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Estimating Historical Sockeye Salmon Abundance Using Stable Isotopes and Nitrogen Budgets
of Central Idaho Lakes

by

Rachel Brinkley

A thesis submitted in partial fulfillment
of the requirements for the degree of
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Committee Approval

To the Graduate Faculty:

The members of the committee appointed to examine the thesis of RACHEL BRINKLEY find it satisfactory and recommend that it be accepted.

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Estimating Historical Sockeye Salmon Abundance Using Stable Isotopes and Nitrogen Budgets of Central Idaho Lakes

Thesis Abstract – Idaho State University (2021)

Idaho's sockeye salmon (*Oncorhynchus nerka*) have been decimated due to factors in (e.g. harvest) and out (e.g. hydropower development) of basin. Extensive management efforts have been aimed at restoring these populations following years of very low spawner returns. However, limited understanding regarding the historical escapement, pre-dam SAR’s, and the historical contribution of MDN emphasizes a need for a frame of reference to inform current and future restoration and management activities. Anadromous salmon have a high proportion of stable isotope \(^{15}\text{N} : ^{14}\text{N}\) relative to other nitrogen sources. As such, the analysis of sediment \(\delta^{15}\text{N}\) is an effective means of constructing historical population estimates. By using temporal shifts in \(\delta^{15}\text{N}\) as determined by sediment cores integrated into lake nitrogen budgets, we quantified historical abundance of spawning sockeye salmon for a suite of Idaho lakes. Our results suggest that current restoration objectives may be as low as 5% of sockeye that historically utilized this watershed for spawning. Initial declines in escapement were on the order of 80% over 10 years following the construction of a downstream dam. Historical smolt-to-adult returns (6-11%) may be higher than previously derived estimates (4%), and the nutrient subsidy via spawning sockeye historically may have contributed as much as 16% of the nitrogen input to the system.

Key Words: Snake River Sockeye, sediment core, historical escapement, recovery goals, sockeye management, Snake River Dams, smolt-to-adult survival, marine derived nutrients
Chapter I: Introduction

Salmon are one of the most iconic keystone species in the Pacific Northwest (Schindler 2003). Over 137 different species depend on Pacific salmon for at least part of their life cycle, and accumulating evidence indicates that many animal’s reproductive cycles and seasonal distributions are directly tied to salmon runs (Cederholm et al. 1999; Gende et al. 2002). Semelparous salmon serve as nutrient pumps that can push vast amounts of marine nutrients from the ocean to headwater streams, subsidizing not only a suite of animal species, but also enhancing primary production and the growth of riparian vegetation. Previous studies indicate that in salmon bearing streams, marine nitrogen propagates across nearly every trophic level (Juday et al. 1932; Cederholm et al. 1999; Gresh et al. 2000; Naiman et al. 2002; Quinn et al. 2018).

Sockeye salmon (*Oncorhynchus nerka*) have life history traits that are unique from other Pacific Salmon and other *Oncorhynchus* species. Sockeye salmon utilize lentic habitats for spawning and rearing (Groot & Margolis 1991; Kline 1993). Sockeye are primarily anadromous, and generally utilize lakes for one to three years prior to migration to marine habitats where they spend 1-4 years before returning to their freshwater nursery lakes where they spawn and die (Groot & Margolis 1991). As sockeye rely on lakes to complete their life cycle, they require more specific homing than that of other pacific salmon, making them more sensitive to habitat loss (Parkhurst 1950).

Within the last century, Snake River Sockeye have declined by over 99%, and they are one of the most imperiled stocks of salmonids in the world (Nehlsen et al. 1991; Kline & Flagg 2014). It is estimated that the Columbia River system historically supported over one million sockeye salmon, and the Salmon River was considered to be one of the most important streams
for anadromous salmon in the Columbia River Basin (Evermann 1894; Groot & Margolis 1991).

This dramatic reduction in abundance occurred due to pressures from a number of factors including intense harvest (1860’s), habitat loss due to lost or impaired river passage (1910-1934), the establishment of the hydropower system (1950’s), irrigation diversion (1900’s), the introduction of non-native species (1920’s and 1930’s), and poisoning (Evermann 1896; Waples et al. 1991; Winans et al. 1996; Selbie et al. 2007). The dramatic decline of salmon in this region is associated with a decline in the input of nutrients via semelparous salmon, and headwater streams in the Pacific Northwest receive no more than 5-7% of the marine derived nitrogen and phosphorus historically delivered to the region via spawning salmon (Selbie et al. 2007; Gross et al. 1998; Gresh et al. 2000).

The establishment of the Columbia River, Snake River, and Salmon River dams, for purposes such as hydropower, irrigation, and navigation, has led to the loss of salmon in this watershed (Rieman et al. 1991; Blumm 1998). The lower Snake River --historically a free-flowing river, serving as the gateway to Idaho’s spawning habitat-- is now a series of 4 reservoirs (Blumm 1998). The Sunbeam Dam, located 20 miles downstream from Redfish Lake on the Salmon River-- completed in 1910-- blocked the passage of anadromous salmon to Sawtooth Valley Lakes. Sunbeam Dam served as a barrier to salmon migration until it was breached in 1934 (Chapman et al. 1990; Waples 1991). While the dam negatively impacted runs of all pacific salmon that used upstream habitats for spawning, it was especially detrimental for sockeye salmon that relied entirely on access to the upstream lakes for spawning and rearing habitat (Bjornn 1968; Parkhurst 1950).

Since the Shoshone-Bannock Tribes successfully petitioned to have the Snake River Sockeye salmon protected under the Endangered Species Act in 1991, there have been extensive
management efforts aimed at restoring these populations (Gross 1995; Griswold et al. 2002). In 2011, the National Marine Fisheries Service (NMFS) identified a recovery goal of 1,000 naturally returning sockeye salmon in Redfish Lake, and 1,500 naturally returning sockeye in two other Sawtooth Valley lakes, combined (Kline & Flagg 2014). However, with limited understanding regarding the number of sockeye salmon that historically used Idaho lakes for spawning, a frame of reference is needed to inform current and future attempts at restoration and management.

The term ‘shifting baselines’ describes the lack of awareness of the magnitude of decline in abundance that has taken place over the twentieth century. It further describes the gradual acceptance of a declining salmon population (Pauly 1993; Licatowich 2017; Thurow 2019). As the baseline regarding what is considered a healthy and recovered fishery is lowered over several decades, there is room for falsely reported ‘recovery’ of a salmon fishery. Without historical data of salmon returns to Idaho’s lakes, they are at an increased risk for shifting-baselines. Again, creating a need for an accurate baseline for assessment of what is considered a healthy fishery.

The pre-development abundance of the Salmon River, with regard to sockeye salmon, is unknown. It may have been relatively low due to factors such as the oligotrophic nature of the watershed, limited spawning grounds, and the fact that the sockeye salmon utilizing these lakes face the longest migration for sockeye in the world (Fulton 1970; Griswold et al. 2003). The largest sockeye salmon return ever reported in this watershed was 4,361 returning adults in 1955, and this was reported as likely being only a small fraction of the returns in the 1800’s (Evermann 1895; Bjornn 1968). One recent estimate of juvenile carrying capacity, coupled with smolt-to-adult returns (SAR’s), suggest that Redfish could support runs of approximately 3,800 sockeye salmon (Gross 1995). However, contradicting reports indicate that, prior to Sunbeam Dam and
European settlement, salmon returns to this region were much higher than these recorded and estimated values. Previous studies have suggested that the Redfish Lake population had already experienced a population bottleneck prior to Bjornn et al.’s population estimates (1968), and initial fisheries explorations in the region indicated that Redfish Lake had sufficient adult Sockeye Salmon returns to sustain a cannery (Evermann 1894). Additionally, it has been suggested that previously derived population estimates do not account for the natural year-to-year variation in sockeye salmon returns and SAR’s, and that it is possible that under some conditions returns to Redfish Lake could have been over 10,000 fish (Gross 1995).

Sockeye salmon gain 95% of their biomass in the ocean and stop feeding prior to migrating back to their nursery lakes. Therefore, when they decompose following spawning, the nutrients that are released into their freshwater nursery lakes are almost exclusively of marine origin (Kline et al. 1993). In the ocean, salmon acquire a relatively high $\delta^{15}$N signature through successive trophic levels in a marine food web. Because of this, anadromous salmon have a high proportion $^{15}$N:$^{14}$N relative to other watershed nitrogen sources. The decomposition of adult salmon introduces this marine nitrogen to the lake food web, where it mixes with nitrogen from the watershed. As the marine derived nitrogen is utilized by the lake food web via phytoplankton, the accumulating sediments store a long-term record of spawning fish abundance over time, in the form of $\delta^{15}$N composition in a sediment record. The analysis of sediment $\delta^{15}$N has proved to be an effective means of constructing historical population estimates of anadromous salmon (Kline et al. 1993; Finney 2000; Satterfield and Finney 2002; Gavin et al. 2017).

Previous isotopic analysis of Redfish Lake, concluded that there was natural variation in sockeye salmon abundance until approximately 150 years ago when dramatic declines occurred,
potentially as a result of pressures from habitat loss and modification and harvest; similar patterns were observed in Pettit lake, with less extreme δ¹⁵N fluctuation in Yellowbelly lake, potentially as a result of a relatively low abundance of sockeye salmon utilizing this lake for spawning (Selbie 2007). While this information may provide evidence of the decline of marine derived input to Redfish Lake there is still uncertainty about the number of salmon that these δ¹⁵N values reflect, and therefore there exists associated uncertainty regarding the historical SAR’s, and the historical relative importance of the marine derived nitrogen subsidy of adult sockeye.

Often, sockeye spawning occurs in large, oligotrophic lake ecosystems, and extensive research has shown that these marine derived nutrients can greatly impact the nutrient dynamics and associated functioning of some freshwater systems (Kline 1993; Cederholm 1999; Naiman 2002). Therefore, the loss of this nutrient input to these systems may have dramatically altered the nutrient and ecosystem dynamics. Marine derived nutrients (MDN) can greatly impact carrying capacity in some systems; however, the relative importance of this nutrient subsidy varies greatly among watersheds. Therefore, understanding historical MDN contributions plays an important role in the restoration of salmon fisheries, and dictates management decisions such as lake fertilization (Griswold et al. 2003). It is estimated that the Pacific Northwest receives only a small percentage of the marine derived phosphorus and nitrogen that was historically introduced to these systems via migrating salmon, and the reduction of marine derived nutrients affects the nutrient dynamics of both freshwater and terrestrial systems (Gresh et al. 2000; Thomas et al. 2002; Kohler et al. 2013). In the Salmon River drainage and the Sawtooth Valley stream-lake ecosystem, formerly salmon-bearing streams now have little to no nutrient
contribution from salmon, and under current conditions salmon-driven nutrient exports can exceed imports (Evans et al. 2019).

SAR’s are commonly used in salmon management in order to quantify the number of adult salmon that successfully complete their life cycle, returning to their natal streams relative to the number of juvenile salmon, of the same cohort, that migrated to the ocean. SAR’s are critical to understanding the future, and the patterns of decline, of salmon populations; however, in much of the Columbia River drainage, and in systems such as this one, pre-dam era SAR’s are unknown. Previous research has indicated that for the period from 1954-2011, 47% of the years resulted in a net salmon-mediated nutrient loss, and that 76% of annual SAR values fell below the threshold for population replacement (Evans et al. 2019). Between 2004 and 2011 SAR’s to Redfish Lake averaged 1.12% with years as low as 0.2% in 2011. Research has shown that a SAR greater than 4.9% would be needed to reach population replacement under current conditions (Kozfkay et al. 2019). Current SAR goals for the region are 4% (NPCC 2014); despite this, there is still a need for a greater understanding of how these recovery goals compare to historical baselines.

This study’s objectives were to estimate the historical abundance of spawning sockeye salmon in the main historical nursery lakes of the Sawtooth National Recreation Area, and to compare population estimates before and after the establishment of Sunbeam Dam. To do this, we refined existing lake nitrogen budgets and used stable isotope data to quantify temporal shifts in sockeye salmon abundance from δ¹⁵N records in sediment cores, as a proxy of marine-derived nutrients from spawning sockeye salmon. These abundance estimates allowed us to compare SAR’s prior to and following the construction of Sunbeam Dam. Abundance estimates and
quantifying current watershed nitrogen flux also allowed us to estimate what proportion of nitrogen input would have historically been of marine origin.

We hypothesize that there were dramatic declines in sockeye salmon abundance in Sawtooth Valley Lakes following the establishment of the Sunbeam, Columbia, and Snake River Dams. If the historical abundance of sockeye salmon that used Sawtooth Valley lakes for spawning is higher than previously thought, this has implications in that SAR’s and the historical contribution of marine derived nitrogen to these watersheds would be underestimated.

*Study Area*

Our study area is located in the Sawtooth National Recreation Area (44°N, 115°W, Fig.1) in central Idaho, and includes four of the six-main potential historical nursery lakes of sockeye salmon in the Upper Salmon River Basin (Redfish, Yellowbelly, Pettit, and Alturas), all of which are designated as critical habitat (Federal Register 58: [December, 28, 1993]). These glacially formed lakes range in volume from 1.9 – 270 (10⁶ m³), and in surface area from 0.24 – 6.15 km² (Table 1) and lie on the east flank of the Sawtooth Mountain Range--draining into the Main Salmon River.
Figure 1. The six main historical sockeye salmon lakes of the Sawtooth Valley. Sunbeam Dam is located 20 miles downstream of Redfish Lake, and historically served as a barrier to salmon movement.

The other two potential historical-sockeye salmon lakes in the Sawtooth Valley -- Stanley and Hell Roaring-- were excluded from the study as they have flushing rates < 0.5 years, and there is strong evidence of dilution effects via nutrient flushing (Holtham 2004; Selbie et al. 2009). Additionally, the inlet to Stanley lake has experienced significant damming via beaver activity over the last 5 years, potentially altering the nutrient dynamics of the system so that they no longer reflect the historical dynamics of the system, and the natural wetlands have been intensively modified to support roads and campsites (USDA 2011). In the spring 2020 there was earthquake activity, dramatically altering the flow and accessibility of the inlet to Stanley Lake.
(44.465°N 115.118°W, 2020-03-21). Similar to Alturas and Yellowbelly, our approach would not produce meaningful modeled reconstructions.

Table 1. The physical and morphological features of the six main historical sockeye salmon lakes in the Sawtooth Valley, Idaho, including the four primary lakes of this study (Redfish, Alturas, Pettit, and Yellowbelly) (Gross 1995).

<table>
<thead>
<tr>
<th>Lake</th>
<th>Area (km²)</th>
<th>Volume (m³ x 10⁶)</th>
<th>Percent volume</th>
<th>Elevation (m)</th>
<th>Mean depth (m)</th>
<th>Maximum depth (m)</th>
<th>Drainage area (km²)</th>
<th>Drainage area/ lake surface area</th>
<th>Water residence time in years (Gross, 1993)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redfish</td>
<td>6.15</td>
<td>269.9</td>
<td>60.8</td>
<td>1996</td>
<td>44</td>
<td>91</td>
<td>108.1</td>
<td>17.6</td>
<td>3.0</td>
</tr>
<tr>
<td>Alturas</td>
<td>3.38</td>
<td>108.2</td>
<td>24.4</td>
<td>2138</td>
<td>32</td>
<td>53</td>
<td>75.7</td>
<td>22.4</td>
<td>1.8</td>
</tr>
<tr>
<td>Pettit</td>
<td>1.62</td>
<td>45.0</td>
<td>10.1</td>
<td>2132</td>
<td>28</td>
<td>52</td>
<td>27.4</td>
<td>16.9</td>
<td>2.2</td>
</tr>
<tr>
<td>Stanley</td>
<td>0.81</td>
<td>10.4</td>
<td>2.3</td>
<td>1985</td>
<td>13</td>
<td>26</td>
<td>39.4</td>
<td>48.6</td>
<td>0.3</td>
</tr>
<tr>
<td>Yellowbelly</td>
<td>0.73</td>
<td>10.4</td>
<td>2.3</td>
<td>2157</td>
<td>14</td>
<td>26</td>
<td>30.4</td>
<td>41.6</td>
<td>0.5*</td>
</tr>
<tr>
<td>Hell Roaring</td>
<td>0.24</td>
<td>2</td>
<td>-</td>
<td>2258</td>
<td>-</td>
<td>-</td>
<td>20.4</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* Residence time calculated using mean annual discharge (Wurtsbaugh personal communication)

The study lakes are oligotrophic and in relatively pristine watersheds, most of which are located in official or de facto wilderness; this area experiences recreational land use that sees dramatic seasonal shifts (Wurtsbaugh 2005; Brown 2008). There is low atmospheric nitrogen deposition (1.17 kg N ha⁻¹ yr⁻¹) (Brown 2008; Wurtsbaugh et al. 2005; NADP site ID15). The bedrock is largely composed of nutrient-poor granite, and primary production is thought to be limited primarily by nitrogen and secondarily by phosphorus (Wurtsbaugh 1997; Marcarelli & Wurtsbaugh 2007).
Chapter II: Methods

To quantify the relative proportions of nitrogen input (primarily nitrate) from the watershed, and from the historical contribution of nitrogen input via anadromous adult sockeye, we used a mixing model. We assume that the nitrogen isotope composition of the sediment reflects the nitrogen isotope composition of the lake water at the time the sediment was deposited. We calculated the $\delta^{15}N$ of the sediment, as a sum of the relative $\delta^{15}N$ contribution from the watershed and from the $\delta^{15}N$ contribution of the nitrogen subsidy provided by spawning sockeye salmon using the following equation:

\[
\text{Equation 1: } \delta^{15}N_{\text{Sediment}} = \delta^{15}N_{\text{Fw}} + \delta^{15}N_{\text{Fs}}
\]

where $\delta^{15}N$ sediment is the isotopic signature for a set historical time period, $\delta^{15}N_{\text{Fw}}$ is the isotopic signature associated with the fraction of dissolved inorganic nitrogen (DIN) from the watershed --measured in the absence of spawning sockeye--, and $\delta^{15}N_{\text{Fs}}$ is the isotopic signature associated with the fraction of nitrogen input via adult sockeye that historically returned to the region to spawn.

All nitrogen inputs were weighted proportionally to the mass of input by source, and were used to calculate an escapement estimate corresponding to sedimentary $\delta^{15}N$ values over a historical time period, using the following equation (Gavin et al. 2017):

\[
\text{Equation 2: } \frac{\text{Sediment } \delta^{15}N}{(\text{Salmon } \delta^{15}N \times \text{ Sockeye mass } \times \text{ Escapement } \times \%N) + (\text{Watershed } \delta^{15}N \times \text{ Watershed N})} = \frac{(\text{Salmon } \delta^{15}N \times \text{ Sockeye mass } \times \text{ Escapement } \times \%N) + (\text{Watershed } \delta^{15}N \times \text{ Watershed N})}{(\text{Sockeye mass } \times \text{ Escapement } \times \%N) + (\text{Watershed N})}
\]

where salmon $\delta^{15}N$ is the $\delta^{15}N$ of snake river sockeye, sockeye mass (g) is the historical mass of a single adult spawner, $\%N$ is the proportion of nitrogen/100 of a single adult spawner,
watershed $\delta^{15}N$ is the $\delta^{15}N$ value of the watershed, and watershed $N$ is the mass (g) of nitrogen input from the watershed.

**Watershed N fluxes and $\delta^{15}N$**

Watershed N input was calculated using inflow of DIN (ppb) and annual water input (m$^3$ yr$^{-1}$) of inlet streams. In our system, net nutrient input is dominated by stream inflow, which makes up as much as 90% of the nutrient input to Redfish Lake (Gross 1995). Annual water input was calculated using previously collected discharge data (Gross 1995; Wurtsbaugh personal communication). Stream discharge of Redfish Lake Creek, Pettit Lake Creek, Alturas Lake Creek, and Yellowbelly Creek were measured during an average water year (1993; Wurtsbaugh personal communication; Gross 1995). In order to assess the contribution from the watershed itself, we quantified the input flux of DIN, $\text{NO}_3^-$, and $\text{NH}_4^+$, the main forms of biologically usable nitrogen.

To quantify watershed nitrogen contribution and current inputs, nutrient and isotope samples were collected from lake inlets monthly from June to October 2018-2020. Water “grab” samples were collected for analysis of total and dissolved nutrients, from approximately the middle of the channel. Unfiltered water was stored in polyethylene containers, rinsed with 0.1 N HCl, and immediately frozen. Additional samples were collected from the same location to assess dissolved nutrients. Dissolved nutrient samples were kept on ice for no longer than 8 hours prior to filtering and were filtered through a 0.45um cellulose acetate filter using a low-pressure vacuum. Filtered samples were immediately frozen, and analyzed for nitrite + nitrate, ammonia, and soluble reactive phosphorus (Steinhart et al. 1993; Budy 1995). All nutrient samples were run at High Sierra Water Lab Inc. Oakland, Oregon.
Nutrient inputs to all lakes were weighted by monthly discharge over each sampling period, as evidence suggests that nutrient concentration was independent of discharge (Appendix A; Wurstbaugh personal communication). In Redfish Lake we accounted for variation spatially, as Redfish has two inlets that contribute nutrients to the lake differently (Gross 1995). Pettit Lake also has two inlets, but nutrient samples were combined as these inlets drain the same watershed, and therefore were assumed to have comparable nutrient dynamics.

Abundance estimates were reconstructed beginning in the 1650’s, as there are reliable long-term climatic and streamflow reconstruction for the Upper Snake River for this time period (Wise 2010). Additionally, tree ring reconstruction of stream flow (Wise 2010) indicates that 1626-1632 represented years of extreme drought (17 years of below average flow). Therefore, reconstructions began after 1632, as current lake retention times and nutrient dynamics may not accurately represent hydrological conditions during this time, and the application of our model during this time period may result in a dramatic overestimate of salmon returns during this period. Year-to-year variability in stream discharge (Appendix B) was accounted for within our sensitivity analysis (see below).

Biofilm

Although nutrient concentrations of the lake inlets were assessed directly, nitrate concentrations were too low for direct $\delta^{15}$N analysis, and we used isotope analysis of biofilm in the inlet streams as a surrogate for inlet $\delta^{15}$N. Primary production in these watersheds is co-limited by nitrogen (Unpublished data 2018-2020; Wurtsbaugh et al. 1997). Therefore, we assumed that the low concentrations of available nitrogen in the system would be assimilated by the biofilm with little fractionation between the stream nitrate and biofilm, as nitrogen concentration greatly impacts the fractionation between nitrate and primary producers (Kline
1993; Waser et al. 1998; Jones et al. 2004). If fractionation does occur, the analysis of biofilm may more effectively account for changes in $\delta^{15}N$ that reflect that of the uptake and sedimentation by phytoplankton in lake sediments, as opposed to the direct analysis of $\delta^{15}N$ of the stream nitrate.

In order to assess the $\delta^{15}N$ of biofilm, we collected a benthic biofilm slurry using 2-3 rocks collected from riffles from the inlet stream as close to the downstream lake as possible for three, separate, monthly (June-October) composite samples. To account for temporal variation in biofilm, rocks were labeled and the same rocks were used each month. At each monthly sampling rocks were scrubbed so the biofilm accumulation and associated $\delta^{15}N$ represents the isotopic signature of the stream conditions monthly, as opposed to the entirety of the growing season. Rocks were scrubbed using a soft brush to create a biofilm slurry. The biofilm slurry was filtered, using a low-pressure vacuum onto a pre-combusted glass fiber filter (GFF), until the GFF was dark in color. Biofilm samples were dried and analyzed for $\delta^{15}N$ (±0.2‰), $\delta^{13}C$ (±0.2‰), and %C/%N ratios at the Idaho State University Stable Isotope Laboratory.

$\delta^{15}N$ Salmon

The contribution of marine-derived nitrogen from anadromous adult salmon was determined over a range of escapement to determine its flux relative to other nitrogen inputs. In order to estimate the historical N contribution from spawning sockeye salmon we used the mean body mass of anadromous Snake River Sockeye from Idaho Fish and Game trapping records, 1312g (1993-2020; Johnson et al. 2016; Evans et al. 2019; K. Tardy personal communication). We used an average nitrogen content of 2.47%, a value based on the wet mass of an adult sockeye salmon (Barto 2004). Therefore, we assumed a nitrogen input equal to 32.4g per adult sockeye.
For the $\delta^{15}$N of salmon, we used a value of 10.97‰ ($\sigma = 0.901$), this mean value was determined from the analysis of tissue samples from adult Sawtooth Valley Sockeye Salmon (2012, $n = 21$). It is unclear if the $\delta^{15}$N of Sawtooth sockeye differs from other populations due to their ocean feeding locations or long migration distance, but this value generally agrees with previously derived $\delta^{15}$N of adult sockeye from other basins in the Columbia River drainage and the broader North Pacific region ($\delta^{15}$N ~11-12‰) (Satterfield & Finney 2002; Johnston et al. 2004; Finney unpublished data 2008).

$\delta^{15}$N Sediment

Sediment $\delta^{15}$N was used to quantify temporal variation in the MDN input. Gravity cores were collected from the Sawtooth Valley Lakes in 1998 and in 2020, and were dated using $^{210}$Pb (Selbie et al. 2007) following the methods of Appleby (2001). Sediment $\delta^{15}$N was measured using a mass spectrometer as described above, and the data has an analytical uncertainty ±0.2‰. The sediment cores, and associated chronologies and $\delta^{15}$N, are from collections taken in 1998. Data from Redfish, Pettit, and Yellowbelly lakes were published in Selbie et al. (2007), and similarly derived data from Alturas Lake are included here. New sediment cores were collected from Redfish Lake in September of 2020.

Mixing Model

We utilized the mixing model (eq. 2) to quantify watershed salmon N contributions to the lake water, and subsequently to the sediments. Flux of watershed N, was based on our nutrient and isotope data, and we assumed that present day contributions from salmon are minor.

Statistical Analysis
We used a Monte Carlo analysis to account for uncertainty and the associated error for variables within our mixing model (Evans et al. 2019). We developed a 95% confidence interval that accounted for variation in salmon δ\textsubscript{15}N and annual watershed DIN input. We ran 10,000 simulations for expected δ\textsubscript{15}N of a given escapement, where salmon δ\textsubscript{15}N and annual watershed DIN input values were randomly sampled from a normal distribution around the mean value. Escapement values sequentially increased by 100 from 0 to 20,000, we used fixed values for variables that lack quantitative variation (% nitrogen of adult salmon, historical salmon mass, and inlet stream discharge; the latter two variables were included in our sensitivity analysis). Monte Carlo analysis was performed in R v4.0.2 (2020-06-22).

Previous studies that utilized the same mixing model (Gavin et al. 2018), indicated that under lower DIN concentrations, sediment δ\textsubscript{15}N is most sensitive to watershed DIN, and spawners per year. Both of these variables were included within our Monte Carlo Analysis.

*Sensitivity of Escapement Estimates*

To assess uncertainty related to individual components of the model that lacked quantified estimates of variation (historical adult salmon mass & discharge), and to isolate the effects of these variables, we performed a sensitivity analysis by which we manipulated the individual parameter within our mixing model to assess the impact this had on our historical population estimate (Loso et al. 2017; Gavin 2018).

To quantify potential variability due to changes in stream discharge, we utilized the discharge recorded downstream (1913-2020) at the upper Salmon USGS gauge (230 km downstream of Redfish Lake). 95% of the variability in discharge of the Upper Salmon River is accounted for by ±25% of the average discharge (55.0 m\textsuperscript{3}/s); we assume that the variability of
the inlet stream exhibits similar variability of the downstream USGS gauge, and therefore inlet stream discharge was perturbed by ±25% to evaluate the models sensitivity to stream discharge.

Comprehensive data on historical anadromous adult weights, and length-weight relationships, are not available. Data on adult sockeye were recorded from 1953-1965, prior to hatchery influence (beginning in 1991). The mean fork length of anadromous adults (21.0 inches) reported in Idaho Fish and Game trapping records (1991-2020), does fall within the range of lengths (19.0 to 25.0 inches) of adult returns 1953-1965 (Bjornn 1968). However, this length does fall on the lower end of historically reported lengths, and evidence suggests that in recent times adult size at return has decreased (Bigler et al. 1996). In order to assess the effects of adult spawner mass on our abundance estimates, we perturbed adult salmon mass by ± 380g, accounting for 68% of the variability (± 1 standard deviation of mass of anadromous adults; 1991-2020; K. Tardy Personal Communication).

SAR’s

Smolt production of Redfish Lake has been estimated for Sawtooth Valley lakes in previous studies (Rieman and Myers 1992; Gross 1995). Production was estimated using a “bottom-up” approach that utilized an empirical relationship between chlorophyll-a concentrations and juvenile kokanee biomass (Rieman and Myers 1992). To determine pre-dam production, we utilized the following relationship (Rieman and Meyers 1992; Gross 1995):

\[ \text{Equation 3: } \log(\text{production}) = 0.394 + 1.06 \log(\text{Chlorophyll a}) \]

where production represents salmon production (kg ha\(^{-1}\) yr\(^{-1}\)), and the chlorophyll a represents the concentration of epilimnetic chlorophyll a (µg/L). Salmon production (# ha\(^{-1}\) yr\(^{-1}\)) was converted to number of smolts using the following equation (Gross 1995):

\[ \text{Equation 4: } (\text{production}) \times 100 = \text{smolts} \]
Where *smolts* is the number of age 1-3 9.6g smolts produced (101mm; Bjornn et al. 1968), assuming that all *O. nerka* production was channeled into sockeye salmon production, as opposed to kokanee production. This equation does not account for the production of age-0 fish, therefore in order to account for this portion of the juvenile sockeye production, we doubled the production estimates (Rieman and Meyers 1992; Gross 1995).

Epilimnetic chlorophyll-α concentrations were quantified monthly, and averaged by year (1992-2019; excluding years of fertilization) for water samples collected using a Van Dorn water sampler (Robert Griswold personal communication). Epilimnetic water samples were put on ice following collection, and were not exposed to light until chlorophyll analysis was complete. Lake water samples were collected from the same GPS points every month. We used this coefficient of smolt production, paired with our historical abundance estimates, to calculate a historical SAR value independent of a migration survival coefficient.

*Marine Derived Nutrients*

The contribution of marine derived nitrogen, relative to nitrogen input via the watershed, was determined over a range of escapement sizes derived from historical escapements using the following equation:

\[
Equation 5: \% MDN = \frac{Salmon \ N \ Input}{Salmon \ N \ Input + Watershed \ N \ Input} \times 100
\]

where *salmon* N input is the mass of nitrogen (DIN) input contributed by spawning sockeye and *watershed N input* is the mass of nitrogen (DIN) contributed by the watershed via stream inflow.
Chapter III: Results

Watershed Nutrient Input

The relative concentration of nitrogen species varied among lake inlets and between months (Appendix B), potentially indicating variation in both upstream and within lake nitrogen processing and availability. However, in most of our study lakes (excluding Yellowbelly lake), DIN input was dominated by NO₃⁻ + NO₂⁻ (Appendix B). The observed nutrient concentrations are similar to previous nutrient concentrations derived from these same watersheds (Gross et al. 1998; Marcarelli & Wurtsbaugh 2007; Marcarelli & Wurtsbaugh 2008).

Our nutrient analysis provided indirect evidence that in these streams, primary production is co-limited by nitrogen and phosphorous (Appendix B); supporting previous studies that utilized primary means of evidence such as bioassays using nutrient diffusing substrata (Thomas et al. 2002; Marcarelli & Wurtsbaugh 2007 2007; Marcarelli & Wurtsbaugh 2008). However, previous analysis of nutrient dynamics of the lake water, suggests that primary production in the lakes is primarily limited by nitrogen (Wurstbaugh et al. 1997).

Watershed Hydrology

We calculated lake residence time for the six main historical salmon nursery lakes using previously collected mean annual discharge data (Wurtsbaugh personal communication; Gross 1995). Our study years, 2018, 2019, and 2020 represented above average, near average, and below average annual discharge, respectively. 2018, 2019, and 2020 had annual discharge values of 66.6 m³/s, 52.5 m³/s, 45.2 m³/s respectively, compared to 55.0 m³/s, the annual average discharge over 107 years (Upper Salmon USGS Gauge, 1913 - 2020). Previously derived nutrient data for 1992 and 1993 represented years of near-average (54.40 m³/s, 1993) and below average drought years (30.46 m³/s, 1992). As 1993 is representative of average conditions in the
Upper Salmon River Basin, it is thus an appropriate year to use for modeling the discharge data within our model.

There is no evidence of a relationship between nutrient concentrations (TN) and stream discharge (Appendix A). Additionally, we observed no significant differences in nutrient concentration with relation to year, regardless of variability in stream discharge (Figure 2).

* Inlets to Redfish Lake, Idaho

Figure 2. Mean NO$_3^-$ (ppb) concentration (±1 Standard Error) of Sawtooth Valley Lake inlet streams collected monthly June-October, 2018-2020.
Abundance Estimates

Figure 3. Historical estimates of returning adult spawners ± 95% CI (salmon yr⁻¹) for Redfish Lake (A), Pettit Lake (B), Alturas Lake (C), and Yellowbelly Lake (D). Frequency of measurements (years) vary between lakes due to differences in sediment core dating and lake sedimentation rates.

As noted in Selbie et al. (2007), some isotope records show a dramatic decline that corresponds to the construction of Sunbeam Dam (Redfish and Pettit Lakes, Figure 3). Prior to the construction of Sunbeam Dam, modeled outputs indicate population sizes that demonstrate natural variation. Prior to the construction of Sunbeam Dam (1652-1910), we estimate a mean of 20,000 spawners yr⁻¹ returning to Redfish Lake and 2,500 spawners yr⁻¹ returning to Pettit Lake.
Two other lakes in the region (Yellowbelly and Alturas) have relatively low estimated escapement (<1,000 spawners yr\(^{-1}\)) with less obvious long-term trends.

The 95% confidence interval, as determined by 10,000 Monte Carlo simulations, suggests that prior to the construction of Sunbeam Dam, between 16,900 and 24,700 spawners yr\(^{-1}\) around an estimated mean of 19,700 spawners yr\(^{-1}\) returned to Redfish Lake annually. For Pettit Lake, the Monte Carlo error envelope is \(\sim \pm 800\) spawners.

**Sensitivity of Escapement Estimates**

Perturbing annual water input by \(\pm 25\%\) results in a mean escapement of 24,000 and 15,300 (spawners yr\(^{-1}\)), respectively. The sediment resolution is approximately 5 years, so therefore annual extremes in discharge are buffered. By running a 5-year smoothing on Upper Salmon River discharge, variability decreases and 95% of variation is accounted for by a range of \(\pm 18\%\) relative to mean flow. Perturbing annual water input by \(\pm 18\%\) results in a mean escapement estimtes of 22,800 and 17,000 (spawners yr\(^{-1}\)). Perturbing average adult salmon mass by \(\pm 380\) grams, \(\pm 34\%\), results in a respective escapement of 16,809 and 24,054 (spawners yr\(^{-1}\)).

**SARs**

Under historical conditions (Pre-Sunbeam Dam) our calculations suggest that Redfish and Pettit Lake could produce approximately 173,800 and 47,600 smolts respectively. With estimated escapements of 19,700 and 2,500 sockeye (yr\(^{-1}\)) we estimate SAR’s for anadromous sockeye in Redfish and Pettit Lake to be approximately 11% and 6% respectively, assuming that all of the *O. nerka* production of the lake was partitioned into the production of anadromous smolts, as opposed to non-migratory life forms. SAR’s would be higher if less of the *O. nerka*
productivity was portioned into anadromous smolt production, making our estimates conservative.

*MDN*

With an annual escapement of 20,000 and 2,500 for Redfish and Pettit Lakes respectively, under pre-dam conditions, MDN historically would have made up as much as 16% of the nitrogen input to the system in both lakes. Note that for overall nutrient budgets, this does not account for nutrient export via out-migrating smolts.
Chapter IV: Discussion

Historical Escapement

Our historical abundance estimates of sockeye in the Sawtooth Valley Lakes indicate that historical returns may be higher than previously derived estimates, using carrying capacity supported by habitat models alone (Gross 1997) because they are not independent of post-Sunbeam Dam migration survival coefficients and SAR’s. Thus, the recovery goal of 1,000 fish returning to Redfish Lake, may be as low as 5% of the historical annual sockeye returns.

Our abundance estimates suggest significant decadal changes in the number of sockeye that historically spawned in Redfish Lake. Natural variation, around an annual mean of approximately 20,000 spawning adult sockeye, was observed prior to the late 1800’s (Figure 3) with decline potentially as a result of intense harvest (1860’s), and impaired river passage (1910-1934) (Kyle et al. 1988; Nehlsen et al. 1991; Waples et. al 1991). In 1910, following construction of Sunbeam Dam, escapement values declined by 80%. While this dam likely completely blocked access to Sawtooth Valley lakes, we observed evidence for a relatively gradual decline in the input of marine derived nitrogen, potentially as a result of the release of MDN retained in the watershed over decades, or perhaps sediment mixing.

At Pettit Lake (Table 1), slightly upstream of and smaller than Redfish Lake, we observe lower historical sockeye abundance (2,500 spawners yr\(^{-1}\)) than that of Redfish Lake (20,000 spawners yr\(^{-1}\)). However, we observe the same temporal patterns in escapement with dramatic declines in the contribution of marine-derived nitrogen following the establishment of Sunbeam Dam, with natural variation in abundance prior to 1910 (Butler and O’ Connor 2004). These same patterns were not observed in all of the lakes, likely as a result of historically lower sockeye salmon abundance.
We do not observe the same temporal declines in $\delta^{15}$N in Alturas and Yellowbelly lakes, potentially as a result of relatively low escapement compared to Redfish and Pettit Lakes. It is possible that with a relatively high annual discharge into the systems, and relatively low retention time for Alturas and Yellowbelly Lakes (1.8 yrs, 0.5 years) dilution effects have dampened the sediment $\delta^{15}$N salmon signals for these lakes (Holtham et al. 2004; Selbie et al. 2009).

Insignificant modeled escapement estimates do not indicate a lack of salmon returning to Alturas and Yellowbelly lakes, but rather suggest that returns to these lakes were too low for reliable escapement estimates using isotopic methods (Loso et al. 2017). Anadromous sockeye have been observed in Alturas lake; 45 adults returned to the lake in 1964 after many years of observing no adult returners, potentially as a result of irrigation diversions below the outlet of the lake (Bjornn et al. 1968; Munther 1975; USFS 1987). Some observations (Evermann 1896; Bjornn 1986) suggest higher salmon populations in Alturas Lake than is suggested by our modeled escapement. This could potentially be biased due to the relatively large amount of high quality stream spawning habitat and accessibility (Bowler 1990; Griswold et al. in Review).

Since the 1920’s the ‘traditional’ sockeye spawning habitat is on the shoals of Redfish and Pettit Lakes, but in the inlet of Alturas lake (Evermann 1896; Bowler 1990). It is likely that, as a result of stream spawning in Alturas Lake, some MDN and the associated isotopic marine signature was exported out of the watershed and is not accounted for in the lake sediment. Evidence suggests that in small streams, predators are capable of transporting over half of the salmon carcasses out of the riparian zone and into the forest (Reimchen 2000; Quinn 2009). Whereas, in lakes, salmon are harder to export by predators, and that more MDN may be retained in the watershed (Quinn 2009). While we assume that in Redfish and Pettit Lakes, with
shoal spawning, most of the MDN is rapidly utilized and retained within the lake (Thomas 2002), any MDN that are exported out of the system would not be accounted for within our abundance estimates, resulting in an underestimate of salmon escapement in this system. Additionally, higher flushing rates in Alturas would mean that more salmon would be needed in-order to create a sediment isotope signature. In initial fisheries explorations in Idaho, Evermann (1986) mentioned that 2,600 lbs of *O. Nerka* were harvested from the lake. Using our mixing model, 2,600 lbs of *O. Nerka* would only change the sediment $\delta^{15}$N by approximately 0.36‰ (Loso et al. 2017), due to high lake turnover.

Non-migratory *O. nerka* have been reported in all four of our study lakes (Hall-Griswold 1990). Kokanee were observed in Alturas and Redfish Lakes during the period of time in which Sunbeam Dam was blocking passage (Locke 1929), and following chemical treatment of Yellowbelly and Pettit Lakes, residual sockeye salmon were found (Bjornn 1968; Hall-Griswold 1990; Kohler et al. 2004). Our abundance estimates account for anadromous *O. nerka* only, and they do not account for populations of non-migratory or residual life forms; so, it is possible that Alturas and Yellowbelly lakes historically had higher proportions of non-migratory life forms -- kokanee-- than anadromous sockeye salmon, potentially as a result of longer migration distances and migration passage.

Differing from the other study lakes, Pettit lake is meromictic and has a monimolimnion below 40m in a small, deep, central depression (Wurtsbaugh 2001). However, this lake, like the other study lakes, is dimictic and primary production is primarily limited by nitrogen (Wurtsbaugh et al. 1997; Wurtsbaugh 2001). Previous studies have indicated that there is a strong relationship between lake sediments and nitrogen limitation, regardless of the typology
(Jones 2004). Therefore, we assume that this had a negligible impact on the sediment signature within the lake as a result of bi-annual mixing and strong N limitation.

It is possible that our modeled escapement estimates could have been affected by anthropogenic nitrogen deposition or sediment diagenesis. However, we did not observe the same temporal declines in $\delta^{15}$N across all of the Sawtooth Valley lakes, suggesting that the temporal patterns we observe in Redfish and Pettit Lakes are not a result of another form of nitrogen transformations or input, such as atmospheric nitrogen deposition or diagenesis, and that the effects of both processes are minor. Previous studies of lakes in this watershed have argued against the changes in $\delta^{15}$N occurring as a result of sediment diagenesis, as changes in $\delta^{15}$N extend beyond the sediment depth that is expected from diagenesis (Holtgrieve et al. 2011), and by observing similar temporal patterns in $\delta^{15}$N decline under both oxic (Redfish) and anoxic (Pettit) conditions, we infer that this decline is due to another factor—migratory salmon—as opposed to diagenic effects.

**Mixing model assumptions**

It has been reported that in these systems the net nutrient input is dominated by stream inflow, which makes up over 90% of the nutrient input to Redfish Lake, dependent on annual discharge (Gross 1995; Wurtsbaugh et al. 1997). Evidence suggests that primary production is limited by nitrogen (Unpublished data; Wurtsbaugh et al. 1997). We assume that marine-derived nutrients made available to the system are rapidly exploited as a result of nutrient limitation, and that there is complete conversion of carcasses to DIN. Therefore, we assume that there is little export from the system, and that there is a uniform $\delta^{15}$N signature spatially within the lake; any MDN lost from the system, or not converted to DIN, would result in an underestimate of sockeye
escapement (Brock et al. 2006; Thomas et al. 2002). We also assume that, as a result of nitrogen-limitation, fractionation during remineralization is low (Jones et al. 2004; Möbius 2012).

Our data and previous studies show that nutrient concentration is independent of discharge (Appendix B). This observation, and the lack of significant annual variability in nutrient concentration (Figure 2), suggest that uncertainty in stream nutrients is not a major factor in the uncertainty of our estimates. Nitrogen deposition in this region is low and has little effect on nutrient cycling and limitation in this system; nitrogen deposition measured in Central Idaho (Swan Valley, NADP site ID15) from 1984-2006 has an average value of 1.17 (kg N/ha/yr), this would equate to 0.03% of nitrogen input to Redfish Lake. If atmospheric nitrogen deposition is currently enhanced, adding to non-Salmon N flux, then our estimates would be too high.

Biofilm is assumed to represent the $\delta^{15}$N signature of the DIN flux into the system if there is minimal fractionation between nitrate and primary producers, because nearly all of the available nitrogen will be utilized (Waser et al. 1998; Jones et al. 2004; Kline 1993). Additionally, we assume that DIN represents the primary input flux of N utilized for primary-production in this system. There is an existing body of literature that suggests that phytoplankton utilize primarily DIN, and only use dissolved inorganic nitrogen (DON) under specific conditions (Doratch 1990). If DON is used by phytoplankton in addition to DIN, our modeled escapements would be underestimated. Similarly, if watershed particulate nitrogen (PN) and DON is transformed or utilized, it would result in underestimated salmon escapements, again suggesting that our abundance estimates are conservative.
Sensitivity of Escapement Estimates

Perturbing the annual water input by ±25%, results in a respective escapement range of about ±25%, which for Redfish is from 24,000 to 15,300 (spawners yr⁻¹). While we assume that this variation accounts for most of the annual variation in discharge, any long-term or extended periods of drought may result in an underestimation of salmon abundance. However, the long-term Upper Salmon Gauge (Appendix A) and paleo-precipitation reconstructions using tree rings (Wise 2010), show no long-term trends, supporting our use of discharge levels in the model. Additionally, sediment δ¹⁵N is an average of nitrogen input for periods of approximately 5 years; therefore, reducing errors due to fluctuations in annual water input, and annual extremes. However, for a five-year drought period (five consecutive years of flows 25% below average; ex. 1930’s Dust Bowl), our modeled escapements for Redfish Lake would have been underestimated by approximately 5,000 adult spawners. By running a 5-year smoothing on Upper Salmon River discharge, variability decreases to ±18%. Perturbing annual water input by ±18% results in a relative escapement of 22,800 and 17,000 (spawners yr⁻¹), potentially serving as a more accurate assessment of potential variation in stream discharge.

Perturbing average adult salmon mass by ±380 grams, results in a respective escapement of 16809 and 24054 (spawners yr⁻¹). While average historical sockeye length falls within the range of lengths recorded 1991-2020, evidence suggests that mass of returning adults is decreasing (Bigler et al. 1996). Our sensitivity analysis indicates that if the average adult salmon mass was historically 30% higher than recorded adult mass -beginning in 1991, our abundance estimates would have been overestimated by approximately 4,000 adult spawners.
SAR’s

Previous studies have estimated SAR’s of 4% for Sawtooth Valley Lakes, for pre-dam conditions, which is lower than other populations of salmon in the Columbia basin (5-34%) (Ricker 1962; Bowels & Cochner 1984; Gross 1995). These studies used a “bottom-up” approach to determine smolt-production in these systems, a method that, without historical escapement, requires the use of migration and marine survival coefficients. However, previously derived migration survival coefficients for this system were developed for the production in the Alturas Lake Creek Drainage, and therefore may underestimate the SAR’s for Redfish and Pettit lake. Alturas lake is 32 miles upstream of Redfish Lake, and historically there have been several irrigation diversions on Alturas Lake Creek increasing stream temperature and impeding river passage (Munther 1974; USFS 1987; Hall-Griswold 1990), and our isotopic sediment data suggests that there was a relatively low MDN signal in Alturas Lake compared to Redfish and Pettit Lakes (Selbie et al. 2007). By estimating escapement using nutrient budgets and isotopic methods, and using the same “bottom-up” approach to determine potential smolt-production, we are able to calculate SAR’s independent of these coefficients.

Our pre-dam SAR estimates (6-11%) indicate that the SAR may be higher than previous estimates, and they may more closely represent the SAR’s of other Pacific salmon stocks in the Columbia River Watershed (5-34%) (Bowels & Cochanner 1984; Ricker 1962). The SAR values derived using our modeled estimates of historical abundance are as much as 165x times higher than modern SAR’s (0.06-3.19%, 2004 -2011), and are higher than the SAR (>4.9%) needed to reach population replacement under current conditions (Ricker 1962; Evans 2019, Kozfkay et al. 2019).

While we utilized the chlorophyll a model to allow for direct comparison with models that utilized marine survival coefficients (Gross et al. 1998), previous studies (Teuscher et al.
compared five methods used to estimate the production potential of Redfish Lake, including the previously described chlorophyll method (Rieman and Meyers 1992). In addition to chlorophyll \( a \), they estimated smolt production using a euphotic volume (Koenings and Burkett 1987), a total phosphorous model (Plante and Downing 1992), a phytoplankton production measure (Stockner et al. 1995), and a stock recruitment model (Bowels and Cochnauer 1984). Our smolt production estimates using the chlorophyll \( a \) method, is slightly lower than the production estimated in 1994 (173,000 vs. 199,000 smolts for Redfish Lake), as a result of lower average chlorophyll \( a \) concentration measured over a longer time period (1992-2019). The comparison of these models, suggested that chlorophyll \( a \) is a conservative estimate of smolt production, and that the primary phytoplankton production (PR) model may more accurately estimate smolt production in this system. Previous estimates of potential smolt production using the PR model estimate production potentials of 260,000 and 63,000 for Redfish and Pettit respectively. Using the PR model coupled with our modeled escapement reconstructions, SAR’s are slightly lower (8% and 4%) for Redfish and Pettit Lakes. Additionally, it is possible that the contribution of MDN in the system could have historically increased chlorophyll concentrations, or higher production, resulting in historically higher smolt production, and a respectively lower SAR (Gross et al. 1998).

\textit{MDN} \\
Previously derived underestimates of historical population size and SAR’s, may have also resulted in an underestimation of the historical contribution of nitrogen and phosphorus via returning adults. With an annual escapement of 20,000 and 2,500 for Redfish and Pettit Lakes respectively, under pre-dam conditions, MDN historically would have made up as much as 16% of the nitrogen input to the system in both lakes - not accounting for nutrient export via out-migrating smolts.
Previous studies have indicated that in this watershed, under modern conditions, sockeye serve as a net nutrient sink, and have for over 60 years (Gross et al. 1998; Evans et al. 2019). Further studies have suggested that even under pre-dam conditions, only 0.1-1.5% of the relative nutrient contribution was historically marine derived, again estimates that were derived lacking reliable historical escapement estimates (Gross 1995). Our model output suggests moderate MDN input, which could have increased lake carrying capacity. However, the proportion of MDN is lower than systems in Alaska that show strong positive MDN-escapement feedbacks (Finney et al. 2000).

Broader Implications

The Columbia River currently serves as the world’s largest ecosystem restoration program, and the plight of Snake River salmon serves as one of the foremost environmental issues of the twentieth century (Lee 1996, Blumm et al. 1998). As of 2017, an estimated $17 billion was spent on Idaho’s salmon recovery by the Bonneville Power Administration (Idaho Statesman 2021). However, these costly management efforts have been carried out with limited knowledge of the historical population sizes of sockeye salmon that used this watershed for spawning. Salmon restoration attempts show no signs of recovering the listed species (Blumm 1998; Thurow et al. 2019).

Providing more accurate historical annual escapement estimates may aid in guiding recovery goals, and prioritizing recovery efforts and management. Additionally, refined estimates of historical abundance will provide an increased understanding regarding pre-dam SAR’s and marine-derived nutrient contribution, and may aid in guiding associated management strategies.
Our historical abundance estimates indicate that the NMFS criteria for ESA down listing, may require that as little as 5% of the historical escapement returns to the Sawtooth Valley lakes, and that current annual increases in salmon populations are marginal (Kline & Flagg 2014). Therefore, our escapement estimates may provide a more accurate baseline for assessment of what is considered a healthy and recovered population, and provides evidence of the negative effects shifting baselines have on current recovery goals.
References


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Appendix A

Figure A-1. Mean annual discharge (m$^3$ s$^{-1}$) measured at the Upper Salmon USGS gauge, 230 km downstream of Redfish Lake. Years with recorded nitrogen concentrations of the Sawtooth Valley Lakes are denoted by red markers. The long-term average (55.0 (m$^3$ s$^{-1}$)) (1913-2020) is denoted by the solid horizontal line.

Figure A-2. Log$_{10}$ transformed TN (ppb) vs. Discharge (m$^3$ s$^{-1}$) for Redfish Lake Creek ($R^2 = 0.06$) (Wurtsbaugh personal communication).
Figure A-3. Monthly average discharge (m$^3$/s) for Redfish Lake Creek for an average water year (1993). Monthly values are averages from 1913-2020.

The C-Q relationship for Redfish Lake Creek, the primary contributor of nitrogen to Redfish Lake, provides additional evidence that nutrient concentration is independent of discharge in this system (Figure A-2, $R^2 = 0.06$). Therefore, the input of nitrogen varies seasonally (Figure A-3) with fluxes of stream discharge. The annual hydrograph of Redfish Lake Creek (Figure A-3), shows extreme seasonal fluctuations, and is strongly related to trends in annual discharge of the Upper Salmon ($R^2 = 0.889$, unpublished data).

Discharge of the Upper Salmon (measured at the Upper Salmon USGS gauge, 230 km downstream of Redfish Lake), does not show evidence of long-term changes in discharge -- supporting paleo-reconstructions of stream discharge on the Snake River (Wise 2010).
Appendix B

Table B-1. Mean nutrient concentrations (ppb) of inlet streams to the main potential historical sockeye salmon lakes of the Sawtooth Valley, Idaho. Samples were collected monthly from June-October.

<table>
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<th></th>
<th>NO3</th>
<th>NO2</th>
<th>NH4</th>
<th>DIN</th>
<th>TKN</th>
<th>TN</th>
<th>SRP</th>
<th>TP</th>
<th>DIN:SRP</th>
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<td>2018</td>
<td>6.4</td>
<td>2</td>
<td>8.4</td>
<td>62.4</td>
<td>68.8</td>
<td>1.8</td>
<td>7.6</td>
<td>4.8</td>
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<td>60.2</td>
<td>67.6</td>
<td>2</td>
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We did not observe significant year-to-year variation in nutrient concentrations (Figure 2, Table B-1). Nutrient concentrations were comparable to nutrient concentrations reported in previous studies that utilized the same collection methods (Marcarelli 2007; Marcarelli 2007; Gross 1995).
Figure B-1. Mean concentrations of NO\textsubscript{3}^- + NO\textsubscript{2}^- (ppb), denoted by the solid line, and NH\textsubscript{4}^+ (ppb), denoted by the dashed line for the inlets to Alturas Lake (A), Pettit Lake (B), Yellowbelly Lake (C), and Redfish Lake (D), measured monthly June - October, 2018-2020. The two inlets to Redfish Lake, Redfish Lake Creek and Fish Hook Creek are denoted by the black and grey lines respectively.

We did not observe systematic seasonal shifts in nutrient concentration across study lakes (Figure B-1). NO\textsubscript{3}+ NO\textsubscript{2} was the dominant form of DIN, with exception of Yellowbelly Lake, potentially as a result of stream-lake interactions and nutrient processing in an upstream lake (Marcarelli 2007; Wurstbaugh 2005).