^{15}$N tracer in a given sample were extrapolated out to the rest of the lake area in the same depth strata. Water column concentrations (DON, seston, zooplankton, and fish) were multiplied by the total volume corresponding to the same depth strata as the sample, and epiphyte, macrophyte, and insect densities were multiplied by the benthic area corresponding to the depth strata of the sample by:

$$N_i = N_x \ast A_l$$

where $N_i$ is the total $^{15}$N tracer in the ecosystem compartment of the lake, $N_x$ is the mass of $^{15}$N tracer in the sample and $A_l$ is the total area (or volume) of the lake of the same depth as the sample. The total mass estimates from samples at each transect/station were averaged to generate one whole lake $^{15}$N estimates ($\pm$ s.d) based on four independent replicates.

For seston calculations the total volume of the lake was separated into volumes of the individual depth strata (surface to 1.5 m, 1.5 m to 4.5 m, 4.5 m to 7.5 m, 7.5 m to 10.5 m...
m, and 10.5 m to 15 m) corresponding to the depths sampled for seston. Zooplankton 
$^{15}$N samples were integrated through the water column and the volume sampled varied 
due to differences in depth among stations. Stations 1 and 2 were both located within the 
deepest portion of the lake (15 m depth); station 3 was at 10.5 m and station 4 was at 4.5 
m depth. The volume of the lake was therefore divided into concentric ovals 
corresponding to the depth strata of each station. Station 4 included 0-5 m; Station 3 5-11 
m and Stations 1 and 2 were averaged and included the volume of the lake between 11 
and 15 m (center of the pelagic zone). Measurements of $^{15}$NO$_3^-$ in water from Bull Trout 
Lake were not successful. Consequently, tracer nitrate in the water column was 
estimated by multiplying concentrations of $^{15}$NO$_3^-$ in the outflow (WSC) by the total 
volume of water in the lake.

Each epiphyte $^{15}$N sample was specific to its macrophyte host, at a specific depth, 
and along one of the four transects. To obtain $^{15}$N mass estimates for epiphytes, the 
density of epiphyte $^{15}$N at a given sample depth was multiplied by the total area of the 
lake at that depth strata, and subsequently by the percentage of the area covered by 
macrophytes of the given species at the given transect and depth (generated from the 
SCUBA macrophyte coverage surveys). Estimates for all three macrophyte hosts at the 
same depth and transect were summed to get a single total for each depth, and all depths 
at a given transect were summed to generate a whole-lake estimate. Depth strata were 1 – 
2.25 m, 2.25 – 3.75 m, 3.75 – 5.25 m, 5.25 -- 6.75 m, 6.75 – 8.25 m, 8.25 – 9.75 m, and 
9.75 – 11.25 m, which encompassed areas surrounding the depths at which samples were 
taken. Macrophytes were almost entirely absent from the 0 – 1.5 m and 11.25 – 15 m 
depth strata, and consequently these depths were not included in the estimate.
Estimates of the mass of macrophytes in the lake were generated by multiplying the mass of macrophyte samples by the total area of the lake at the given depth strata and by the percent cover of the given species at that depth. These mass estimates were multiplied by the atom ratio of macrophyte $^{15}$N samples to generate an estimate of $^{15}$N within the macrophyte pool.

Estimates of $^{15}$N tracer in benthic invertebrates and fish were done by multiplying $^{15}$N atom ratio values for each taxa by biomass estimates from the literature (g m$^{-2}$) and by the total lake area to obtain whole-lake $^{15}$N estimates for fish and insects. For the mass balance analysis and estimates of uptake and turnover, all insect taxa were grouped together to generate one estimate for the compartment. Although this approach yielded less accurate and detailed information than for other groups, the pools of isotope in the invertebrates and fish were small; thus these estimates should have had little impact on the overall isotope budget (see below).

Tracer uptake and turnover rates were calculated for each of the lake ecosystem compartments. Uptake rates for ecosystem compartments were estimated as the slope of the line fit to the natural log of delta $^{15}$N vs. time during the injection period. Net turnover rates (day$^{-1}$) were estimated from the decline of del $^{15}$N values in each ecosystem compartment as the slope of the curve (exponential) of del $^{15}$N vs. time (days since the start of the injection).

Results

*Hydrodynamics* - The cold Spring Creek water inserted into the metalimnion and epilimnion of BTL and the highest concentrations of Br$^-$ were generally between 3 and 9
m (Fig. 3). Minimal Br⁻ tracer was found at 12 m, indicating that there was limited underflow and/or mixing into the hypolimnion. Epilimnetic and metalimnetic concentrations of Br⁻ decreased rapidly following the termination of the injection, and then more slowly over the rest of the summer. By late July, average concentrations throughout the entire water column were ~12 mg m⁻³ (hydraulic residence time ~ 55 days). In contrast, hypolimnetic Br⁻ concentrations peaked at about 15 mg m⁻³ near the end of the injection and these elevated concentrations were sustained or increased slightly in the late summer when deep mixing occurred (Fig. 3). I used the integrated mass of bromide in the lake to estimate an overall turnover rate from 1-July to 12-September of 0.016 day⁻¹ as the tracer was exported slowly, especially as water residence time increased (Figs. 3 and 5).

Nitrogen Dynamics - Tracer ¹⁵N was quickly transformed from inorganic (¹⁵NO₃⁻) to organic forms as it was incorporated into the lake food web upon delivery from Spring Creek (Fig. 6; Appendix A). The highest and most rapid enrichment of the biota was in the seston (avg peak value 485‰; Fig. 6), within the first few days of the injection. However, after the injection ended on 30-Jun, the tracer moved out of this compartment in an exponential decline indicating short-term storage of the tracer and rapid turnover. Seston in the epilimnion became much more enriched than the hypolimnion with the highest del values sampled at 3 and 0.5 m (Fig. 7a). There was a short time lag before hypolimnetic seston became enriched and peak enrichment was only 238‰ on 21-Jul (9 m). While the tracer rapidly moved into and out of the epilimnetic seston, the rate of uptake and turnover was much slower within the hypolimnion.
Concentrations of tracer $^{15}\text{N}$ (Fig. 7b) followed a different distribution than delta values due to the presence of relatively high seston biomass in the deep chlorophyll layer (Fig. 3). Although $^{15}\text{N}$ was most concentrated in the epilimnion shortly after the injection, it was rapidly lost from that layer via sedimentation and washout so that by late July and early August the highest concentrations of tracer $^{15}\text{N}$ were found at 9 and 12 m. The specific uptake rate of the whole-lake seston pool from 20-Jun – 29-Jun was 0.50 day$^{-1}$ and the turnover rate after the addition ended was 0.038 day$^{-1}$. The turnover rate of the epilimnion (0.04 day$^{-1}$) was faster than that of the hypolimnion (0.03 day$^{-1}$).

Nitrogen ($^{15}\text{N}$) enrichment of seston in Warm Springs Creek (outflow) peaked at 399‰ following the termination of the tracer addition (Fig. 6). Concentrations of $^{15}\text{N}$ tracer also peaked right around the end of the injection at 39 µg/m$^3$ (Fig. 8) and declined immediately after the injection. The flux of $^{15}\text{N}$ tracer moving out of the lake as seston followed the same trend and peaked at 2.8 g $^{15}\text{N}$ day$^{-1}$ near the end of the injection.

Zooplankton enrichment peaked shortly after that of the seston and reached similarly elevated values. Average $\delta^{15}\text{N}$ values of zooplankton peaked at 483‰ (Fig. 6) and were highest at stations 3 and 4 (mean = 523 ‰) where there were only epilimnetic and metalimnetic organisms. Our vertically-integrated samples did not allow us to confidently assess the vertical distribution of zooplankton, but the differences between stations suggest that zooplankton in the upper, warmer strata, grazed more and became labeled more quickly than those in deeper strata. Delta values for zooplankton increased rapidly and as a compartment had a specific uptake rate of 0.41 day$^{-1}$. Additionally, the tracer was lost fairly quickly and the turnover rate was 0.03 day$^{-1}$. 
Epiphytes and macrophytes - Due to sedimentation of organic material out of
the water column onto submerged macrophytes, the epiphyte compartment includes both
eiphytic algae growing on macrophyte hosts and sedimented material that collected on
leaves and stems. Enrichment of epiphyte samples was moderate (peak of ~62 ‰)
compared to that of seston and there was a time lag (24 days) between the end of the
injection and peak enrichment of epiphytes (sestonic peak enrichment was reached before
the end of the injection; Fig. 6). There was not a dramatic difference (range 64-96 ‰) in
eiphyte enrichment among depths although the highest enrichment values were observed
at 6 m. While there was a difference in enrichment between macrophyte genera, I was not
able to separate this from the effect of depth given that the distribution of macrophyte
genera was largely influenced by depth. The specific uptake rate (0.18 day⁻¹) and
turnover rate (0.018 day⁻¹) were much lower than that of the seston and zooplankton
indicating longer-term storage within the compartment.

Enrichment of submerged macrophytes (Potamogeton spp., Elodea spp., and
Chara spp.) within the lake was only 4 – 10 fold above background. The highest delta
¹⁵N value for any macrophyte sample was 18.5‰ (Fig. 6); however, average values for
each depth and station were never greater than 9.5‰. Individual macrophytes took up
minimal ¹⁵N tracer; however, due to the large mass of macrophytes (~ 30 metric tons dry
weight) in the lake there was a noticeable mass of tracer within the compartment (see
below). The specific uptake rate for macrophytes was calculated to be 0.13 day⁻¹ and the
turnover time was not calculated due to sustained or increased enrichment through the
end of the season.
Sedimentation rates out of the water column varied substantially throughout the lake. Rates of sedimentation were the greatest at station 4 (4.5 m depth, near the outflow) followed by station 3 (10.5 m depth). Therefore, rates of sedimentation reaching the benthos were the lowest in the deepest portion of the lake. Delta values of sedimented materials peaked at 394‰, and followed the same trend as those of the seston (Fig. 6). Peak gross sedimentation rates ranged from 0.2 to 1.1 g $^{15}$N day$^{-1}$ among stations and net sedimentation was on average 76% of gross sedimentation.

Enrichment of BTL sediments with $^{15}$N above background was not observed, as delta values of sediment samples did not increase following the injection. While we hypothesize that a substantial portion of the tracer were stored within the sediments, we were unable to directly estimate this mass.

Enrichment of fish and insects within the lake was minimal compared to other lake compartments. Nevertheless we were able to follow the tracer into these compartments. Of the insect taxa sampled, damselflies (Odonata-Zygoptera: 50‰) and then mayflies (Ephemeroptera: 43‰) labeled the highest, while amphipods ($Gammarus$ sp.: 16.6‰) and brook trout (3.6‰) became enriched to a lesser extent. The specific uptake rate of the insect compartment (average for all taxa combined) was 0.08 day$^{-1}$ and the turnover rate 0.003 day$^{-1}$. Delta values in fish increased from 8‰ (background) to a maximum of 12‰ in mid-August. I did not estimate uptake and turnover rates of the fish because mass of tracer within the compartment was still increasing at the termination of sampling.

$Tracer$ $Mass-Balance$ - Following the termination of the 10-day tracer injection (on 30-June-08) 21% of $^{15}$N tracer was within the seston compartment, 17% in the
macrophyte-epiphyte complex, <1% in the insect/fish compartment, 6% exported as seston in the outflow stream, 4% exported as nitrate in the outflow stream, 2% had sedimented out of the water column and 13% was unaccounted for (Fig. 8). Although the seston rapidly assimilated $^{15}$N early in the experiment, 36% of the tracer in the lake remained as nitrate on the last day of the injection (based on estimates of $^{15}$NO$_3^-$ concentration in Warm Spring Creek). This amount may be somewhat overestimated because the calculation assumed that equal amounts of nitrate were mixed into all depth strata, but in reality, the hypolimnion received much less tracer (at least as estimated by bromide concentrations). Due to high stream flows (and therefore low residence time) during the injection, a substantial portion of the tracer was quickly lost via the outflow stream as both nitrate (4%) and seston (6%). The greatest uptake of any biological compartment was in the seston, however, the tracer was rapidly lost from the compartment (see below).

The mass balance and fluxes over the whole season are depicted in Fig. 9 and additional data is provided in Appendix B. As shown previously, seston quickly assimilated the most $^{15}$N (62 g on 30-Jun), but as the summer progressed, tracer within this pool sedimented out of the water column (50 g cumulative sedimentation by 12-Sep) or was exported from the lake via the outflow stream (cumulative 42 g). By the end of the season only 7% of the maximum accumulation of tracer remained within the seston compartment and only 8% in the nitrate compartment. In contrast, 54% of the maximum accumulation of tracer remained in the epiphyte/macrophyte compartment at the end of the season. Measures of both seston and nitrate export via WSC were cumulative and increased through the season; however, the majority of tracer had been exported by mid
July and additional exports were minimal between July and September. While our estimate of fish and benthic invertebrates was combined, the estimated mass in fish was <0.5 g and therefore the majority of that estimate is tracer within the invertebrate compartment.

Discussion

This whole-lake tracer experiment provided a unique opportunity to study nitrogen dynamics on an ecosystem scale. Given the influence lakes have on downstream water chemistry (Baron and Campbell 1997; Brown et al. 2008), we hoped to improve the current knowledge of in-lake nitrogen processing. To serve as a proxy for labile nitrogen delivered from the watershed, $^{15}$N was injected to the inflow stream as nitrate, given that the majority of inorganic nitrogen delivered to BTL in the spring is nitrate. While the mass of $^{15}$N added was not sufficient to fertilize in-lake production, it allowed us to follow the flow paths of stream-delivered nitrate into and through the food web throughout the growing season. The $^{15}$NO$_3^{-}$ tracer experiment comparatively quantified the roles pelagic and benthic primary producers play in the BTL food web. Additionally, it exposed the path taken by stream water and nitrate through the BTL ecosystem. This study may continue to pave the way for future whole-lake tracer experiments, which will help to advance the field of limnology (Kling 1994).

 Hydrodynamics and Nitrogen Movement - While $^{15}$N and Br$^{-}$ were delivered to the lake by the inflow stream, the movement of nitrogen through the lake differed from that of the path taken by water that was measured with the bromide tracer. Both tracers were found in greatest concentrations in the upper 6 m during the injection, however the
concentrations of $^{15}$N increased markedly at the 9 and 12 m depths (as the concentrations in the epilimnion decreased) following the termination of the injection. Little $^{15}$NO$_3^-$ was initially exported from the lake due to immediate uptake by lake biota and ecosystem “drag” on nitrogen as opposed to water. The drag on nutrients by biota is conceptually identical to nutrient retardation used by engineers, where the movement is slowed due to the non-conservative nature of the tracer. While concentrations of Br$^-$ throughout the different depth strata were fairly similar 3 weeks after the termination of the injection, concentrations of $^{15}$N in seston were highest in the hypolimnion due to sedimentation of the tracer out of the epilimnion. Therefore, even as epilimnetic waters were exported from the lake, the sedimentation and vertical migration of organic material kept nitrogen within the lake ecosystem. If I compare the removal of the two tracers from the system, the turnover rate of $^{15}$N in seston was 0.038 day$^{-1}$ while the turnover rate for the Br$^-$ pool was only 0.016 day$^{-1}$. Losses of the $^{15}$N tracer from the seston pool included export via the outflow stream (0.008 day$^{-1}$), but also consumption by zooplankton and sedimentation out of the water column contribute to the greater turnover rate of the tracer. The only loss of the Br$^-$ tracer was to the outflow stream and the increasing hydraulic residence time by mid-summer contributed to the slow turnover rate for the tracer out of the lake. However, when I look at loss of total $^{15}$N (not just pelagic) from the system, the loss rate of Br$^-$ is actually faster (0.016 day$^{-1}$) than total $^{15}$N (0.007 day$^{-1}$) further demonstrating the “drag” on nutrients as they move through the lake.

While enrichment of seston in the lake’s outflow was substantial, it was not to the extent of the epilimnetic seston in the lake. This may be an indication that the depths we sampled within the lake did not provide us with sufficient resolution of tracer dynamics.
within the different stratified layers. While we assumed that samples at a depth of 0.5 would be a proxy for the surface water, the tracer enrichment at 0.2 m depth (approximate depth of the outflow point) may have differed from that of 0.5 m.

Estimates of $^{15}$NO$_3^-$ within the lake were complicated by high analytical errors, presumably caused by faulty laboratory procedures and the difficulty with working with NO$_3$-N concentrations frequently <5 µg N L$^{-1}$. Therefore I relied upon estimates of $^{15}$NO$_3^-$ concentrations in the outflow to extrapolate to the lake. Whereas we feel this estimation technique is valid, concentrations in the lake could have varied from the south to the north and estimates may have been overly influenced by concentrations at the north end by the outflow. Therefore, there is some uncertainty involved in extrapolating $^{15}$NO$_3^-$ concentrations in the WSC to entire volume of the lake. The estimate of $^{15}$NO$_3^-$ within the lake peaked at the end of the injection (37% of the tracer). However, this pool was rapidly depleted to a small mass for the rest of the season as nitrate concentrations were reduced to <2 µg L$^{-1}$.

Pelagic vs. Benthic Pools - Nitrogen inputs to BTL delivered during spring runoff are taken up quickly by organisms within the lake, indicating strong reliance on inorganic nitrogen delivered from the upper watershed. Additionally, pelagic organisms have first chance at assimilating inorganic nitrogen delivered by the inflow due to the hydrodynamics of the lake-inflow stream interaction. The pelagic primary producers took up a greater portion of the nitrogen delivered to the lake than their benthic counterparts. However, I found that a substantial portion of the $^{15}$N tracer ended up in the benthic primary producer compartment. I must note, however, that estimates of epiphytes included nitrogen sedimented out of the water column and onto macrophytes. The pelagic
seston may have become more enriched with the tracer than benthic epiphytes due to the smaller size of the seston compartment and the secondary pathway of nitrogen uptake in epiphytes from benthic or macrophyte sources, which likely dilutes the tracer signature. These findings are vastly different from those of Axler and Reuter (1996) who found periphyton activity to account for >70% of nitrogen tracer depletion in Castle Lake (CA), however, the different methods of tracer addition in the two experiments may explain some of the discrepancy. First, the $^{15}$N tracer experiment done by Axler and Reuter (1996) was done in mesocosms within the littoral zone of Castle Lake. Results from this experiment may not be easily applicable to the whole-lake. Additionally their method of $^{15}$N addition to the mesocosms did not mimic the natural delivery of nitrogen to the lake ecosystem. Nitrogen was added to the “lake” in a pulse, in concentrations beyond tracer levels and the whole system was then mixed manually. In BTL the inflow stream is inserted directly into the pelagic zone and particularly into the upper metalimnion (Fig. 4) and therefore watershed-derived nutrients do not reach the littoral zone before passing through the pelagic portion of the food web. The majority of nitrogen delivered by the inflow stream appears to stay within the epilimnion before it is transported vertically via sedimentation or exported from the lake via the outflow stream.

The benthic portion of the BTL food web may not have access to nutrients delivered by the inflow stream until they arrive at the water-sediment interface either via mixing or sedimentation out of the seston. This may be due in part to the hypsometry of the lake and the hydrodynamics of how the inflow is inserted into the pelagic zone above the deepest portion of the lake (Fig. 4). During the mid summer, hypolimnentic $^{15}$N concentrations in the seston increased where Br$^-$ concentrations did not, indicating
transfer of $^{15}$N via sedimentation and not mixing (c.f. Figs. 3 and 7). However, all of
the sedimenting N may not reach the lake bed, as organic matter is hydrolyzed within the
water column, and at the fastest rates in the epilimnion (Ohle 1962). The highest rates of
sedimentation were measured at the shallowest station (4), as there is little time for N to
be hydrolyzed before it reaches the macrophytes or sediments, whereas, at stations 1 and
2 there is much more time and space for hydrolization of organic material before it settles
to the benthos.

Benthic primary producers generally have much more biomass than pelagic
primary producers (e.g. Vadeboncoeur et al. 2002; Tobias et al. 2003) and therefore serve
as a large sink for nitrogen. Many have argued that benthic primary production may be
more important than pelagic primary production in oligotrophic lakes (Axler and Reuter
1996; Vadeboncoeur et al. 2001). However, the benthic primary producers likely obtain
some of the needed N (and other nutrients) from the pelagic organisms via mineralization
of detritus that moves out of the water column via sedimentation. We estimate that as
much as 40% of tracer found within the epiphyte compartment was delivered via
sedimentation. Additionally, the complex of benthic primary producers may hold onto
nitrogen longer than pelagic organisms due to cycling within the benthic complex
(Carpenter and Lodge 1986; Tobias et al. 2003). Multiple studies in estuaries have
described uptake of remineralized nutrients from the sediment-periphyton community by
microphytobenthos, where nutrients are maintained within the benthic complex (Dong et
al. 2000; Tobias et al. 2003). In their 2003 estuarine nitrogen tracer study Tobias et al.
found that benthic processing was almost two orders of magnitude more important than
pelagic sinks for the $^{15}$N tracer. However, the Tobias study took place in a small estuary
where there is a much larger surface area to volume ratio. In BTL both the pelagic and benthic zones appear to be important for nitrogen cycling through the lake food web.

Epiphytic algae proved to be an important sink for nitrogen entering BTL. My estimates indicated that a substantial amount (14%) of the nitrogen tracer was taken up by epiphytes by the end of the injection. However, given the association of epiphytes with their macrophyte hosts and our method of sampling, this estimate is not free of error. The method of epiphyte removal from macrophyte hosts was assumed, but not proven, to be 100% efficient. After sampling macrophytes and attempting to remove epiphytes from the plants, it is possible that epiphytic algae remained on the macrophyte hosts. Therefore, estimates of $^{15}$N in epiphytes may have been underestimated while estimates of $^{15}$N in macrophytes may have been over estimated. Taking this into consideration, it may be valuable to consider epiphytes and macrophytes together as a single benthic plant assemblage and combine estimates of tracer uptake in the two compartments. Combining epiphyte and macrophyte $^{15}$N pools, we estimate that this combined benthic primary production compartment achieved maximum accumulation (57 g (18%) of the $^{15}$N tracer) on the last day of the injection but held on to the majority of this tracer into mid August.

While the pelagic portion of the lake appears to take up N first, the benthic compartment may hold onto nutrients and fuel production through the entire season. Once nitrogen enters the benthic compartment, via uptake of dissolved N in the water overlying the sediments or from sedimentation out of the surface waters, it is likely cycled within the sediment-benthic plant interface before it is made available to be incorporated back into the pelagic food web. The sediment-macrophyte-epiphyte complex may be very active in nutrient cycling as epiphytes rapidly assimilate nutrients
released by sediments and macrophytes (Carpenter and Lodge 1986). Conversely, as the lake stratifies and nutrients are transferred out of the pelagic zone, they may become “lost” from the pelagic zone to the profundal zone. While sediments may be subject to resuspension, those within the deepest water may not be subject to resuspension (Kalff 2002). These nutrients enter the hypolimnion via sedimentation, as there is very little mixing between stratified layers during this time. Therefore pelagic primary producers must rely on new inputs of nutrients from the littoral zone, the inflow stream or other sources to continually fuel production whereas the benthic zone may hold onto and recycle nutrients (Saunders and Kalff 2001). Additionally, nutrients released within the water column may not become re-available for uptake due to immobilization by bacteria (Uehlinger 1986).

The highest enrichment of $^{15}$N within the lake was within the seston and zooplankton compartments. The seston became the most enriched and took up the greatest mass of the $^{15}$N tracer compared to other measurable pools in the lake. The zooplankton compartment became enriched to nearly the same extent as the seston. However it is possible that detritus (including seston) was a component of zooplankton samples. Unidentifiable (seston or dead zooplankton) detritus was captured within the zooplankton nets and included on the filters analyzed for $^{15}$N and may have inflated the tracer signature of zooplankton samples. Even though the zooplankton became highly enriched, the total mass taken up by the compartment was minimal (2% of total tracer) due to the low biomass of zooplankton within the lake (mean of 7 mg C m$^{-3}$). Therefore, zooplankton appear to play a small role in the BTL ecosystem nutrient budget. Therefore in comparison to primary producers, these higher trophic levels appeared to take up a
small portion of the total nitrogen delivered by the inflow stream. Aquatic insects and fish also took up a minimal mass of $^{15}$N. Within the insects, predatory damselflies took up the tracer slower than grazer mayflies or detrivore amphipods, however became enriched to a greater extent by the end of the summer. The turnover rate I estimated for insects was much slower than that of the seston and zooplankton, which is consistent with what we know about body size and turnover rate (Brown et al. 2004). Likely due to the large body size and slow tissue turnover in trout; the compartment never became a significant sink for the tracer.

**Sediments** - While a substantial portion of the $^{15}$N tracer likely entered the BTL sediment compartment (Axler and Reuter 1996; Nydick et al. 2004; Lockwood 2009); I was unable to quantify an estimate based on the samples we collected. We hypothesize that the total sediment nitrogen pool is so large that the $^{15}$N signature was overwhelmed by the massive pool of nitrogen (99.7% $^{14}$N). This likely occurred in the benthic plant compartment to some extent. Given that epipelic algae grows at highest density on the surface of the sediments, we may have had better luck observing the tracer enrichment if we had separated the top 5 mm of the sediments for separate analysis. The mass of nitrogen that enters the lake sediments comes from at least two different sources. One of these is from the uptake of dissolved N (by primary producers and bacteria) out of the water column and another is from sedimentation out of the water column. However, in areas covered by macrophytes (63% of lake area) sedimentation initially deposits N within the macrophyte complex and not onto the sediment surface. A portion of the tracer that was classified as “unknown” in the mass-balance likely entered into the sediment compartment. Denitrification has been found to be negligible within the system and is
therefore not a likely sink for tracer (M. Baker, unpublished), at least during the spring-summer period. Where there may be other compartments that may have assimilated the tracer but were not quantified in this study, I feel that it is likely that a large portion of the unaccounted for tracer entered into the sediments.

Given that the majority of nitrogen tracer experiments have been done in streams, it is valuable to compare our findings with those. Hall et al. (2009) found that the majority of export of a $^{15}$NO$_3^-$ tracer in Spring Creek (Bull Trout Lake’s inflow stream) was by seston. However, the majority of uptake of $^{15}$N tracer was within the benthic compartment, which may have simply been exported as seston due to scour. High assimilatory N removal in Spring Creek is perhaps not surprising given its low given low inorganic N concentrations and high demand for the nutrient (Hall et al. 2009). This describes the situation with BTL as well. Had nitrogen from Spring Creek been delivered to BTL differently, we may have observed a dominance of uptake by benthic primary producers as well. Additionally, Hall et al. described long residence times of nitrogen within benthic compartments. While I did not quantify the residence time of N within benthic algae, our data demonstrates that nitrogen is held within the benthic complex. Finally, Hall et al. stress the importance of the hyporheic zone within Spring Creek, especially during high discharge. Within the stream, nitrogen can be transported out of the system and permanently or temporarily lost via hyporheic flow. Given a substantial mass of tracer that was unaccounted for, we must consider possible pools that make up the “unknown” compartment within our mass balance. While nitrogen is not likely lost from BTL to the hyporheic zone, it may be buried within the sediments and the interstitial waters, and never returned to the water column.
Through this tracer study we quantified the roles of pelagic and benthic compartments in incorporating watershed-derived nitrogen into the BTL ecosystem. Pelagic primary producers appear to have a competitive advantage in initially incorporating this inorganic nitrogen largely based on hydrodynamics of the inflow nutrient delivery. While uptake occurs in the epilimnion, nitrogen is quickly passed down to the hypolimnion and on to the surfaces of macrophytes in the littoral zone via sedimentation. Even though BTL is dominated by littoral habitats, the hydrodynamics of Spring Creek entering into BTL do not result in immediate delivery of nitrogen to benthic plants. While a large portion of the $^{15}$N tracer was incorporated into the epiphyte compartment, this uptake occurred slower than that into the seston and may have been partially due to sedimentation out of the epilimnion. This experiment demonstrates the lesser role that the upper levels of the food web play in nutrient assimilation as very little tracer was found in zooplankton, insects and fish.

REFERENCES


Figure 1. Location of the Bull Trout Lake watershed in Central Idaho, USA. Bull Trout Lake is the large lake in the watershed cutout of the figure and feeds the South Fork Payette River.
Figure 2. a) Temperature profiles of Bull Trout Lake throughout the spring and summer of 2008. Curves represent stratification of the water columns and horizontal rectangles on each curve represent the measured Secchi depth at the given date. b) Distribution of chlorophyll a in the Bull Trout Lake water column at five different dates during the summer of 2008. During the whole study the maximum chlorophyll concentrations were in the metalimnion and migrated progressively deeper as the summer progressed.
Figure 3. a) Hydrograph of the outflow of Bull Trout Lake (Warm Springs Creek) during the summer of 2008 (solid line). The theoretical hydraulic residence time for a fully-mixed lake is shown in the dotted line. b) Concentrations of bromide tracer in different depth strata of Bull Trout Lake. Errors bars represent standard error of estimates. Horizontal thick black line represents the duration of the bromide and $^{15}$N tracer injection.
Figure 4. Bathometric map of Bull Trout Lake showing the sampling stations and sampling transects. The red star indicates the site on Spring Creek where the tracers were injected. Numbered stars are pelagic stations while numbered black lines are benthic transects. Depth isopleths are in meters.
Figure 5. Loss of $^{15}\text{N}$ and Br$^-$ tracers from the Bull Trout Lake ecosystem. Dotted curve (highest in the figure) represents the loss of total $^{15}\text{N}$ tracer from the ecosystem ($r^2 = 0.59$). Solid line represents the loss of Br$^-$ tracer from the lake ($r^2 = 0.65$) and the partially dotted line (lowest in the figure) represents the loss of $^{15}\text{N}$ tracer from the seston ($r^2 = 0.99$). Equations are from exponential curves fit to the decline data for each tracer. The exponents of the loss curve indicate the turnover ratios for the two tracers.
Figure 6. Delta $^{15}$N values throughout the 2008 season for ecosystem compartments in Bull Trout Lake. Horizontal thick black line represents the duration of the injection.
Figure 7. a) Delta $^{15}$N values throughout the 2008 season for Bull Trout lake seston separated by each depth strata for which we sampled. Error bars represent the standard error of samples. b) Concentrations of $^{15}$N tracer in the Bull Trout Lake seston by depth strata. Error bars represent the standard error of samples.
Figure 8. Mass-balance of $^{15}$N tracer within Bull Trout Lake at the end of the 10-day injection (30-June-08). The whole “pie” represents the total mass of tracer and the individual “slices” are the mass found within each labeled compartment on day 9.
Figure 9. Mass-balance of $^{15}$N tracer within Bull Trout Lake throughout the whole summer. The total height of the figure represents the total mass of tracer (306 g) entering the lake. The thickness of each individual shaded band represents the mass of tracer in the given compartment. Zooplankton (checkered) and insect + fish (solid black) are found towards the middle of the figure but are hardly visible due to the small mass. Cumulative fluxes are shown for sedimentation and export of seston and $^{15}$NO$_3$ . "Unknown" represents tracer that was not accounted for in the sampling, or cumulative errors in other compartment estimates.
CHAPTER III

A MODELING APPROACH TO ASSESSING THE EFFECT OF MULTIPLE LAKES IN A SEQUENCE ON NUTRIENT TRANSPORT

Introduction

Lakes have traditionally been viewed as discrete entities within watersheds, reflecting the reluctance of aquatic ecologists to consider streams and lakes within watersheds as a single ecosystem (Jones 2010). Although some watershed-scale studies have assumed lakes to be unimportant in affecting nutrient transport (e.g. Sickman et al. 2003), others have suggested that lakes can significantly decrease or alter the timing of nutrient export (Baron and Campbell 1997; Brown et al. 2008). More recent work has shown lakes to be extremely important within watersheds, influencing the transport of nutrients and water downstream (Kling et al. 2000; Brown et al. 2008). Specifically, lakes have been shown to prolong nitrogen transport through watersheds by buffering spring transport and converting inorganic N to organic N through uptake and transfer (Brown et al. 2008). While lakes can be sinks for certain nutrient species such as nitrate (Kling et al. 2000), they have also been shown to be sources of dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) to downstream ecosystems (Brown et al. 2008; Marcarelli and Wurtsbaugh 2007). Given the potential for lakes to influence nutrient
transformations and transport, their importance within their watersheds cannot be underestimated.

Ecologists have begun to explore the effect of the physical characteristics of watersheds on downstream water chemistry. Focusing specifically on lakes, studies have correlated variation in water chemistry within lakes with physical variables within their watersheds. In some cases, nutrient concentrations may be largely influenced by the geology and land cover of the catchment (Swanson et al. 1988; Johnson et al. 1997). The parent geologic material (Duarte and Kalff 1989), percent of forest cover (Hood et al. 2003), and the amount of lake area (Brown et al. 2008) relative to stream area are all factors that can dramatically influence nutrient concentrations and nutrient flow within watersheds. Given the influence that lakes can have on nutrient transport, the percent of lake cover in addition to the size and location of lakes within watersheds also have the potential to significantly influence nutrient processes at the watershed scale (Kratz et al. 1997; Riera et al. 2000). Other variables also influence flow paths and therefore the speed at which water travels as runoff. The size and location of lakes (which determine hydraulic residence time), and the proportion of the watershed that contributes runoff that passes through a given lake, are highly influential in determining the proportion of runoff in the watershed that is subject to the influence of the lake (Jones 2010). Collectively, the number, size and position of lakes in a watershed may all be important in addition to the location of lakes in determining downstream water chemistry.

As described above, traditional perspectives on lakes have depicted the systems as net nutrient sinks (Jansson 1979; Persson and Broberg 1985). Nutrient pulses delivered by the inflow streams are slowed down when they reach the lake, assimilated and
maintained within the lotic biota, and/or settled down to the hypolimnion or sediments where they may be “lost” from the food web. However, certain attributes of lakes may cause them to serve as nutrient sources within their watersheds.

The nutrient balance in a given lake is influenced by many factors including loading from the inflows and the biological community within the lake. In high elevation, nutrient-poor watersheds, streams carry the majority of nutrients during high flow periods and therefore nutrients are transported through the streams without adequate time for uptake by stream biota. However, once these flows enter into lakes, velocities are slowed dramatically and contact time between biota and organisms increases. The effects of a single lake within a watershed may be compounded by the presence of other lakes downstream by exacerbating or negating the effects of the first lake. Multiple, linked lakes are a common feature of many watersheds, particularly those in glaciated areas.

In this study I analyzed and modeled nutrient transport and other limnological parameters in glaciated watersheds of the Sawtooth Mountains of Idaho. The study was part of a larger Stream-Lake Interaction (SLI) project aimed at investigating the effects complex watersheds (multiple lakes connected by stream channels) have on downstream water chemistry in comparison to simple (stream only) watersheds. To examine the nutrient dynamics within a single small oligotrophic mountain lake, (Bull Trout Lake (BTL)) and test the hypothetical effects of multiple lakes in series within the watershed, I applied a one-dimensional lake water quality model. Empirical data was collected; the model was populated and then calibrated using these data and literature values. Using this calibrated model, I simulated the response of multiple lakes in series to assess their biological and chemical responses.
Study Site

Bull Trout Lake is located in the Boise National Forest, just northwest of the Sawtooth National Recreation Area (central Idaho, 44° 17’ 58” N, 115° 15’ 16” W) and forms part of the headwaters of the South Fork Payette River (Fig. 10). The lake is a 0.29 km² moraine-dammed system at 2118 m elevation that drains an 11.7 km²-glaciated watershed. Mean lake depth is 4.3 m with a maximum depth of 15 m. The lake is oligotrophic with an average epilimnetic summer chlorophyll concentration of 1.1 µg L⁻¹. Lake water residence time ranges from 7 days during peak spring snowmelt to 150 days during summer baseflow conditions. Bull Trout Lake is dimictic, and in 2008 mixed completely by late May and again in early October. Spring Creek forms the inflow to BTL and is a second-order, gravel-bed stream. The outflow is Warm Springs Creek.

Bull Trout Lake contains dense submergent macrophyte beds between 1.5 and 9 m depths (i.e., the epilimnion and metalimnion) that total approximately 30 metric tons of dry weight during mid-summer (Epstein, Chapter 1) with a C:N ratio of 11:1. Primary macrophyte species in BTL include Potamogeton praelongus, Elodea canadensis, and Chara spp. Senescence of these macrophytes is known to occur from mid-July to late-September (Carpenter 1980; Janse et al. 1998).

Stream hydrographs are dominated by spring snowmelt, and the area is typically snow covered from mid-November to late-May or early-June. Bull Trout Lake watershed is mostly undeveloped (>99% forested) with only limited recreational land use and low
wet atmospheric N-deposition (~1.0 kg ha\(^{-1}\) yr\(^{-2}\); NADP 2001). Lakes in the Sawtooth Mountains are oligotrophic, and primary production is co-limited by phosphorus (P) and nitrogen (N) availability (Wurtsbaugh et al. 1997).

Methods

Hydrologic Data Collection

To populate and calibrate our BTL model, limnological data was collected prior to and throughout the 2008 ice-free season. Stream discharges (Q) were measured weekly using a flow meter and top-setting wading rod (Flo-mate 2000, Marsh-McBirney Inc., Frederick MD), and stream stage was measured hourly with capacitance rods (Tru-Track, Inc., Christchurch, New Zealand) from April 2007 through October 2008. Bull Trout Lake inflow and outflow gauging stations were located 60 and 560 stream meters upstream and downstream of BTL, respectively, and stream stage-discharge relationships were established to estimate continuous stream discharge (Fig. 11). Lake bathymetry with 1-m depth isopleths was generated using hypsographic data analyzed by Arp et al. (2006). Daily rain and snow precipitation data was obtained from the Banner Summit SNOTEL (NRCS 2010), which is located 2 km from the lake at an elevation of 2140 m. Daily mean wind data was obtained from the United States Forest Service Ranger Station in Stanley, ID, 28 km SE of BTL.

Sample Collection and Chemical Analysis

Stream water samples were collected at BTL inflow and outflow gauging stations every 2-3 days during the ascending and descending limbs of the 2008 snowmelt hydrograph peak, and weekly throughout summer baseflow. I filtered replicate stream-
water samples through ashed 0.7 µm glass-fiber filters (Whatman GF/F, Maidstone, UK), for DOC, DON, NO\textsubscript{3} -N, NH\textsubscript{4}\textsuperscript{+} -N, and PO\textsubscript{4}\textsuperscript{3-} -P (soluble reactive phosphorus; SRP) analysis. Filtered stream water samples for DOC were acidified with HCl to a pH <2 and stored in the dark until analysis, while filtered stream-water samples for NO\textsubscript{3} -, NH\textsubscript{4} +, SRP and DON were frozen until analysis. DOC concentrations were measured on a Shimadzu TOC analyzer (OI Corporation model 700, College Station TX) using wet persulfate oxidation (Menzel and Vacarro 1964). All other dissolved nutrient analyses were measured colorimetrically on an Astora autoanalyzer including TDN using persulfate oxidation following procedures by Valderrama (1981), NO\textsubscript{3} -N by colorimetric analysis via cadmium reduction (detection limit 0.6 µg/L) and NH\textsubscript{4} + -N by colorimetric analysis via phenolhypochlorite (detection limit 0.9 µg/L; Solorazo 1969). DON was calculated as total dissolved N (Valderrama 1981) minus dissolved inorganic N (NO\textsubscript{3} - and NH\textsubscript{4} +). PO\textsubscript{4} -P was measured by ascorbic acid molybdenum reaction for soluble reactive phosphorus (detection limit 0.57 µg/L; Murphy and Riley 1962). I also collected unfiltered water samples for total nitrogen (TN) and phosphorus (TP) analysis. TN and TP were measured colorimetrically on an Astoria autoanalyzer (Astoria Pacific International, Portland OR) following Valderrama (1981), with respective detection limits of 5.7 and 2.5 µg/L.

Weekly to biweekly throughout the summer, measurements of temperature, DO, Secchi depth transparency, and Chl \( \alpha \) were taken in BTL. Temperature and DO were measured at 0.5, 1, 3, 5, 8, 12, and 14 m depths with a YSI Model 85 meter (Yellow Springs, OH). Water transparency was measured using a 25 cm-Secchi disk. Chlorophyll \( \alpha \) was measured by filtering 50 mL of lake water collected at 3 and 11 m depths (to assess
both surface and deep chlorophyll layers), 25-mm diameter GF/F filters, freezing, and subsequently extracting them in 95% ethanol for >12 h in the dark at room temperature. Chlorophyll fluorescence was measured on a Turner 10-AU fluorometer (Turner Designs, Sunnyvale, CA) following Welschmeyer (1994). Particulate organic carbon (POC) samples were collected by filtering a known volume of (both lake inflow, outflow, and lake 3 m depth) water through a pre-combusted GF/F filter until clogged. Filters was then dried at 60°C for 48 hours and analyzed at the University of California Davis Stable Isotope Facility’s elemental carbon (C) analysis using a PDZ Europa ANCA-GSL elemental analyzer (Sercon Ltd., Cheshire, UK).

Model Description and Assumptions

The Lake2K model (Chapra and Martin 2004) incorporates water, heat, and nutrient mass balances, along with light, ice, vertical mixing, sediment flux, primary and secondary production models to depict a vertically stratified lake (Fig. 3). The model is designed to simulate seasonal patterns in a stratified lake (epi-, meta-, and hypolimnion) and model predictions include ice melt, temperature, water clarity, as well as concentrations of inorganic and organic nutrients, dissolved oxygen (DO) and phytoplankton (Chl a).

The Lake2K model simulates a lake as a one-dimensional conical system consisting of three vertical layers (Chapra and Martin 2004; Fig. 12). The volumes of the two deeper layers are held as fixed, whereas the epilimnion is allowed to change as a balance between the inflow and outflow change. The inflow (representative of all flows entering the lake from tributaries, and direct point and non-point sources) is routed into
one of the three layers based on the density of the incoming water relative to that of each stratified layer. The source of the lake’s outflow is designated by the user and can be routed from any of the three vertical layers. Mixing between the stratified layers is by turbulent diffusion, and vertical diffusion coefficients are typically calibrated. The biological component of the model includes phytoplankton, however, no benthic primary production is included in the model.

In the BTL model, volumetric discharge inflows and outflows were assumed to be identical and the outflow was then set to exit the lake via the epilimnion (i.e. surface outflow). The inflow discharge was set equal to the measured outflow discharge to achieve constant volume. These assumptions were made because the BTL inflow enters the lake through a large sand-gravel delta, where both surface and groundwater inflows enter, and additionally via non-channelized hill slope runoff along the lake margin (Arp et al. 2006), making stream inflow discharge data unrepresentative. In the model I also assumed that the temperature and chemistry of the water entering the lake via subsurface flow paths was similar to those measured in the spring-fed inflow stream.

Adaptations of the Lake2K Model

As previously mentioned, within Lake2K the inflow stream is routed into the stratified layer that is most similar in density (i.e., the plunging inflow phenomenon; Effler et al. 2009). Tracer experiments in BTL and other mountain lakes in the region, however, have shown that the cold inflow streams normally do not plunge to the hypolimnion (Fleenor and Schladow 2000; Wurtsbaugh, unpublished data). Rather, the lake inflow water entrains substantial quantities of epilimnetic water and enters into the
intersection between the lower epilimnion and the upper metalimnion (Fleenor and Schladow 2000). To account for this inflow pattern, the model was modified to insert the inflow water into both the epilimnion and metalimnion, at 65 and 35% of the inflow volume, respectively, throughout the whole modeling period (regardless of the density gradients). This split of the inflow insertion was most appropriate based on previous tracer studies (Wurtsbaugh, unpublished data).

Model Population and Calibration

Bull Trout Lake was modeled for the ice-free season from 2 June 2008 through 1 October 2008. The BTL Lake2K model was populated with inflow discharge and water chemistry data, lake morphometry dimensions, meteorological data, and lake water chemistry data representing initial conditions. From mid-July through the rest of the summer, BTL outflow exported a greater TN load than the inflow stream imported. Thus it became clear that there was an additional source of nitrogen inputs within the lake (likely from benthic processes or groundwater inputs, which are assumed to be insignificant in this study). The Lake2K model does not account for benthic processes that are known to influence lake biogeochemistry, such as benthic algae (including N-fixers) or macrophyte nutrient uptake from the sediments and subsequent release into the water. According to Marcarelli and Wurtsbaugh (2009), benthic N-fixation contributes at least 2-4% of the TN load in BTL. Therefore to account for this contribution, I added this daily lake-scaled N-fixation rate as an additional NH$_4^+$ input to the lake via the inflow stream. Additionally adjustments (described below) were made for macrophyte nutrient inputs.
Submerged macrophytes are capable of mobilizing nutrients from the sediments directly via root uptake and can be a source of nutrients to the water column (Barko et al. 1991). To account for dissolved organic matter inputs to the lake from macrophytes, I added additional DOC (0.6 mg C/L), DON (0.06 mg N/L), and P\textsubscript{org} (2 µg P/L) inputs to the lake via the inflow nutrient fluxes beginning on 15 July 2008 until the end of the modeling period, 1 October 2008. This addition assumed ~6% day\textsuperscript{-1} of the macrophyte OM is converted to DOM through mortality and excretion, less than the 10% observed by Rich and Wetzel (1978) and I assume DOC is 45% of DOM (Craft et al. 1991). These additional inputs were 11% of the total inflow DOC load, 29% of the total inflow DON load and 19% of the total inflow P\textsubscript{org} load for the modeled time period.

I utilized water chemistry and temperature data for the epilimnion and hypolimnion for calibration of the model. I completed a sensitivity analysis with a separate model run representing a 5% increase and decrease for each of the ~45 parameters (in isolation) that the model-user is able to manipulate within the model. Following initial calibration efforts and a sensitivity analysis, I determined that the BTL Lake2k Model was relatively insensitive to changes in many of the parameters included in Lake2K. The root sum of squares (SSR) was calculated for the predicted results for NO\textsubscript{3} and DOC compared to the predicted results of the base case model run (representing the calibrated model). If the resulting SSR values were greater than 90 for NO\textsubscript{3} and/or greater than 10 for DOC, then the given parameter was utilized in model calibration. Our calibration efforts focused on nine parameters: organic carbon, nitrogen and phosphorus hydrolysis and settling rates; dissolved organic carbon oxidation rate; nitrification and denitrification rates; and maximum phytoplankton growth rate (Fig. 12). Calibration was
guided by literature values for similar lake systems and experimental manipulation of
the model.

Model Scenario

Following the adaptation, population, and calibration of the model, I generated a
clear depiction of the lake system. From the model output, I was able to quantify the
fluxes of heat, nutrients, and water into and out of the system. Based on our empirical
data and contrary to common perspectives of sub-alpine lakes being nutrient sinks, BTL
appeared to serve as a nutrient source within its watershed. The overarching question I
was interested in is: What is the effect of multiple lakes in series on nutrient transport
through watersheds? More specifically, will exported nutrients from a nutrient producing
lake become trapped in downstream lakes or will additional lakes have a compounding
effect of increasing nutrient fluxes downstream? To examine this question, I connected a
series of four BTL Lake2K models to form a hypothetical system where the inflow water
chemistry of the downstream lake was composed of the model results of the lake
upstream (including inputs from benthic N-fixation and macrophytes). Each lake was
named by its position within the sequence of lakes in the watershed, Lake 1 being the
first in the series and Lake 4 the furthest downstream. The outflow water chemistry of
Lake 1 was compared to that of Spring Creek (the inflow) and the outflows of each
consecutive downstream lake. Concentrations of macronutrients were compared between
the five different systems for the duration of the modeling period.

Whereas changes in average concentration of nutrients reveal ecosystem process
dynamics, they may not portray watershed level changes in nutrient transport. Therefore I
additionally provide results in terms of total nutrient fluxes (total mass per summer) to show changes in the total mass of nutrients moving within the modeled lakes. To demonstrate the effect of each lake on water chemistry, I describe the net change in flux of nutrients out of each lake as $\Delta X_Y$, where $\Delta$ represents the change in flux ($1 - ((\text{outflow mass} / \text{inflow mass}) * -1)$), $X$ is the nutrient of concern (POC, DOC, $N_{\text{Org}}$, $NO_3^-$, $NH_4^+$, $P_{\text{Org}}$ or $P_{\text{Inorg}}$), and $Y$ is the lake of focus (1, 2, 3 or 4). Positive values would then be representative of an increase in flux out of the lake and a negative value a decrease in flux.

**Results**

**BTL Observed and Predicted Trends**

The calibrated BTL Lake2K Model produced physical, biological and chemical results similar to those observed in BTL during 2008. Predicted concentrations for outflow water chemistry ranged from +/- 6 to 30% of empirical observations with most predicted values within +/- 15% of the observations (Fig. 13-15). With a much greater surface area to collect solar radiation, epilimnetic temperatures in BTL were consistently much warmer than the inflow stream (Spring Creek), and therefore annual temperature variation was greater within the lake (Fig. 13a). Summer epilimnetic temperatures warmed from around 5°C in late May to around 17°C into late August, while temperatures in Spring Creek never warmed beyond 7°C. Rapid warming of the epilimnion occurred from the start of the modeling period until mid-July when temperatures were fairly constant (~17°C) until cooling commenced in late August (Fig. 13a).
The trend of the predicted nutrient concentrations through the growing season followed those of the observations, with the highest concentrations moving through the lake during spring runoff and concentrations otherwise increasing into the late summer. For example, observed and predicted NO$_3^-$ concentrations were >2 $\mu$g/L in the early spring, decreased to near 0.1 $\mu$g/L in late June and July, and then increased to above 2 $\mu$g/L during fall turnover in October (Fig. 13c). Organic N (Fig. 13b), NH$_4^+$ (Fig. 14a) and chlorophyll $a$ (Fig. 14b) followed a very similar pattern, whereas phosphorus concentrations fluctuated much less through the season (Fig. 14c, 15a). Note that the concentrations of organic nutrients do not include the living stock of phytoplankton.

The measured water chemistry dynamics of BTL outflow were moderated by the lake and therefore much less variable than those in Spring Creek. This trend was reproduced in the BTL Lake2K Model, as flashy inflow dynamics were somewhat buffered by the lake. Particulate organic carbon appeared to hydrolyze or settle out within the lake, with predicted outflow concentrations much lower than those of the inflow (Fig. 15b). The highest concentrations of POC were delivered in the spring with decreasing concentration in all lakes through the rest of the summer. Similarly, predicted DOC concentrations were highest in the spring with a decreasing trend through the rest of the summer, with the exception of slight increases in mid-July and mid-September (Fig. 15c). Predicted concentrations of DOC leaving the lake were greater than those entering the lake, as DOC was produced within the lake ecosystem. The modeled dynamics of NH$_4^+$ followed a similar pattern to those of the inflow stream with increasing concentration in August (Fig. 14a). The outflow of BTL followed a similar trend to the inflow; however, concentrations increased earlier in the season than those in the inflow stream, indicating a
source of NH$_4^+$ other than the inflow or conversion of nitrogen forms. Concentrations of NO$_3^-$ and N$_{Org}$ out of the lake were lower than those in the inflow whereas the opposite trend was true for NH$_4^+$, likely due to the conversion of nitrate to organic N (algal uptake and growth), N-fixation and macrophyte inputs (Fig. 13a, b, 14a). Organic phosphorus concentrations peaked in the spring and dropped to a stable lower concentration through the rest of the summer (Fig. 15a). Both modeled P$_{Org}$ and P$_{Inorg}$ concentrations were lower in BTL than in the inflow stream (Fig. 14c, 15a); where P$_{Org}$ likely was hydrolyzed or settled out of the water column and P$_{Inorg}$ was consumed in primary production.

Lakes in Series Model

The multi-lake model predicted patterns similar to those of subsequent lakes downstream, with increases in temperature and nutrient concentrations (Fig. 16, 17, 18). In general, temperature and nutrient concentrations increased in each subsequent lake; however, the magnitude of change between lakes decreased. Warm water flowing out of Lake 1 (max temp 17.2°C) was further heated in Lake 2 and so on in downstream lakes until reaching a maximum summer water temperature of 19.7°C in Lakes 3 and 4 (Fig. 16a). A maximum temperature was approached in the downstream lakes, such that the increase between Lakes 3 and 4 was minimal.

Changes in average POC concentrations during the summer were dramatic from Spring Creek inflow to Lake 1 and from Lake 1 to Lake 2; however, changes were less dramatic from Lake 2 to Lake 3 (Fig. 16b). The model indicated that the majority of POC was lost in Lakes 1 and 2, and POC concentrations in Lakes 3 and 4 were nearly identical. The Lake 1 outflow concentration dynamics followed a pattern similar to that
of the inflow stream, only with time lags before increases in concentration and muted peak concentrations. Incremental increases in DOC concentrations were found in each of the four lakes with the seasonal trend similar to that of Spring Creek. The predicted increases in concentration of DOC in downstream lakes were likely due to hydrolysis of POC and macrophyte inputs (Fig. 16c).

Modeled total nitrogen, organic nitrogen and NH$_4^+$ concentrations increased in each downstream lake (Fig. 17a-c), likely due to phytoplankton death, macrophyte senescence and the hydrolysis of organic N. The modeled NO$_3^-$ concentrations were reduced in downstream lakes; late spring NO$_3^-$ was likely depleted by phytoplankton uptake, however, the modeled increase in concentrations through the late summer may be due to a combination of reduced phytoplankton uptake, nitrification of NH$_4^+$ and release from benthic sediments. Modeled organic nitrogen concentrations increased substantially in each downstream lake (Fig. 17a). Total nitrogen (TN) concentrations within the lake decreased through June (post peak runoff) and subsequently increased through the rest of the summer. Concentrations of TN increased in each downstream lake during all parts of the modeling period reflecting the production of NH$_4^+$ and N$_{org}$ in each lake.

Modeled P$_{org}$ concentrations in all lakes decreased following spring runoff and stayed fairly constant throughout July and August (Fig. 18b). Concentrations increased from Lake 1 to Lake 4 and the seasonal trend stayed consistent between lakes. The trends in P$_{inorg}$ concentrations in all lakes followed the dynamics of the inflow stream; however, there was a time lag and the extent of the variation was muted (Fig. 18a). Additionally, the trend in P$_{inorg}$ concentrations mirrored that of Chl $a$, demonstrating phosphorus limitation of primary production. In general, predicted P$_{inorg}$ concentrations decreased
dramatically in Lake 1, but were fairly constant in downstream lakes. Chlorophyll \( a \) dynamics followed a fairly consistent trend as Chl \( a \) increased incrementally in each downstream lake, following the dramatic increase from the inflow to Lake 1 (negligible Chl \( a \) was present in Spring Creek; Fig 18c). However, the increase in Chl \( a \) in each lake was of decreasing magnitude, demonstrating decreased production in each downstream lake (Chl \( a \) production data not shown). The increased mass of phytoplankton in downstream lakes was primarily due to exports from upstream lakes in addition to some production within each lake.

Despite sedimentation and other losses, the total flux of total macronutrients (C, N and P) increased with number of lakes. In general, inorganic forms were depleted while organic nutrients were increasingly produced with additional lakes. Values of the net change in flux (negative values indicate a net reduction in nutrient flux) are shown in Fig. 19a-c. In general the change in fluxes were greatest in Lake 1 and decreased from Lakes 2 to 4.

The greatest change in nutrient fluxes occurred within Lakes 1 and 2, while the \( \Delta \) values decreased in magnitude in Lakes 3 and 4 for all nutrient species (Fig. 19a-c, Table 1). Nitrate was lost within all four lakes; however, the mass lost in Lake 1 was much greater than in any other lake (Fig. 19a). Nitrate was continually depleted in all downstream lakes but the total mass lost (taken up) was minimal in Lakes 3 and 4.

Ammonia was produced in all lakes but the greatest increase was in Lake 1. Similarly \( N_{\text{org}} \) increased in all lakes, however the greatest increase in flux was in Lake 2. POC decreased in all four lakes while DOC increased (was produced). The majority of POC
was lost in Lake 1 while the net change in Lake 4 was close to zero (Fig. 10b). Inorganic P decreased within all lakes while P$_{\text{org}}$ was produced (except for in Lake 1; Fig. 19c).

**Discussion**

Modified Model

I was able to accurately depict the summer dynamics of BTL using a simple 3-layer, one-dimensional lake model. During the collection and analysis of empirical data, I determined that there were significant inputs of nutrients to the lake from a source other than the inflow stream, largely from benthic sediments (and macrophytes) and/or nitrogen fixation. These benthic primary producers play a crucial role in delivering nutrients that may otherwise not be available into the water column, and subsequently making the lake a nutrient source within its watershed (on a single-season time scale). The role of BTL as a nutrient source in the watershed is not unique, as others have indicated that lakes may act as sinks or sources depending on the season (Brown et al. 2008). However, some studies have depicted lakes strictly as nutrient sinks, due to sedimentation and nitrification (Harrison et al. 2008). This analysis of BTL observations shows that the lake exported around 10% more N than it received in 2008, while in New Zealand lakes and reservoirs Alexander et al. (2002) found that TN removal ranged from 1 – 87%. My estimate of a 10% increase in nitrogen flux is rough given that our model predictions were on average within just 15% of observed values. Nevertheless, in seven lakes within the Sawtooth Mountains, Goodman (2010) found that DOC increased from inflow to
outflow in lakes. While other studies have documented nutrient regeneration in lakes (Shaus et al. 1997), few have shown net production. Even though I suggest Bull Trout Lake acted as a nutrient source during the summer of 2008, I have not gathered enough information to make conclusions about other seasons or years.

Given the limited flux of nutrients delivered from the upper watershed in the inflow stream, the large mass of submerged macrophytes, and the large pool of nutrients buried within the sediments, these macrophytes appear to be an important conduit, transferring nutrients from the sediments into the water column. Rooted macrophytes have been shown to mine nutrients from the sediments (especially when concentrations in the sediments are higher than those in the water column) and release these nutrients to the water column during senescence (if not before; Barko et al. 1991). There are other potential pathways for nutrient inputs to the water column (i.e., inputs of shallow hyporheic flows with higher nutrients than those measured in Spring Creek); and further investigation of these pathways is warranted.

Lakes in Series Model

The results showed that the effect of multiple lakes in series appears to be important, causing substantial increases in downstream water temperature and nutrient concentrations. Some have suggested that landscape position of lakes can influence chemical concentrations; however, the trend with distance downstream can be both positive (Kratz et al. 1997) and negative (Kling et al. 2000). This analysis is the first (to my knowledge) that quantifies and compares the potential net nutrient flux through a series of lakes and between each successive lake downstream. Results showed that the
“lake effect” of incorporating, converting, and buffering the transport of nutrients was most pronounced in the first two lakes in the series, while those downstream of these lakes had a minimal effect on water chemistry and nutrient transport.

The model suggests that multiple factors interact to cause the increase in nutrient flux to downstream lakes. Increased temperatures, export of nutrients from upstream lakes and the internal loading of nutrients from N-fixation and macrophytes were largely responsible for the changes. Cold water delivered by Spring Creek warmed dramatically within Lake 1; however, heating in downstream lakes was limited as inflows to subsequent lakes were warm due to epilimnetic releases from warming upstream lakes. Given a limited heating potential (the meteorological conditions were the same for all of the modeled lakes), the increase in temperature in each subsequent lake was diminished. With the warming temperatures in downstream lakes and the direct inflow into the metalimnion, metalimnetic temperatures approached those of the epilimnion, allowing more mixing to occur in the lowest lakes of the sequence. This mixing caused increased variability in epilimnetic nutrient concentrations in the form of rapid jumps in concentration following mixing with the more highly concentrated metalimnion and hypolimnion. Warmer temperatures also increased the rate of chemical and biological reactions and potentially influenced the biological community.

Nutrient Dynamics

The majority of POC inputs entered the four-lake system via the Lake 1 inflow and the reduction of POC in downstream lakes was of a smaller magnitude, mainly due to settling and hydrolysis in Lake 1. Particulate carbon was collected from the landscape
and transported by Spring Creek but was delivered to the downstream lakes in diminished concentrations. Dead phytoplankton and macrophyte-derived detritus are the likely sources of POC generated within the lakes (Carpenter 1980, Hessen et al. 2003). Dissolved organic carbon increased due to hydrolysis of POC and macrophyte inputs, with a reduced increase in each downstream lake as POC was depleted and not produced substantially in downstream lakes. While analyses of series of lakes are lacking, it has been suggested that the presence of lakes may result in either the increase or decrease in DOM in downstream streams. Similar to our result, Brown et al. (2008) found greater concentrations of DOM downstream of lakes and suggest that lakes collect the pulse of nutrients delivered in spring runoff and slowly release them later in the season. Contrarily, Larson et al. (2007) found DOM was less abundant in streams below lakes due to increased residence time in lakes that could allow for microbial mineralization and photic degradation. However, their study was done in the upper peninsula of Michigan in mixed coniferous and deciduous watersheds. This contrasting result may be due to high DOM concentrations and DOM of different quality from deciduous forest within the watersheds they studied.

The source of NH$_4^+$ to downstream waters was likely the release from the sediments, N-fixation and hydrolysis of N$_{org}$ in the water column. Ammonia may remain concentrated in the water column due to low phytoplankton production that became limited by phosphorus availability and release from sediment and macrophyte sources (Dugdale 1965). Organic nitrogen is lost via sedimentation and hydrolysis; however, it is replenished in the water column via phytoplankton death and macrophyte inputs (Otsuki et al. 1972; Carpenter 1980). NO$_3^-$ was rapidly lost due to phytoplankton uptake and was
seldom replaced by any source other than the inflow stream to Lake 1, suggesting that nitrification is minimal in this system. The predicted depletion of $P_{\text{inorg}}$ in each lake was largely due to phytoplankton uptake and settling. Numerous studies have found that $\text{NO}_3^-$ and phosphorus are commonly depleted, due to uptake and sedimentation, and organic nitrogen is produced (Hillbricht-Ilkowska 1999; Brown et al. 2008). For the majority of the season modeled N:P ratios were well above Redfield (Redfield 1934), indicating P limitation, and the trend of Chl $\alpha$ concentrations mirrored that of $P_{\text{inorg}}$. This depletion of P may have resulted in limitation of primary production and subsequent excess of N in the water column. Even though $P_{\text{org}}$ was lost in each lake in hydrolysis and settling (organic), it was produced in each lake through macrophyte inputs and phytoplankton production, and therefore the lakes were net sources of $P_{\text{org}}$.

Our findings contradict the dogma of lakes as nitrogen (and other nutrient) sinks (Saunders and Kalff 2001). However, this result is based on observations from five months in 2008 and not an annual or multi-year nutrient budget. The four lakes in sequence appear to accumulate nutrients in their epilimnia irrespective of allochthonous terrestrial inputs (since we did not include these inputs), potentially resulting in more productive downstream waters. Some of this increase in nutrient concentrations is due to warming temperatures and the ensuing more frequent mixing between stratified layers. The remainder of the increase can be attributed to the transfer of nutrients from upstream lakes and autochthonous production/nutrient mining. Each lake has internal loading from N-fixation, phytoplankton production, and macrophytes in addition to the flux of nutrients from the upstream lakes. While some nutrients are lost to sedimentation, it appears that most are taken up and/or converted to another form and exported to the
downstream waters. Further depletion of some nutrients may be inhibited by nutrient limitation. In addition to nutrient accumulation in downstream lakes, phytoplankton (Chl $a$) was exported from one lake to the next and therefore Lake 4 had the highest Chl $a$ concentrations in the modeled four-lake system.

Strengths and Limitations

This research provides the development and application of a valuable tool in limnological research. Once calibrated, the Bull Trout Lake 2K model is easily manipulated and quickly run for hypothesis testing. I applied this model to investigate a watershed configuration found in nature; however, the model could be easily applied to explore other hypothetical situations or environmental changes. Our model incorporates benthic primary producers including submerged macrophytes, the role of which may be overlooked or underappreciated in other systems. Additionally, many lake models do not include compartments for benthic primary producers and submerged macrophytes, which proved to play a large role within the BTL ecosystem.

As with all ecological models, the application of this tool has its limitations; given that the BTL Lake2K model is a simplification of a lake ecosystem. While the model incorporates the basic components, fluxes, and characteristics of a lake, many other processes are either simplified or omitted. The hydrology of the lake is represented by a 1-dimensional cone vertically stratified into three layers receiving inputs from a single inflow and outflow in addition to precipitation. While I was able to modify the insertion of the inflow stream into the lake, this distribution of inflow water into the epilimnion and metalimnion may not have been accurate for all flow conditions, time periods, or all
modeled lakes. Additionally, there is no way to differentiate overland flow, groundwater, fixation or benthic inputs from the flux of water and nutrients delivered by the inflow fluxes. While this is a reasonable depiction of some lakes, this model may not be appropriate for certain lake ecosystems. Nonetheless, lake models are valuable tools that have the capacity to improve our understanding of lake functioning.

The addition of a nutrient flux from benthic plant origin was fixed in all models, so that each lake had the same influx of nutrients from benthic sources. While this flux was accurate and was used to calibrate the model, the incorporation of a benthic primary production compartment into the model might have provided a more realistic depiction of interaction with the lake ecosystem. For example, nutrient inputs in Lake 1 may have provided a sufficient nitrogen flux downstream to where nitrogen fixers would not be active due to sufficient N in the water column. This would be depicted if the benthic primary producers were incorporated into the model instead of our manual input of a constant nutrient flux.

The multi-lake model demonstrates the influence multiple lakes in series may have on downstream water chemistry. Given the diversity of drainage configurations found in nature, I am interested in the influence of lakes in series, particularly in contrast to single-lake and lake-less drainages. However, our modeling scenario did not take into account the stream channels that usually occur between lakes, as within the model outflow water from one lake was directly routed into the next lake downstream. This was an over-simplification as some have indicated that there may be a reset distance in which streams below lakes are capable of returning water conditions back to the pre-lake condition (Stanford and Ward 2001; Arp and Baker 2007). However, estimates of this
reset distance in Sawtooth watersheds are relatively long: Arp and Baker (2007) found only a 50% recovery in 2-4 km for sediment size and channel shape; Garrett (2010) found reset distances of 6 – 8 km for temperature. Consequently, full recovery may not be reached within 20 km downstream (Arp and Baker 2007) and many of the watersheds in the Sawtooth Mountains are shorter than this. In contrast, Maciolek and Tunzi (1968) found complete removal of lake seston (phytoplankton, bacteria and detritus in the water column) in streams after greater than 2 km of stream channel. Therefore, the flux of Chl a from one lake to the next downstream lake depends on the distance between lakes and also discharge (Vadeboncoeur 1994). Our modeled results thus demonstrate the maximum flux of seston from one lake to the next. In small, subalpine watersheds such as those in the Sawtooth Mountains of Idaho, the influence of lakes may be demonstrated in water chemistry entering downstream lakes, as stream lengths may not be sufficient to allow for water chemistry reset. This modeling scenario represents the maximum influence of lakes in sequence, therefore demonstrating the potential for increased nutrient flow through small, lake-populated watersheds.

**Conclusion**

With the use of a simplified one-dimensional lake model I developed an effective tool for modeling water chemistry dynamics in a small sub-alpine lake. Field data showed that in 2008 Bull Trout Lake functioned as a nutrient source within its watershed, and exported a greater flux than it receives from Spring Creek. I suggest that the source of these nutrients may be the lake sediments, and nutrients are re-incorporated into the water column via benthic macrophytes and nitrogen fixation in the epiphytes. In depicting a
hypothetical multi-lake watershed, this modeling process highlighted the importance of
lakes in the landscape as nutrient processors. Multiple lakes appear to have a
compounding effect on the accumulation of nutrients; however, the most dramatic effect
appears to be from the first two lakes (mainly the first lake). Subsequent lakes
downstream continue to produce nutrients, but have a much lesser effect on watershed
level changes in water chemistry. This research highlights the importance of lakes within
their watersheds, provides an example of the application of a useful tool, and supports
other research within the field of landscape limnology.

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Table 1. Average temperature (°C) and mass of macronutrient flux (kg) into and out of each modeled lake.

<table>
<thead>
<tr>
<th></th>
<th>Lake1 inflow</th>
<th>Lake1 outflow</th>
<th>Lake2 outflow</th>
<th>Lake3 outflow</th>
<th>Lake4 outflow</th>
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<td><strong>Average Temperature</strong></td>
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<td>15.29</td>
<td>15.68</td>
<td>15.79</td>
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<tr>
<td><strong>POC (kg)</strong></td>
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<td>1,052</td>
<td>706</td>
<td>637</td>
<td>625</td>
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<tr>
<td><strong>DOC (kg)</strong></td>
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<td>7,779</td>
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<td>9,241</td>
<td>9,619</td>
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<td><strong>OrgN (kg)</strong></td>
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<td>384</td>
<td>414</td>
<td>435</td>
</tr>
<tr>
<td><strong>NH₄⁺ (kg)</strong></td>
<td>13.7</td>
<td>22.6</td>
<td>24.2</td>
<td>25.3</td>
<td>25.9</td>
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<tr>
<td><strong>NO₃⁻ (kg)</strong></td>
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<td><strong>OrgP (kg)</strong></td>
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<td><strong>InorgP (kg)</strong></td>
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<td><strong>Chla (kg)</strong></td>
<td>0</td>
<td>5.7</td>
<td>8.3</td>
<td>9.5</td>
<td>10.1</td>
</tr>
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</table>
Figure 10. Location of the Bull Trout Lake watershed in Central Idaho, USA. Bull Trout Lake is the large lake in the watershed cutout of the figure and feeds the South Fork Payette River.
Figure 11. Hydrograph for Spring Creek inflow to Bull Trout Lake during the modeling period.
Figure 12. A graphical depiction of the Lake2K model. The model depicts a conical lake that is vertically stratified. Inputs into the system are water, watershed-derived nutrients, heat and an additional flux of nutrient representing benthic production. Outputs include water, nutrients, heat and chlorophyll \( \alpha \). The parameters used in calibration are shown in a box within the depiction of the epilimnion in the figure.
Figure 13 a-c. Measured values for temperature, $N_{\text{org}}$ and $NO_3^-$ in Spring Creek (Bull Trout Inflow) and measured and predicted values within Warm Springs Creek (Bull Trout Lake outflow. In frame A) the diamonds represent predicted epilimnetic values, filled triangles are metalimnetic, stars represent hypolimnetic values, and the open triangles are measured values from the inflow. The points are values from samples taken in 2008 (open triangles represent measurements from the inflow and filled triangles represent the outflow) and lines are predictions from the epilimnion of the BTL Lake2K Model, Boise National Forest, Idaho.
Figure 14 a-c. Measured values for NH$_4^+$, Chl $a$, and P$_{\text{inorg}}$ in Spring Creek (Bull Trout Inflow) and measured and predicted values within Warm Springs Creek (Bull Trout Lake outflow). The points are values from samples taken in 2008 (open triangles represent measurements from the inflow and filled triangles represent the outflow) and lines are predictions from the epilimnion of the BTL Lake2K Model, Boise National Forest, Idaho.
Figure 15 a-c. Measured values for $P_{org}$, POC, and DOC in Spring Creek (Bull Trout Lake inflow) and measured and predicted values within Warm Springs Creek (Bull Trout Lake outflow. The points are values from samples taken in 2008 (open triangles represent measurements from the inflow and filled triangles represent the outflow) and lines are predictions from the epilimnion of the BTL Lake2K Model, Boise National Forest, Idaho.
Figure 16 a-c. Measured values for temperature, POC, and DOC in Spring Creek (Bull Trout Lake inflow) and predicted epilimnetic values for Lakes 1-4. Temperature data is shown for all three stratified layers within the lake.
Figure 17 a-c. Measured values for $N_{\text{org}}$, NH$_4^+$, and DOC in Spring Creek (Bull Trout Lake inflow) and predicted epilimnetic values for Lakes 1-4.
Figure 18 a-c. Measured values for $P_{\text{inorg}}$, $P_{\text{org}}$, Chl $a$ in Spring Creek (Bull Trout Lake inflow) and predicted epilimnetic values for Lakes 1-4.
Figure 19 a-c: Change in flux of (a) nitrogen, (b) carbon, and (c) phosphorus for the four-modeled lakes. Change is flux is the total mass transported through the outflow of the given lake minus the total flux into that lake.
CHAPTER IV
CONCLUSION

Lakes are highly important players in nutrient processing and transport through watersheds. While this has not always been widely recognized, contemporary research continues to demonstrate the large influence lakes have on downstream water chemistry. In this research I employed and developed effective methods and tools that could be more widely utilized in studies of lakes. In two research projects I utilized different techniques to characterize nitrogen flow through both a single lake and a multiple-lake watershed. I applied a $^{15}$N stable isotope tracer experiment to a whole ecosystem to study the flow of inorganic nitrogen through the ecosystem. My research demonstrates the strong reliance of lake organisms on inorganic nitrogen delivered by the inflow stream, the importance of both pelagic and benthic primary producers in nutrient uptake, and the relatively small role played by larger organisms within the food web. Taking this perspective on lakes a step further, I developed a user-friendly lake model for our system of focus, which allowed me to explore the effect of the lakes within the watershed. I was able to quantify Bull Trout Lake as a source of nutrients within its watershed during the 2008 growing season. Additionally I suggest that benthic nitrogen fixation and the senescence of benthic macrophytes are important sources of nutrients to the water column and Warm Springs Creek. This research indicates that if there were additional lakes immediately downstream of Bull Trout Lake, they would further increase nutrient loading to downstream waters. However, the majority of watershed-level changes in nutrient transport would occur within Bull Trout Lake and to some extent the next lake
downstream, as changes in flux from more than 2 total lakes are minimal. Together these two research projects stress the important role that lakes play within watersheds in altering the movement of nutrients downstream as they dramatically alter the water chemistry of streams from inflow to outflow. I hope that this research both provides valuable information for the field of limnology and also an example of research methods that could be further implemented in other research.
Appendix A

Enrichment of Bull Trout Lake Ecosystem Compartments
Average (by station) delta $^{15}$N values integrated through the water column.

### Seston

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<td>6/29/08</td>
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<tr>
<td>7/1/08</td>
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</tr>
<tr>
<td>7/6/08</td>
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</tr>
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</tr>
<tr>
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<td>9/12/08</td>
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### Zooplankton

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<tr>
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<td>39</td>
<td>9</td>
</tr>
<tr>
<td>13-Sep</td>
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<tr>
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<tr>
<td>14-Sep</td>
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Appendix B

Mass of Tracer in Bull Trout Lake Ecosystem Compartments
Mass estimates for $^{15}$N tracer in Bull Trout Lake ecosystem compartments.

**Seston**

<table>
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**Zooplankton**

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**Epiphytes**

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**Macrophytes**

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Benthic Invertebrates

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Appendix C

Hypsometry of Bull Trout Lake
Bull Trout Lake hypsometry.

<table>
<thead>
<tr>
<th>&quot;Depth&quot; (m) from bottom</th>
<th>Cumulative Volume (m$^3$)</th>
<th>Cumulative Area (m$^2$)</th>
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