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An Ecological Comparison Between Resource Subsidies: Pacific Lamprey (*Entosphenus tridentatus*) and Pacific Salmon (*Oncorhynchus* spp.)

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AN ECOLOGICAL COMPARISON BETWEEN RESOURCE SUBSIDIES: PACIFIC LAMPREY (*ENTOSPHENUS TRIDENTATUS*) AND PACIFIC SALMON (*ONCORHYNCHUS SPP*.)

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by
Jocelyn Wensloff
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Graduate Studies

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ABSTRACT

AN ECOLOGICAL COMPARISON BETWEEN RESOURCE SUBSIDIES: PACIFIC LAMPREY (*ENTOSPHENUS TRIDENTATUS*) AND PACIFIC SALMON (*ONCORHYNCHUS SPP.*)

by

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Historically, oligotrophic Pacific Northwest (PNW) streams received annual returns of spawning anadromous fish that provided resource subsidies in the form of marine-derived nutrients (MDN), thus driving stream food web productivity. To date, many studies in the PNW have focused on Pacific salmon (*Oncorhynchus* spp.) as a resource subsidy, overlooking other anadromous fish species such as Pacific lamprey (*Entosphenus tridentatus*). Both Pacific salmon and Pacific lamprey are culturally important to PNW tribes for ceremonial, medicinal, and subsistence purposes, and have been since time immemorial. Unfortunately, both salmon and lamprey populations are in decline. Historically, lamprey have been disregarded and actively eradicated by non-tribal resource managers, and although they have recently been included in restoration considerations, their role as a resource subsidy is still poorly understood. In order to better understand how Pacific lamprey can subsidize stream food webs, I used a nutrient diffusing substrate (NDS) array amended with Pacific lamprey and tule fall Chinook salmon tissue to compare the basal food web response in the summer and fall, when lamprey and salmon spawn, respectively. This study was conducted in the upper Yakima River basin where the Yakama Nation has an active adult lamprey translocation program.

I measured chlorophyll *a* as the autotrophic food web response and community respiration (CR) as the heterotrophic food web response. Chlorophyll *a* responded equally to lamprey and salmon but was significantly higher in the summer. Alternatively, CR had a higher response to salmon compared to lamprey and was significantly higher in the fall. Differences observed in food web response were dictated by season, where chlorophyll *a* nutrient response ratios (NRRs) were roughly twice as high as in the summer and CR NRRs were roughly twice as high as in the fall. Stoichiometric differences in lamprey and salmon tissue likely facilitated this response and had C:N:P ratios of roughly 187:37:1 and 60:13:1 respectively. These results indicate that Pacific lamprey are equivalent to salmon as a resource subsidy for the autotrophic food web in the summer when lamprey would normally spawn and suggest that increased lamprey populations will drive stream food webs that support both lamprey and salmon.

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To the streams, fish, and lamprey, thank you for inspiring and persisting.

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CHAPTER I

INTRODUCTION

Fluvial systems connect landscapes through their unidirectional transport of water and nutrients from their headwaters, across vastly distant ecotones, and ultimately to the ocean. The structure and productivity of stream food webs are often dictated by the influx of resource subsidies from the surrounding landscape (Cummins 1974; Vannote et al. 1980). Resource subsidies are additions of nutrients, organic materials, or organisms, derived outside of the receiving ecosystem that can increase primary and secondary production in the receiving ecosystem (Polis et al. 1997). Early studies on resource subsidies focused on influxes of allochthonous resources via leaf-litter from the surrounding riparian habitat into streams which provide nutrients (Webster et al. 2000), and food sources for aquatic macroinvertebrates (Cummins et al. 1989). This initial understanding of a resource subsidy has since expanded to include resource subsidies in many forms and across multiple ecosystems. For example, terrestrial organisms can act as resource subsidies as demonstrated by mass drownings from wildebeest migrations which can provide up to 1,100 tons of biomass to stream food webs and contribute a large amount of added nutrients to the system (Subalusky et al. 2017). Although stream food webs rely on influxes of resource subsidies, they can simultaneously provide a resource subsidy to the surrounding riparian habitat. For example, during aquatic macroinvertebrate emergence, the macroinvertebrates can act as a resource subsidy and dictate where predators such as spiders accumulate in the receiving riparian ecosystem (Marczak and Richardson 2007). Although these studies have expanded the literature base for resource subsidies, one of the most commonly studied resource subsidies in the Pacific Northwest (PNW) are Pacific salmon (*Oncorhynchus* spp.), which transport marine-derived nutrients (MDN) to freshwater systems through their anadromous life history (Gresh et al. 2000).

Pacific salmon spend their early lives in freshwater, migrate to the ocean to accumulate biomass, and return to their natal streams to complete their life cycle. As returning adults, they transport carbon (C), nitrogen (N), and phosphorous (P) subsidies from the ocean to the receiving freshwater ecosystem (Polis et al. 1997; Lundberg and Moberg 2003). These subsidies from runs of semelparous salmon provide carcass and egg material which enter the food web directly through consumption by aquatic macroinvertebrates (Chaloner et al. 2002), juvenile anadromous (Bilby et al. 1996) and resident fish species (Kaylor et al. 2020), or terrestrial scavengers such as the American dipper (*Cinclus mexicanus*; Tonra et al. 2015), or bears (*Ursus* spp.; Shakeri et al. 2018). Alternatively, salmon can contribute indirectly to food webs, where the decomposition of their post-spawn carcasses releases nutrients which can stimulate the autochthonous production of benthic biofilms to provide a food source for aquatic macroinvertebrates, juvenile and resident fish species (Morley et al. 2016; Kaylor et al. 2020), and other higher consumers (Tonra et al. 2015). In some systems, marine-derived N sources may be extremely important in stream food webs as some studies have found that ^{15}N composes 30-73% of the organismal N in stream consumers after salmon addition (Chaloner et al. 2002; Tonra et al. 2015; Morley et al. 2016).

Unfortunately, many Pacific salmon runs are extinct or declining across their historic range (Nehlsen et al. 1991), which can directly impact stream food webs. Many anthropogenic factors have contributed to salmon declines, such as the construction of hydropower dams, over-fishing, logging, mining, irrigation infrastructure and flow regulation, and continued urban growth (Nehlsen et al. 1991). Decreased salmon returns directly impact the MDN influx added to PNW stream food webs, as it is estimated that only 6-7% of historic salmon MDN are entering these systems (Gresh et al. 2000). Diminished MDN inputs from anthropogenic impacts can rapidly decrease stream productivity (Bilby et al. 1996), a process termed cultural oligotrophication (Stockner et al. 2000). Cultural oligotrophication can elicit a positive feedback loop in which decreased MDN input decreases stream productivity which decreases juvenile salmonid survival, which decreases spawner abundance thus decreasing MDN input (Wipfli et al. 1998; Naiman et al. 2002). Understanding this feedback loop and the importance of salmon as a resource subsidy (see Janetski et al. 2009) has led to multiple responses to mitigate cultural oligotrophication. For example, from 1999 through 2019 the state of Washington has invested approximately $1 billion in various projects to improve salmon populations (WSRC 2020). Additionally, various resource managers have attempted to offset the positive feedback loop by adding salmon carcasses or artificial salmon carcass analog pellets directly into salmon-bearing streams (Pearsons et al. 2007; Kohler et al. 2012). This salmon-centric approach has allowed researchers and resource managers to understand the ecological importance of resource subsidies via annual anadromous returns; however, less charismatic anadromous species such as Pacific lamprey (*Entosphenus tridentatus*) have largely gone unnoticed in terms of their ecological importance by non-tribal resource managers.

Pacific Lamprey

Pacific lamprey are a member of the ancient jawless fish superclass, Agnatha, and are a native member of PNW ichthyofauna (Close et al. 1995; Close et al. 2002). They are an anadromous, semelparous species, that begin their life as larval, filter-feeding organisms burrowed in fine stream sediment for 3-8 years (Close et al. 2002; Dawson et al 2015). Once they transform into juveniles (Clemens 2019), they migrate to the oceans and undergo a parasitic phase for up to 3.5 years (Beamish 1980; Clemens et al. 2010), accumulating a large amount of MDN before returning to the rivers to spawn. Spawning generally occurs between April and July (Beamish 1980), however the time spent in freshwater prior to spawning depends on the specific life history characteristics. Ocean-maturing Pacific lamprey will spawn within several weeks of re-entering freshwater, whereas stream-maturing lamprey can hold for up to 2 years in river systems prior to spawning (Close et al. 2004; Miller 2012; Clemens et al. 2013).

Similar to Pacific salmon, Pacific lamprey contribute to both direct and indirect food web pathways. Larval or migrating juvenile Pacific lamprey are often cited as a predation-buffer against migrating salmon (Close et al. 2002; Clemens et al. 2010) due to their poor swimming ability and high lipid content (Whyte et al. 1993), and they can stimulate direct food web pathways via predation by sculpin (*Cottus* spp.), white sturgeon (*Acipenser transmontanus*), rainbow trout (*O. mykiss*) and other consumers (Merrell 1959; Poe et al. 1991; Close et al 1995). Furthermore, as returning adults, they provide carcass and egg material during and after spawning events, which can further drive direct food web pathways (Beamish 1980; Close et al. 2002). Alternatively, they can contribute to indirect pathways during their larval stage where they filter feed and assimilate 30-

40% of the detritus, diatoms, and algae they ingest, thus breaking down larger particles into sizes that are available for filter feeding aquatic insects (Moore and Mallatt 1980; Merritt et al. 1984). Additionally, lamprey have a life history such that they could subsidize stream food webs with MDN similar to Pacific salmon, but there have been very few studies that have investigated Pacific lamprey as a resource subsidy. Dunkle (2017) utilized an adapted mechanistic periphyton biomass model to predict that post-spawn Pacific lamprey carcasses may contribute a small-scale, localized response that creates a hotspot of food web activity due to the small population and body size of Pacific lamprey. Moreover, Dunkle et al. (2020) found that complex in-stream habitat can facilitate this process by contributing to carcass loading at specific locations within the stream. Although there are limited studies with Pacific lamprey, studies on anadromous sea lamprey (*Petromyzon marinus*) in Maine suggest that lamprey may contribute similarly to indirect food web pathways like salmon, where post-spawn carcasses can increase downstream biofilms as a food source for aquatic macroinvertebrates and larval lamprey (Weaver et al. 2016; Weaver et al. 2018a). Furthermore, Hogg et al. (2013) found evidence of a positive feedback loop where the presence of larval lamprey increased subsequent spawner abundance and MDN inputs from adult lamprey increased larval growth rate and survival (Weaver et al. 2018b).

Currently, Pacific lamprey are listed as a species of concern by United States Fish and Wildlife Service due to declining populations and face a “high risk” of extirpation in most of the watersheds where they still exist (Renaud 1997; Wang and Schaller 2015). However, Pacific lamprey populations could historically be found in streams from Japan to Baja California and were understood to have large populations which could compose the dominant biomass in some coastal rivers (Kan 1975; Close et al. 2002; Miller 2012). There is not an agreed quantitative historical estimate, however daytime counts at Bonneville Dam were as high as 400,000 prior to 1969 although runs in the Columbia River basin were likely much higher than this as a Nez Perce tribal member reported that up to 500,000 lamprey were commercially harvested at Willamette Falls alone in the 1800s (CRITFC 2011).

The sharp decline in Pacific lamprey populations is multi-faceted. Pacific lamprey share many of the same threats as Pacific salmon (Clemens et al. 2017), however other actions such as systematic extermination and commercial harvest additionally contributed to the decline. Rotenone treatments were a common method used to rid streams of non-salmonids during the 1940s-1980s (Close et al. 1995). For example, a 1967 rotenone treatment in the Umatilla River killed around 1 million fish of varying age groups (Close et al. 1995), and a 1969 rotenone treatment in the North Fork John Day River killed 33,000 adult Pacific lamprey (Figure 1; ODFW 2002). Although lamprey were actively exterminated in some basins, there was a commercial harvest at Willamette Falls which began in 1941, peaked in 1946 with 500,000 adults harvested, and ended in 2001 after just 12,276 were harvested (Close et al. 1995; ODFW 2002; Close et al. 2009). These factors are compounded with a general lack of awareness by various resource managers, and an overall negative bias towards lamprey due to invasive sea lamprey in the Great Lakes (USFS 2011).

Declines in Pacific lamprey were first noticed by Native American tribal members along the Oregon coast and inland Columbia River basin (ODFW 2002; Close et al. 2004). Since then, PNW tribes have been at the forefront of Pacific lamprey research, restoration, and conservation actions. In 2004, the Columbia River tribes organized a summit where 12 tribes from California, Oregon, and the Columbia River basin along with federal, state, and local partners committed to conserve this unique species (Wang and Schaller 2015). These tribes are now collaborating with other governing entities to spearhead Pacific lamprey research to "…restore natural production of Pacific lamprey to a level that will provide robust species abundance, significant ecological contributions and meaningful harvest…" throughout their historic distribution (Yakama Nation Fisheries 2020).

Tribal Conservation in the Columbia River Basin

Pacific Northwest tribes have a deep cultural connection with Pacific lamprey. In addition to relying on Pacific lamprey as a source of food, many tribes have used lamprey for medicinal and ceremonial purposes since time immemorial (Close et al. 1995; Close et al. 2002). The decline in lamprey populations has directly impacted tribal members' legal harvest opportunities and ability to maintain traditional ecological knowledge surrounding this species (Close 1995; Close et al. 2002; Close et al. 2004; Miller 2012). In order to restore Pacific lamprey populations and maintain the cultural connection, many PNW tribes have contributed to lamprey restoration and research; however 4 Columbia River basin treaty-tribes in particular have banded together and been extensively involved in lamprey restoration, conservation, and research within the Columbia River basin (Figure 1).

In 1977, the Confederated Tribes of the Umatilla Indian Reservation (CTUIR), the Confederated Tribes of Warm Springs (Warm Springs), the Nez Perce Tribe (Nez

Perce), and the Confederated Tribes and Bands of the Yakama Nation (Yakama Nation) created the Columbia River Inter-Tribal Fish Commission (CRITFC n.d.a; Figure 1). This collective body was formed to facilitate and coordinate with local and international entities to ensure its member treaty-tribes' fishing rights are maintained into perpetuity (CRITFC n.d.a). Since the inception of CRITFC, the organization, along with the member treaty-tribes, have spearheaded many lamprey restoration efforts, and they actively provide non-tribal entities with invaluable traditional ecological knowledge regarding historic lamprey distribution, abundance, and ecological role to guide conservation efforts on their traditional and ceded lands and beyond (CRITFC 2011; CRITFC n.d.b). In 2011, CRITFC and its member tribes, created a comprehensive restoration plan, the "Tribal Pacific Lamprey Restoration Plan for the Columbia River Basin," dedicated to restoring Pacific lamprey populations in the Columbia River mainstem and tributaries with targeted goals (CRITFC 2011). This plan intends to halt Pacific lamprey declines and rebuild healthy populations that allow Pacific lamprey to fulfill their ecological role while increasing opportunities for tribal members to exercise their rights to sustainably harvest and maintain traditional ecological knowledge surrounding this species (CRITFC 2011). Although CRITFC has made historic progress in terms of lamprey restoration, each member tribe has collaboratively and individually contributed to increase lamprey populations.

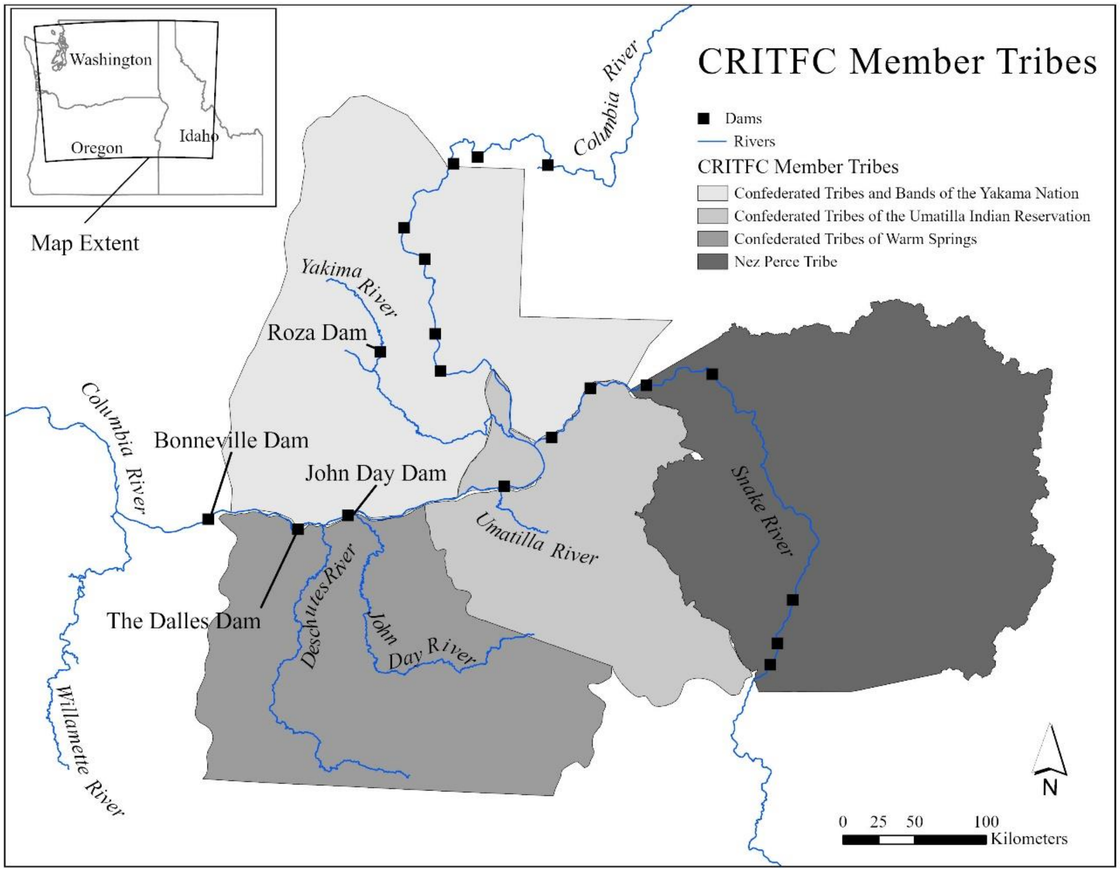

Figure 1 Ceded lands of Columbia River Inter-Tribal Fish Commission member treaty-tribes across Washington, Oregon, and Idaho, USA. Clock-wise beginning with the ceded lands of the Nez Perce Tribe (darkest grey) is the Confederated Tribes of the Umatilla Indian Reservation, the Confederated Tribes of Warm Springs, and the Confederated Tribes and Bands of the Yakama Nation. Major rivers and several Columbia River mainstem dams receiving tribal Pacific lamprey restoration work are shown.

The CTUIR was one of the first treaty-tribes to focus on Pacific lamprey research and to improve lamprey populations. In 1998, they began including night counts for adult Pacific lamprey returns at Bonneville Dam to obtain better data about Pacific lamprey numbers as traditional ecological knowledge suggested that lamprey mainly move at night when they first re-enter river systems (Close 2000; Close et al. 2004; Miller 2012). Although there was an 8-year delay before the U.S. Army Corps of Engineers also included night counts for Pacific lamprey at all of the passage structures on Bonneville

Dam (CRITFC 2011), night counts are now included as a recommendation to improve the accuracy of lamprey population estimates (Pacific Lamprey Technical Workgroup 2017). Additionally, in efforts to increase lamprey populations, the CTUIR began a translocation program in 1999 that successfully transplanted 2,600 Pacific lamprey adults by 2007 (Close et al. 2009). Today, CTUIR and the Yakama Nation lead the way in the development of artificial propagation methods and have successfully produced thousands of larvae with outplanting plans that build on their prior successes (CRITFC n.d.b; Lampman et al. 2016; Lampman et al. 2020; Yakama Nation Fisheries 2020). As a result of CTUIR efforts, populations of larval and spawning adult Pacific lamprey have increased in the Umatilla River basin (Close et al. 2009; USFS 2019; Ward et al. 2012).

Similarly, the Warm Springs have been active in many areas of lamprey research and have contributed to knowledge around lamprey habitat requirements and improving population estimates. Warm Springs biologists began a study in 2002 dedicated to determining lamprey species composition, adult abundance, and larval distribution within the Deschutes River basin in Oregon (Graham and Brun 2004). They found larval lamprey in 4 of the 13 streams surveyed with larval lamprey presence positively associated with depositional areas, fine sediment, wood presence, and low stream flows (Graham and Brun 2004; Graham and Brun 2006). After the 2010 removal of the Powerdale Dam from the Hood River in Oregon, Warm Springs biologists monitored the return of Pacific lamprey and later found 1- and 2-year old larvae above the old dam site (CRITFC n.d.b). From 2010-2016 the Warm Springs biologists worked on improving estimates of escapement, the portion of a returning anadromous population that avoids harvest, at Willamette Falls and estimated that an average of 60,689 adults passed the fish structures, a 50-60% decline in historic abundance (Baker and McVay 2016; USFS 2019). During this time, Warm Springs also improved estimates for escapement and abundance at Sherars Falls on the Deschutes River (CRITFC et al. 2018).

The Nez Perce began an active translocation program in 2006 with the goal of reestablishing self-sustaining lamprey populations in the Snake and Clearwater River basins, largely in Idaho (CRITFC 2011; Ward et al. 2012). To start this program, they collected lamprey from dewatered fishways at the Dalles and John Day dams in the Columbia River, and later also collected lamprey during upstream migration at Bonneville, the Dalles, and John Day dams (CRITFC et al. 2018). As a result of the translocation program, spawning and larval lamprey have been documented in Asotin Creek (Snake River basin) and Lolo Creek (Clearwater basin) where they had not been detected since the 1980s, and 2004-2006 respectively (CRITFC et al. 2018; Ward et al. 2012). The Nez Perce extended their translocation project to include the Salmon River basin in 2012 (CRITFC et al. 2018), and as of 2018, the Nez Perce has released 2,805 adult lamprey into the Clearwater, Salmon, and Snake River basins (Poirier 2019).

In 2011, the Yakama Nation and CRITFC organized the first international forum focused on recovery and propagation of lamprey, and now the Yakama Nation has a successful artificial propagation program that produces thousands of larval lamprey per year with the eventual goal of larval outplanting (Greig and Hall 2011; Lampman et al. 2020; Yakama Nation Fisheries 2020). Additionally, the Yakama Nation has an active translocation project modeled after CTUIR efforts that successfully translocated 15 adults into Status Creek (Yakima River basin) in 2012 (CRITFC 2011; Yakama Nation Fisheries 2020). Since then, the Yakama Nation has translocated adult Pacific lamprey into the Yakima, Naches, Wenatchee, and Methow rivers (Lampman 2017a; Lampman 2017b; Lampman 2017c). Translocation efforts in the Yakima River basin have included the upper Yakima basin above Roza Dam, where Pacific lamprey were locally extirpated (Figure 1). Although Roza Dam is a known Pacific lamprey barrier (Lampman et al. 2014), the Yakama Nation translocated 102 adults above the dam in efforts to restore populations throughout the Yakima River and began passage improvement on Roza Dam (Lampman et al. 2015). Larval lamprey release pheromones which can attract spawning adults (Sorensen et al. 2005; Yun et al. 2011) and are therefore an important mechanism for improving Pacific lamprey populations. If Pacific lamprey populations increase in the Yakima River, and throughout the Columbia River basin, they will contribute increased MDN to these streams and will likely contribute to stream food web productivity (Close et al. 2002).

Stream Food Web Response to Anadromous Subsidies

Although a resource subsidy benefits the receiving ecosystem (Polis et al. 1997), environmental conditions can dictate the food web response via changes in the benthic biofilm. Benthic biofilms are a symbiotic community of autotrophic and heterotrophic microbiota that convert dissolved water column nutrients and organic matter into particulate matter that can be transferred to higher consumers, making them an integral part of the basal food web in stream networks (Cummins 1974; Weitere et al. 2018). Understanding how biofilms respond to resource subsidies shows the potential for food web assimilation of the subsidy. After initially increasing in response to a resource subsidy, biofilms can then decrease due to macroinvertebrate grazing (Claeson et al.

2006), or due to scouring from active spawner disturbance (Cak et al. 2008; Janetski et al. 2009). In some cases, the biofilm may not respond at all if light limitation attenuates demand by autotrophic-dominated biofilms (Ambrose et al. 2004). In most cases, studies have documented increased benthic biofilms (biofilms) as an initial response to carcass additions (Wipfli et al. 1998; Fisher et al. 1999; Janetski et al. 2009; Weaver et al. 2016), particularly if nutrients limit biofilm growth.

Biofilm nutrient limitation status can vary among streams and across seasons which may influence the initial, indirect food web response, and the autotrophic and heterotrophic biofilm communities can differ in their response to the same subsidy (Tank and Dodds 2003; Marcarelli et al. 2009; Hoellein et al. 2010). For example, some studies have found stream biofilms are typically N and P co-limited and have higher P retention during the spring (Hoellein et al. 2007; Hall et al. 2002). Similar trends were seen in the fall, except that some autotrophic communities expressed primary N limitation with secondary P limitation (Morley et al. 2016). Nutrient limitation in the fall is partly attributed to the greater addition of leaf litter, which requires a large amount of microbial processing. For example, Webster et al. (2000) found that by excluding leaf and wood litter, P and ammonium retention was reduced suggesting that microbial colonization on the surface of leaf and wood litter outcompeted other heterotrophic processes such as fungal biomass accumulation (Tank and Webster 1998). The nutrient requirements by microbes during leaf decomposition may help explain why coho salmon (*O. kisutch*) carcasses alleviated autotrophic communities, despite all but 1 heterotrophic community remaining mostly P limited (Rüegg et al. 2011). This suggests that the elemental composition of the resource subsidy in combination with the stoichiometric demand of biofilms can further influence the food web response.

Anatomical differences between Pacific lamprey and salmon may contribute to stoichiometric differences in the resource subsidy that may influence the food web response. For example, salmon and other teleost fish, have calcified bones which can hold up to 40% of organismal P, whereas lamprey are composed of cartilage and keratin which are lower in P (Parmenter and Lamarra 1991; McPhail 2007). Prior to my study, the elemental composition of Pacific lamprey was unknown, however Weaver et al. (2015) reported sea lamprey in Maine were composed of 54% C, 11.2% N, and 1% P, and had a C:N:P molar ratio of 207:30:1. Although Pacific salmon molar ratios vary by species, Rüegg et al. (2011) reported unpublished data from D. Chaloner that estimated pink salmon (*O. gorbuscha*) to have a molar ratio of 139:24:1. Molar ratios may ultimately determine how the autotrophic or heterotrophic community may benefit from added nutrients based on the stoichiometric demand of consumers (Elser et al. 1996).

Although both Pacific lamprey and Pacific salmon share anadromous life histories and similar distributions (Wicks-Arshack et al. 2018), they differ in the seasonal timing of their life histories which may influence nutrient delivery and stream food web response. For example, Pacific lamprey typically spawn from April through July when biological activity is beginning to increase from warming temperatures and increased light availability (Beamish 1980; Crandall and Wittenbach 2015). Alternatively, Pacific salmon, although there are some variations, typically spawn in the fall and winter at a time with less biological activity due to cooler temperatures and less light availability (Wydoski and Whitney 2003). Therefore, it is possible that resource subsidies from spawning timing differences influence fungal biomass, bacterial density, or stable isotope ($\delta^{13}C$ and $\delta^{15}N$) enrichment of biofilms (Samways et al. 2015). Moreover, lamprey are smaller than salmon; Pacific lamprey can reach 70 cm in length and can weigh as much as 453.5 g whereas Pacific salmon typically range from 50-92 cm and weigh anywhere from 1800-10,000 g on average depending on the species (Wydoski and Whitney 2003). The drastic differences in fish sizes may alter the quantity of nutrients delivered to streams in runs of equal numbers.

Given the large amount of money being invested to improve salmon returns, and the simultaneous increased attention around Pacific lamprey, it is important to understand how seasonal timing of lamprey life history will influence the food web response. For example, as the Yakama Nation works to increase Pacific lamprey populations in the upper Yakima River basin, an area that has not had Pacific lamprey for several decades, it is important to understand how the added MDN will influence the stream food webs. Understanding how autotrophic and heterotrophic biofilms respond to lamprey tissue compared to salmon will help predict the indirect food web response to lamprey restoration efforts. This will allow resource managers, the Yakama Nation, and other tribes to gain greater insight into how lamprey restoration efforts might impact stream food webs in the upper Yakima basin and similar oligotrophic systems.

Study Questions and Hypotheses

This study sought to elucidate the role of Pacific lamprey as a resource subsidy compared to Pacific salmon. This was done by comparing the stream biofilm response to lamprey and salmon tissue in streams above Roza Dam, and how that response varied by environmental and seasonal factors, and by differences in the elemental composition of fish species. In this study, I aimed to answer: 1) Are streams in the upper Yakima River basin nutrient limited, and how does nutrient limitation change seasonally? 2) Do autotrophic and heterotrophic biofilms respond differently to salmon and lamprey compared to added nutrients? 3) Do stream biofilms respond similarly to lamprey and salmon tissue, and does the response differ between summer and fall? 4) What is the elemental composition of Pacific lamprey compared to Pacific salmon? 5) Can seasonal differences in stream temperature, light availability, and canopy cover predict stream biofilm response?

Given the oligotrophic conditions of the upper Yakima basin, I hypothesized that the streams would be nutrient-limited, especially in the summer when more light activity may stimulate nutrient demand via autotrophic biofilms. I expected biofilm communities to respond similarly to nutrient and fish tissue treatments; however, I did not expect a difference in biofilm response between lamprey and salmon treatments. Due to the presence of bones in salmon, I expected Chinook salmon to have higher P content than lamprey, but I did not expect a difference in nitrogen or carbon content. Finally, I expected that season will be the primary predictor in biofilm response given that light availability and temperature are largely controlled by season.

CHAPTER II

METHODS

Site Selection and Study Design

I selected five study sites in the Upper Yakima River basin in Kittitas County (Figure 2). Sites were selected on the Yakima River, Teanaway River, Swauk Creek, Taneum Creek, and Manastash Creek. Locations at these sites were selected based on accessibility, riparian canopy openness, lack of a passage barrier, and similarity to suitable Pacific lamprey spawning grounds defined by median substrate size (median = 27 mm, Stone 2006; median = 24 mm, Gunckel et al. 2009). Open canopy sites were given preference in order to reduce any potentially confounding influence of light-limitation on autotrophic biofilm growth when comparing the food web response among study sites (Ambrose et al. 2004).

At each site, I measured the seasonal change in nutrient limitation of autotrophic and heterotrophic benthic biofilms using a nutrient diffusing substrate (NDS) array. In 2020, I deployed NDS arrays from 06 June to 04 August (summer) and from 02 October to 10 November (fall). Summer months were selected based on typical lamprey spawning periods (Close et al. 2002), however COVID-19 setbacks delayed my earliest sampling until June; fall months were selected based on typical salmon spawning periods in the Yakima basin (Yakama Nation 2019). The seasonal separation also allowed a comparison between two distinctly different “metabolic” time periods in these streams: summer when autotrophic metabolism was expected to dominate in the high light conditions, and fall when heterotrophic metabolism was expected to dominate due to leaf litter inputs and increased shading.

I measured general stream habitat characteristics to further explain the biofilm response. I estimated canopy openness using a spherical densiometer (Spherical Crown Densiometer, Convex Model A, Forestry Suppliers; Jackson, MS, USA), and I measured stream velocity using a portable flow meter (Flo-Mate 2000, Marsh McBirney; Loveland, CO, USA) to calculate discharge at a representative channel cross-section. Additionally, during NDS deployment and retrieval, I measured *in situ* temperature and dissolved oxygen using a portable, handheld YSI (YSI ProODO, YSI Inc.; Yellow Springs, OH, USA), and I collected water samples for stream ammonium (NH_4^+) , nitrate (NO_3^-), soluble reactive phosphorous (SRP), and dissolved organic carbon (DOC) concentrations. I also measured photosynthetically active radiation (PAR; Odyssey Photosynthetic Active Radiation Logger, Dataflow Systems Inc.; Christchurch, New Zealand) as pulses s^{-1} at one-minute intervals during several representative days at each site during NDS deployment. Finally, during the summer NDS deployment, I calculated median substrate size from the cumulative substrate measured along the intermediate axis (n =100 per site) via a Wolman Pebble Count (Wolman 1954). In contrast to all other measurements which occurred in both seasons, substrate was measured only in the summer because there was no sediment-mobilizing stream discharge between summer and fall deployment, so a change in median substrate size was not expected.

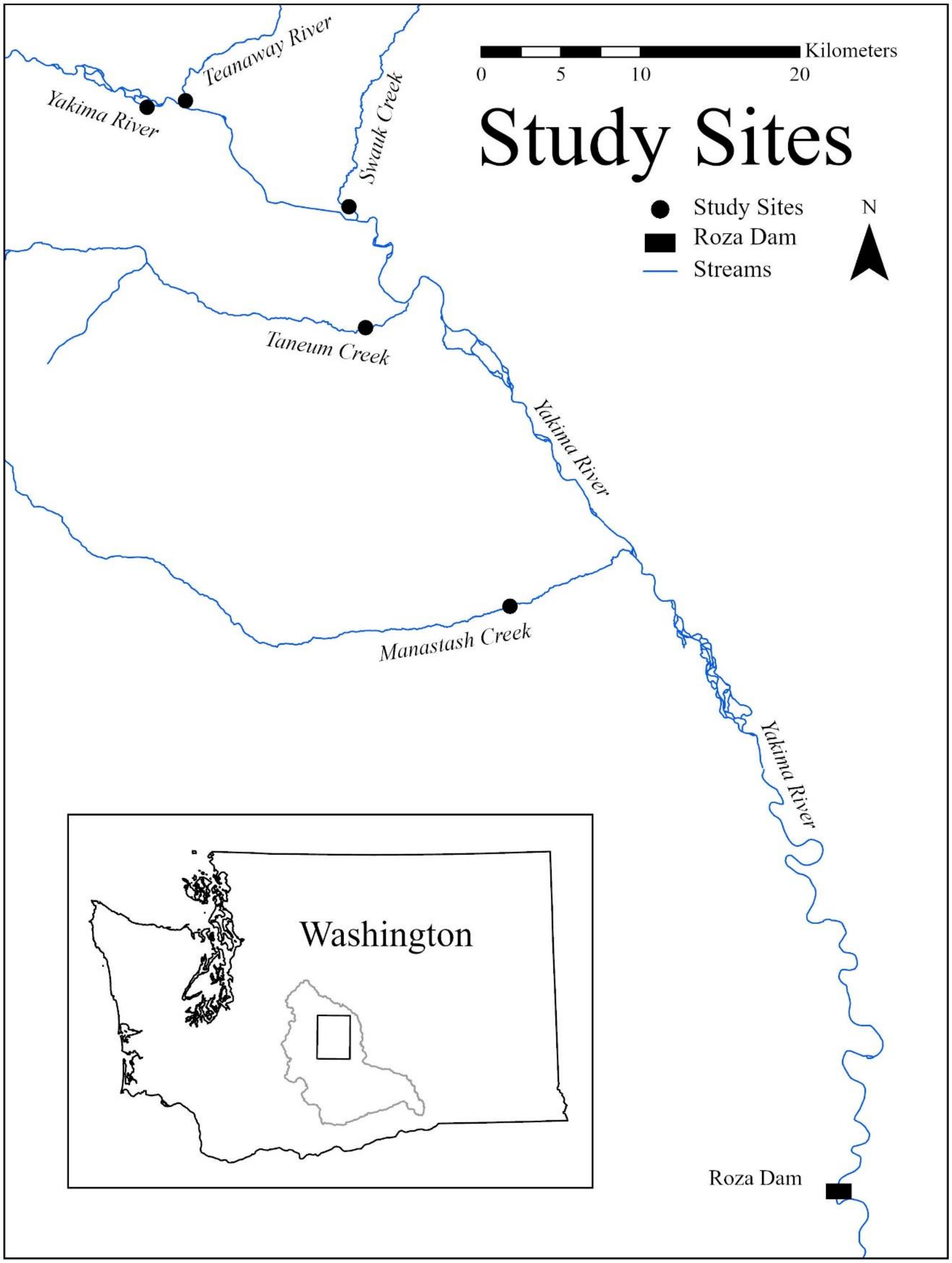

Figure 2 Map of study sites located in the upper Yakima River basin in Kittitas County, Washington. The inset map shows the location of study sites relative to the Yakima River basin (shown in grey outline in the inset map) in Washington, USA.

Preparation of Salmon and Lamprey NDS Treatments

In order to use fish tissue for NDS treatments, I received 22 sexually mature Pacific lamprey carcasses (both pre- and post-spawn) from the Yakama Nation. Although I had hoped to acquire coho salmon carcasses because they normally spawn during the fall when I deployed NDS, they were unavailable. Instead, I received 9 pre-spawn tule fall Chinook (*O. tshawytscha*) carcasses from U.S. Fish and Wildlife Service. Additionally, in order to examine if the elemental composition of the stream-maturing ecotype might change from the time of re-entry to the time when they spawn (due to the potential for altered stoichiometry to influence biofilm activity), the Yakama Nation provided 6 stream-maturing ecotype lamprey carcasses that had recently returned to the Columbia River system (fresh migrants). Individual whole carcasses were homogenized and combined with all other individuals of the same species and migration status to create three separate fish treatments for NDS arrays: salmon (+salmon, n = 9), sexually mature lamprey (+ lamprey, n = 22), and fresh migrant lamprey (+fresh migrant, n = 6) treatments.

For the lamprey preparation, individual whole lamprey carcasses were weighed and homogenized using a commercial grade food processor. Female lamprey carcasses included the eggs that remained after a subsample of eggs was removed for separate elemental analysis (described below), but some carcasses in the NDS lamprey treatment were post-spawn. Salmon heads were removed anterior to the operculum and were not homogenized due to lack of necessary equipment. The skeleton and caudal fin were homogenized in a scientific blender with milliQ water (MΩ = 18.2), then added to the remaining tissue, which was homogenized in a commercial grade food processor. Salmon and sexually mature lamprey treatments were included in each NDS array deployed in both seasons at all sites. However, the fresh migrant tissue was only included in a single summer deployment in Swauk Creek in order to compare biofilm response to fresh migrant lamprey tissue and sexually mature lamprey tissue.

Nutrient Diffusing Substrata

I used NDS arrays to measure stream nutrient limitation status and response to added nutrients following methods outlined by Tank et al. (2017). Nutrient diffusing substrata were composed of 0.5 M nutrient solutions in a 2-4% agar gel (based on number of solutes) poured into 30 mL polyethylene plastic cups. Nutrient diffusing substrate nutrient treatments included a 2% agar used for the control (agar only), +N (ammonium chloride), +P (potassium monobasic phosphate), and +C (glucose), 3% agar used for +N+P (ammonium and phosphate), +N+C (ammonium and glucose), and +P+C (phosphate, and glucose), and 4% agar used for +N+P+C (ammonium, phosphate, and glucose). Each treatment was topped with either a porous glass disk which selects for the autotrophic community (Tank and Dodds 2003), or a cellulose sponge disk which selects for the heterotrophic community (Johnson et al. 2009).

Salmon and sexually mature lamprey tissue were included as 2 additional NDS treatments that differed in preparation. The first treatment was 2% agar amended with either 3 grams of homogenized mature lamprey tissue (+lamprey, LA) or salmon tissue (+salmon, SA) in a 10% *w/v* mixture (Rüegg et al. 2011). Based on elemental analysis (described below), LA had concentrations of 4.36 mol C/L, 0.87 mol N/L, and 0.03 mol P/L, and SA had concentrations of 4.16 mol C/L, 0.93 mol N/L, and 0.07 mol P/L. The second tissue treatment was composed of approximately 25 mL of ground lamprey (LT) or salmon (ST) tissue, bound in a nylon stocking that had been soaked in milliQ water for 24 h and placed in the polyethylene NDS cup. Both tissue treatments were also topped with a porous glass disk or cellulose sponge in a fully crossed design. Additionally, fresh migrant tissue was included as an agar (FMLA) and a tissue in nylon (FMLT) treatment in a single summer deployment in Swauk Creek. As my study progressed, I began to run out of mature lamprey tissue, so I added 2 additional sexually mature pre-spawn lamprey carcasses provided by the Yakama Nation to the previously homogenized sexually mature lamprey tissue and included them in the fall LT treatment for Teanaway and Swauk deployments. Elemental analysis found no difference in elemental composition between mature and fresh migrant tissue, so adding new individuals to the lamprey treatments for two streams was unlikely to introduce excessive variation compared to the initial lamprey treatments.

To assemble the NDS arrays, treatments were randomly placed on L-bars (n = 8 bar^{-1}) and secured with waterproof silicone and zip ties (Figure 3). Each treatment (n = 11 treatments) was replicated 5 times with each top (glass or sponge) per deployment, and these arrays were deployed in each of the 5 study streams (n =110 cups per stream, Figure 4). Deployments were replicated in summer and fall (n = 550 season^{-1}), and each deployment lasted 11-15 days, a length of time sufficient to colonize biofilm based on prior studies in this area (C. Arango, unpublished data).

Nutrient diffusing substrate arrays were deployed with a minimum of 1 day between deployments to allow 24 hours after retrieval for processing the NDS tops. After retrieval, net primary production (NPP) and community respiration (CR) were measured in the laboratory using a modified light-dark bottle method (Tank et al. 2017; Tank and

Dodds 2003). First, NPP (μg O_2 cm^{-2} h^{-1}) was measured by incubating filters in the light and measuring the change in dissolved oxygen, then CR (μg O_2 cm^{-2} h^{-1}) was measured by incubating filters in the dark and measuring the change in dissolved oxygen. Gross primary production (GPP; μg O_2 cm^{-2} h^{-1}) was then calculated by adding NPP and the absolute value of CR (Tank et al. 2017: Johnson et al. 2009). These values represent the stream biofilm metabolic activity of autotrophs (GPP) and heterotrophs (CR) in response to the various nutrient and tissue treatments. Negative values of GPP and positive values of CR were excluded from the analysis.

After the light/dark bottle incubation, glass filters were frozen until NDS processing was complete for each season whereupon chlorophyll *a* biomass (μg cm^{-2}) was measured using a hot ethanol extraction method (Sartory and Grobbelaar 1984) as an additional autotrophic food web response to the NDS treatments. The disks were placed in a plastic centrifuge tube with 10 mL of 95% ethanol buffered with $MgCl_2$. The tubes were then heated to 79°C for 5 minutes, mixed, and measured within 24 hours. Samples were then analyzed fluorometrically using a Turner Designs benchtop fluorometer (Trilogy Laboratory Fluorometer, Turner Designs; Sunnyvale, California, USA) at excitation and emission wavelengths (λ) of 436 nm and 680 nm.

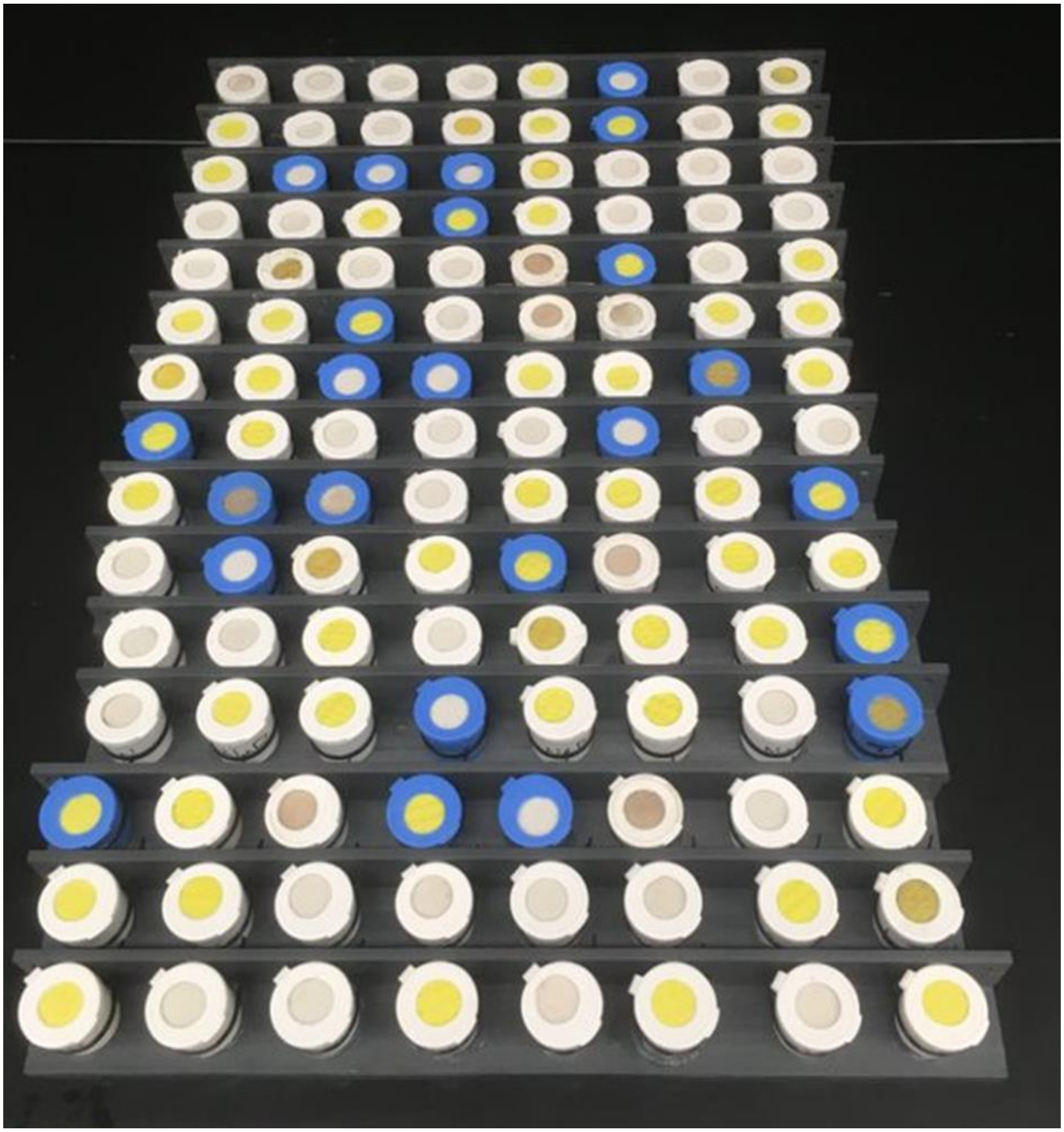

Figure 3 Nutrient diffusing substrate array for a single stream prior to deployment. Each treatment (nutrient and filter top; white top = porous glass, yellow top = cellulose sponge) was randomly placed on an L-bar and secured with silicone and zip-ties. The color of the plastic cup does not indicate any difference in treatment. Each treatment is replicated 5 times per filter top.

Figure 4 Nutrient diffusing substrate array deployed in the Yakima River in June 2020. The L-bars were secured in the stream with rebar stakes at the upstream end.

Water Quality

To understand how background stream nutrient levels influenced the biofilm response, water quality samples were collected by filtering site water through a glass fiber filter (1.0 μm pore size) into an acid-washed HDPE bottle rinsed with filtered site water. Water samples were stored on ice until I returned to the lab, at which point they were frozen for later analysis of NH_4^+, NO_3^-, SRP, and DOC. Ammonium was measured with the fluorometric method (Taylor et al. 2008) using a Turner Designs benchtop fluorometer at excitation and emission wavelengths (λ) of 350 nm and 410 nm. Nitrate was measured using the cadmium reduction method (Brewer and Riley 1965) and SRP was measured using the molybdate method (Murphy and Riley 1962), both using a Seal AQ1 Discrete Analyzer (Seal AQ1, Seal Analytical; Mequon, Wisconsin, USA). The cadmium reduction method combines nitrite (NO_2^-) and NO_3^-, but since NO_2^- is usually below detection, hereafter we refer to these values as NO_3^-. For DOC analysis, samples were acidified to $pH \leq 2$ to purge inorganic carbon, and then measured with the infrared method (APHA 2017) using a Shimadzu TOC-L autoanalyzer (TOC-L Total Organic Carbon Analyzer; Shimadzu, Kyoto, Japan).

Elemental Composition and Stable Isotopes

Prior to homogenizing fish carcasses to create the 3 separate NDS treatments, a subsample of ground individual carcass tissue, homogenized within individual, was collected for elemental composition and stable isotope analysis. These samples were collected from 10 of the least deteriorated mature lamprey carcasses (n = 5 pre-spawn female, n = 5 male of which 3 were post-spawn and 2 pre-spawn), 5 pre-spawn male salmon, and 6 fresh migrant lamprey (n = 3 female, n = 3 male; Table 1). I was unable to compare male and female salmon due to the limited availability of sexes in the salmon carcasses. Finally, a sample of Pacific lamprey eggs was collected from each sexually mature female lamprey and included as distinct tissue samples in elemental analysis (n = 5).

Table 1 Lamprey and salmon tissue samples used in elemental composition and NDS treatments.

Carcass Type	Sex	Elemental Composition	NDS Treatment	Total n
Sexually Mature Lamprey	Female	5*	15	22**
	Male	5	7	
Fresh Migrant Lamprey	Female	3	3	6
	Male	3	3	
Salmon	Male	5	4	9

*A sample of eggs were taken from each sexually mature female lamprey and included as a sample for elemental composition.

**Once the sub-sample for elemental composition was collected the remaining homogenized tissue was added to the NDS treatment, therefore “NDS Treatment” count includes carcasses in “Elemental Composition” count.

To analyze elemental and stable isotope composition, tissue samples were dried at 60°C until a constant weight was achieved, usually 24-48 hours (Weaver et al. 2018a). Samples were then ground by hand using a mortar and pestle, weighed into 1.0-1.5 mg subsamples, and sealed in tin capsules. Three analytical replicates per individual were sent to Washington State University’s Stable Isotope Core Laboratory in Pullman, WA to analyze the % C, % N, δ^{13}C, and δ^{15}N composition. Isotope samples were converted to N_2 and CO_2 using an elemental analyzer (ECS 4010, Costech Analytical; Valencia, California, USA) and measured using a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinniganm; Bremen, Germany). Lipids in tissue samples can negatively bias δ^{13}C values (Focken and Becker 1998). To mitigate this, I included an additional sample from each individual which received a Soxhlet/lipid extraction wash to provide a lipid correction factor to δ^{13}C values from the 3 analytical replicates (Anthony, Roby, and Turco 2000). Hereafter, only lipid corrected values are reported. Stable isotope ratios of N and C are expressed in parts per thousand or per mil (‰) and are calculated as:

$$\delta^{15}N \text{ or } \delta^{13}C = ([R_{sample} - R_{standard}] / R_{standard}) \times 1000$$

where R is the ratio of ^{15}N:^{14}N or ^{13}C:^{12}C. The isotopic composition of air and Vienna Peedee Belemite were used as standards for N and C respectively. Additionally, two analytical replicates per individual were sent to University of Idaho's Analytical Sciences Laboratory for phosphorous analysis where samples received a nitric acid digestion followed with inductively coupled plasma optical emission spectroscopy (Optima 8300 ICP-OES, PerkinElmer; Waltham, Massachusetts, USA).

Statistical Analysis

All data analyses were performed using R 4.0.3 (R Core Team 2020). Habitat and water quality data were compared between seasons using a paired Mann-Whitney U test due to small sample size. PAR data was collected for an unequal number of days at each site during the NDS deployments; therefore, PAR was ranked from highest to lowest from 1-10 (Table 3) based on the average pulses s^{-1} over deployment duration and used as a predictive variable in models relating habitat parameters to stream biofilm response to added nutrients.

Nutrient limitation status of GPP, CR, and chlorophyll *a* was determined by a multi-factor analysis of variance (ANOVA) with the presence or absence of each nutrient as a main factor (Tank and Dodds 2003; Tank et al. 2017). Only presence or absence of N and P were included as main factors for GPP and chlorophyll *a* as I did not anticipate autotrophs to benefit from added organic carbon due to their ability to photosynthesize and store carbon compounds (Everson et al. 1967). When necessary, data were transformed to meet the assumptions of ANOVA, and if transformation did not help the data meet model assumptions, untransformed data were used in a nonparametric factorial analysis via the aligned rank transformation (ART; Wobbrock et al. 2011) in the ARTool package (Kay and Wobbrock 2016). If a single factor or interaction was significant, I used interaction plots to evaluate nutrient limitation status.

Pearson or Spearman correlations were used to determine how well the tissue treatments in agar alleviated nutrient limitation compared to the added nutrients in agar according the methods outlined in Rüegg et al. (2011). The +N+P treatment was used in the autotrophic comparison, whereas the +N+P+C treatment wasused in the heterotrophic comparison. Because primary productivity was extremely low in the fall and many GPP calculations were 0, chlorophyll *a* was used as a proxy for autotrophic activity in all autotrophic-heterotrophic comparisons when season was a factor. To compare the autotrophic (chlorophyll *a*) and heterotrophic (CR) biofilm response to salmon and lamprey directly, I used an ANOVA with species interacting with treatment (i.e., tissue in agar versus tissue in nylon) and blocked by season. In a separate analysis restricted to the Swauk Creek summer deployment, I used a one-way ANOVA to compare calculated GPP, chlorophyll *a*, and CR response to fresh migrant (just arrived in the Columbia River) and mature (arrived on spawning grounds) lamprey tissue to understand how tissue from different stages of migrating lamprey influenced biofilm response. I compared the elemental composition and stable isotopes of mature lamprey and salmon, and among different lamprey tissue samples (sexually mature male, sexually mature female, fresh migrant male, fresh migrant female, and eggs) using an ANOVA or

Kruskal-Wallis test depending on whether or not data met assumptions for a parametric analysis as described below.

Linear mixed effects models, using “lme” function in the “nlme” package (Pinheiro et al. 2021), were used to predict how environmental variation (i.e., PAR, stream temperature, canopy cover, background nutrients, and season) influenced the biofilm response (chlorophyll *a* or CR) to the added nutrients, lamprey, and salmon treatments. For the models, biofilm response was quantified as the nutrient response ratio (NRR), which is the response to a given treatment relative to the response on the control within each stream+season which allows comparisons among streams and between seasons (Tank and Dodds 2003; Johnson et al. 2009). Tissue in agar was used as opposed to the tissue in nylon in order to compare explanatory variables to the nutrient treatments. Site was modeled as a random effect, and explanatory habitat characteristics were modeled as fixed effects (Table 2).

Data were tested for equal variance using Levene’s test, in the “car” package (Fox Weisberg 2019), and data was tested for normality using the Anderson-Darling test in the “nortest” package (Gross and Ligges 2015). All data were transformed where appropriate in order to meet model and analysis assumptions, and the significance of all statistical tests was determined at $\alpha = 0.05$.

Table 2 Variables used in linear mixed effects models to best explain chlorophyll *a* and CR. PAR = photosynthetically active radiation, DIN = dissolved inorganic nitrogen, N = nitrogen, P = phosphorus, C = carbon, DOC = dissolved organic carbon.

Response	**Random Effect**
Chlorophyll *a*	Site
Community respiration	
Fixed Effect	
Discharge (m^3/s)	Phosphate
PAR	DIN
Canopy openness (%)	Molar N:P
Season	Molar C:N
Temperature (°C)	Molar C:P
DOC	

CHAPTER III

RESULTS

Study Sites

Median substrate size, temperature (°C), dissolved oxygen (mg/L), stream discharge (m^3/s), PAR, and canopy openness (%) varied among sites but not between seasons. Median substrate size ranged from 31-77 mm (Figure 5). Temperature ranged from 12.25-23.75°C in the summer and 4.85-13.50°C in the fall, but the difference between seasons was not significant (Mann-Whitney U test, $p = 0.1$), and there was no seasonal difference between dissolved oxygen (Mann-Whitney U test, $p = 0.1$; Table 3). Discharge did not vary seasonally (Mann-Whitney U test, $p = 1$); however, relative to the other discharge measurements, Yakima was an outlier in the summer, and Teanaway was an outlier in the fall (Table 3). The 5 highest PAR ranks occurred in the summer, whereas the lowest occurred in the fall, albeit the difference was not significant (Mann-Whitney U test, $p = 0.06$). Percent canopy openness did not differ between seasons (Mann-Whitney U test, $p = 0.4$) and had low variability among sites (Table 3). There was no seasonally significant difference between NH_4^+, NO_3^-, SRP, DOC, or molar N:P, C:N, or C:P (Mann-Whitney U test, $p > 0.05$; Figure 6).

Table 3 Habitat characterization of study sites. Temperature (Temp) and dissolved oxygen (DO) were measured during the deployment and retrieval of NDS arrays, and site average (1 standard error) is reported. Discharge and canopy openness were only measured during NDS deployment. Photosynthetically active radiation (PAR) was measured as a proprietary unit (pulses s^{-1}) and reported here as rank data, 1= high, 10 = low

Season	Site	Temp (°C)	DO (mg/L)	DO (%)	Discharge (m^3/s)	PAR	Canopy Openness (%)
Summer	Taneum	15.50 (1.45)	9.30 (0.42)	92.70 (1.3)	0.46	1	100
	Manastash	16.95 (0.35)	9.24 (0.95)	95.45 (0.17)	0.93	3	99
	Yakima	12.25 (0.95)	10.13 (0.2)	94.50 (0.19)	4.51	2	95
	Teanaway	23.75 (2.45)	8.18 (0.45)	96.45 (0.415)	0.90	4	99
	Swauk	21.50 (0.3)	8.91 (2.45)	100.75 (0.28)	0.12	5	100
Fall	Taneum	13.50 (2.0)	9.89 (0.05)	94.75 (0.43)	0.79	6	99
	Manastash	9.00 (4.1)	10.93 (1.4)	93.90 (0.92)	0.70	7	99
	Yakima	12.70 (1.9)	9.71 (1.95)	91.35 (0.205)	0.15	9	100
	Teanaway	5.55 (0.85)	11.78 (0.15)	93.45 (0.275)	3.53	8	96
	Swauk	4.85 (0.75)	11.98 (0.55)	93.35 (0.295)	0.27	10	100

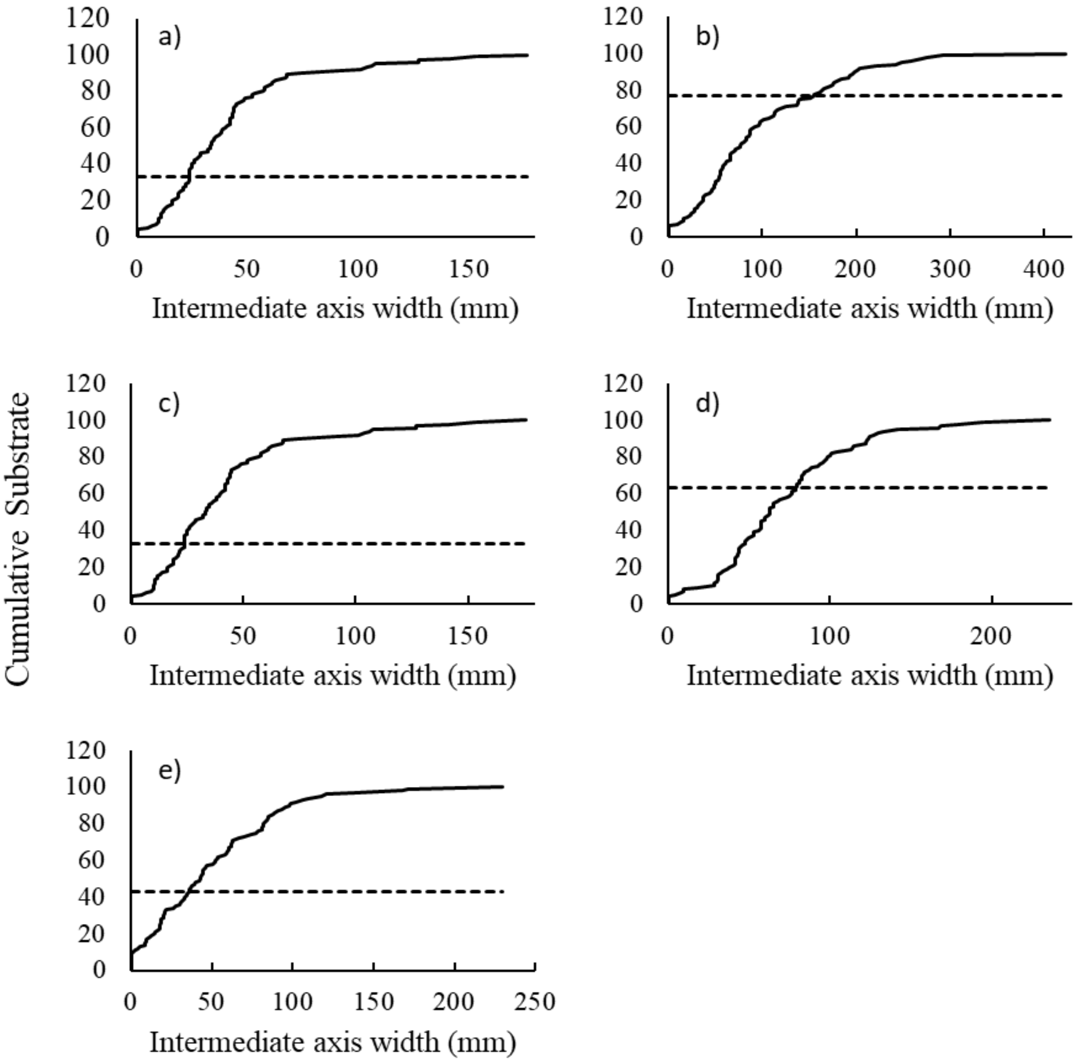

Figure 5 Cumulative substrate (n =100) measured along the intermediate axis, and median (dashed line) for a) Taneum, b) Manastash, c) Yakima, d) Teanaway, and e) Swauk.

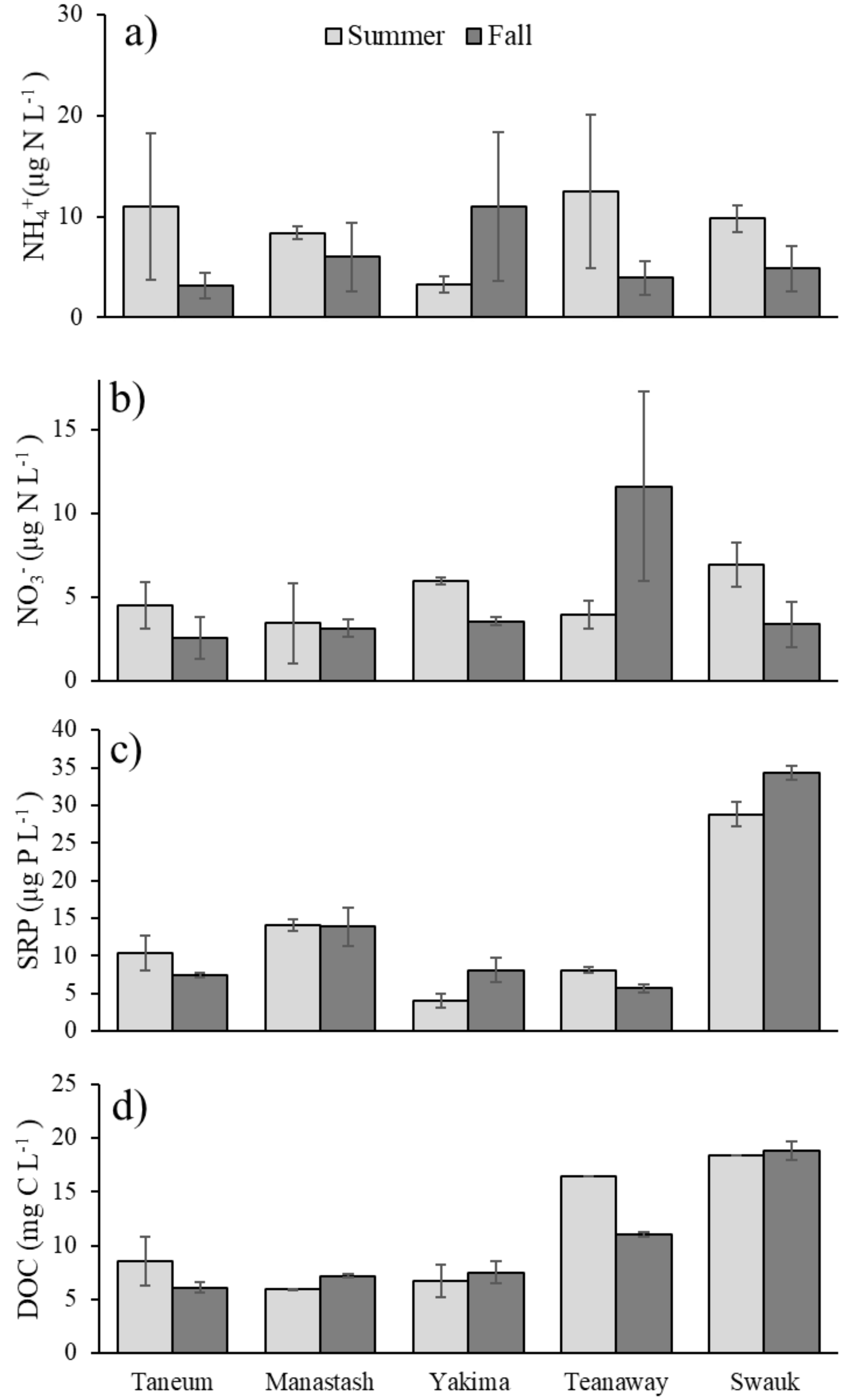

Figure 6 Mean a) ammonium (NH_4^+), b) nitrate (NO_3^-), c) soluble reactive phosphorus (SRP), and d) dissolved organic carbon (DOC) concentrations for each study site in summer and fall +/- 1 standard error. Teanaway and Swauk DOC only had 1 sample in the summer, therefore they do not have error bars.

Nutrient Limitation Status

Autotrophic nutrient demand shifted seasonally. In the summer, both GPP and chlorophyll *a* were N limited in 4 out of 5 sites. Gross primary production was not limited at Swauk Creek and chlorophyll *a* was N+P co-limited at Teanaway. In the fall, there was a shift towards no limitation, or an increase in the importance of P as a limiting nutrient. GPP was not limited in 4 out of 5 sites but was N limited in Teanaway although productivity was extremely low in all sites which resulted in a heavily zero-skewed GPP dataset. Surprisingly, GPP was inhibited by N at 3 sites and by P at 1 site during the fall. Chlorophyll *a* was N limited at Manastash and Yakima, N+P co-limited at Taneum and Swauk, and not limited at Teanaway (Figure 7).

Compared to patterns revealed by autotrophic metrics, heterotrophic limitation was more varied among sites and between seasons. In the summer, all sites were N limited except for Yakima which was N+C co-limited. Interestingly, C appeared to inhibit CR in Teanaway in the summer. The incidence of C and/or P limitation increased in the fall when Taneum, Manastash, and Swauk were N+P+C co-limited, Teanaway was C+P limited, and Yakima was C limited (Figure 7).

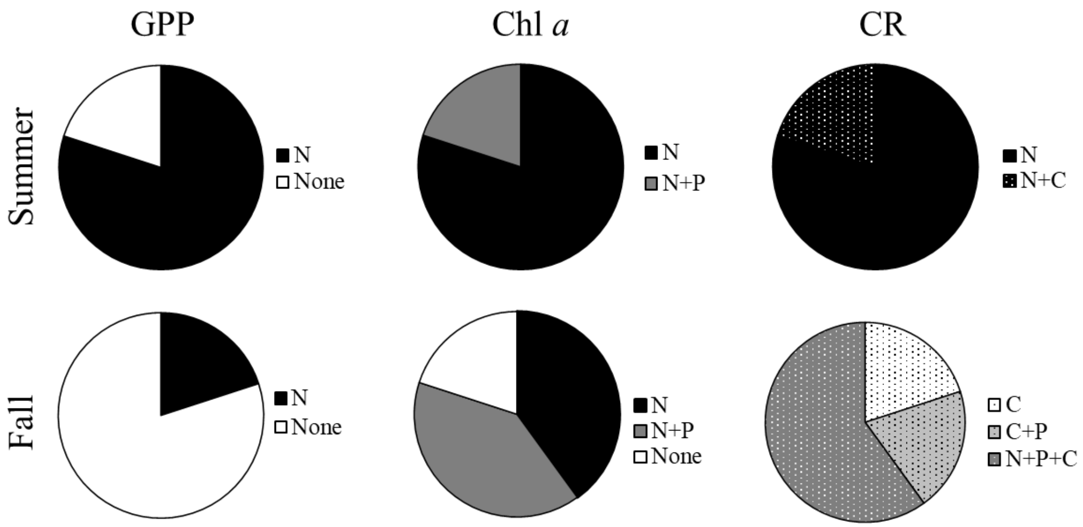

Figure 7 Nutrient limitation for gross primary production (GPP), chlorophyll *a* (Chl *a*), and community respiration (CR) for all 5 study sites in summer and fall. Limitation was either by N = nitrogen, P = phosphorous, C = carbon, or some combination, or was not limited by any nutrient used in the NDS (None).

Biofilm Response to Nutrient and Tissue Treatments

Tissue and nutrients relieved biofilm nutrient limitation, but the autotrophic food web response to either treatment was inconsistent for GPP and chlorophyll *a*. Biofilm NRR for GPP from the tissue in agar (LA and SA) was generally not correlated with the added nutrients (+N+P). The only significant GPP correlation between +N+P treatment and tissue was with SA in the fall (r = 0.59, p = 0.004), but this was likely driven by the heavily zero-skewed GPP values as it was not correlated with LA in either season or with SA in the summer (Figure 8).

Unlike GPP, NRR for biofilm chlorophyll *a* in response to salmon and lamprey was generally correlated with the NRR of the added +N+P. Both LA and SA were positively correlated to the +N+P treatment in the summer (r_{LA} = 0.39, p_{LA} = 0.04905; r_{SA}= 0.68, p_{SA} < 0.001), but not in the fall (Figure 8). Interestingly, there were several instances where the +N+P treatment elicited a higher response than either tissue treatment (summer NRR was 10-15 for nutrients versus < 10 for tissue). The higher mean NRR for chlorophyll *a* suggests that algal biomass does not necessarily scale with autotrophic productivity measured as GPP.

The NRR for biofilm CR from the added tissue was generally correlated with NRR from the +N+P+C treatment. The LA treatment was correlated to the +N+P+C treatment in the summer ($r = 0.59$, $p = 0.003$, Figure 8), but not in the fall, whereas SA was correlated in both the summer ($r = 0.61$, $p = 0.002$, Figure 8), and fall ($r = 0.41$, $p = 0.04$, Figure 8). Interestingly, both LA and SA elicited a consistently higher response than +N+P+C in both seasons, a trend not seen in the autotrophic response (Figure 8).

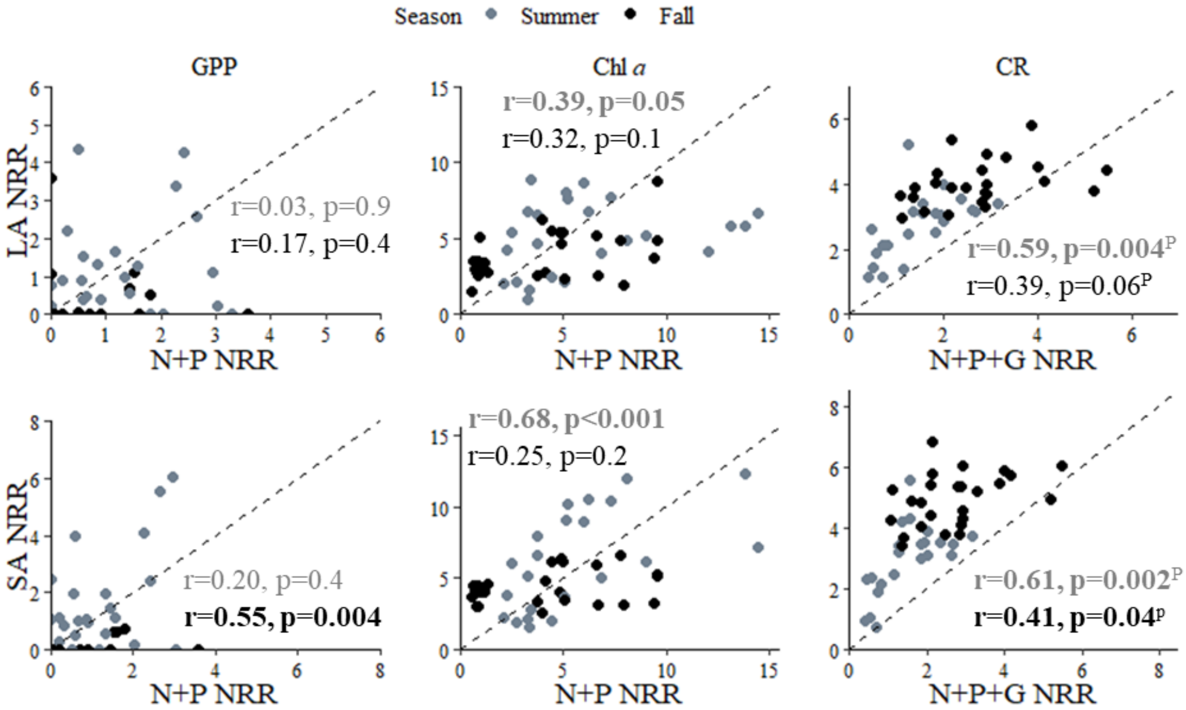

Figure 8 Correlation plots comparing nutrient response ratios (NRR) of tissue (LA = lamprey in agar, top row; SA = salmon in agar, bottom row) to added nutrient treatments in agar across seasons. Gross primary production (GPP) and chlorophyll *a* (Chl *a*) response to tissue treatments are compared to the +N+P treatment whereas community respiration (CR) response to tissue is compared to the +N+P+C treatment. The dashed line is the 1:1 line. Correlations performed with a Pearson's correlation are indicated with (^{P}) next to test statistics, other correlations are Spearman's rank correlation; significant p-values are bolded.

Biofilm Response to Lamprey and Salmon Tissue Treatments

When comparing the seasonal response of chlorophyll *a* to lamprey and salmon tissue in different treatments (agar versus nylon), I found that season was a better predictor than either tissue type or treatment. There was no difference in chlorophyll *a* response between lamprey and salmon, or between tissue in agar and tissue in nylon in either summer or fall. However, chlorophyll *a* was significantly higher in the summer compared to the fall (ANOVA, p = 0.001; Figure 9) where mean NRRs were roughly

40% higher. In contrast, CR was higher in the fall compared to the summer (ANOVA, $p < 0.001$; Figure 10a), where mean NRRs were roughly 60% higher. CR had a higher response to salmon compared to lamprey, and the tissue in nylon treatment elicited a higher response than the tissue in agar treatment (ANOVA, $p_{\text{Species X Amendment}} = 0.04$, Figure 10b).

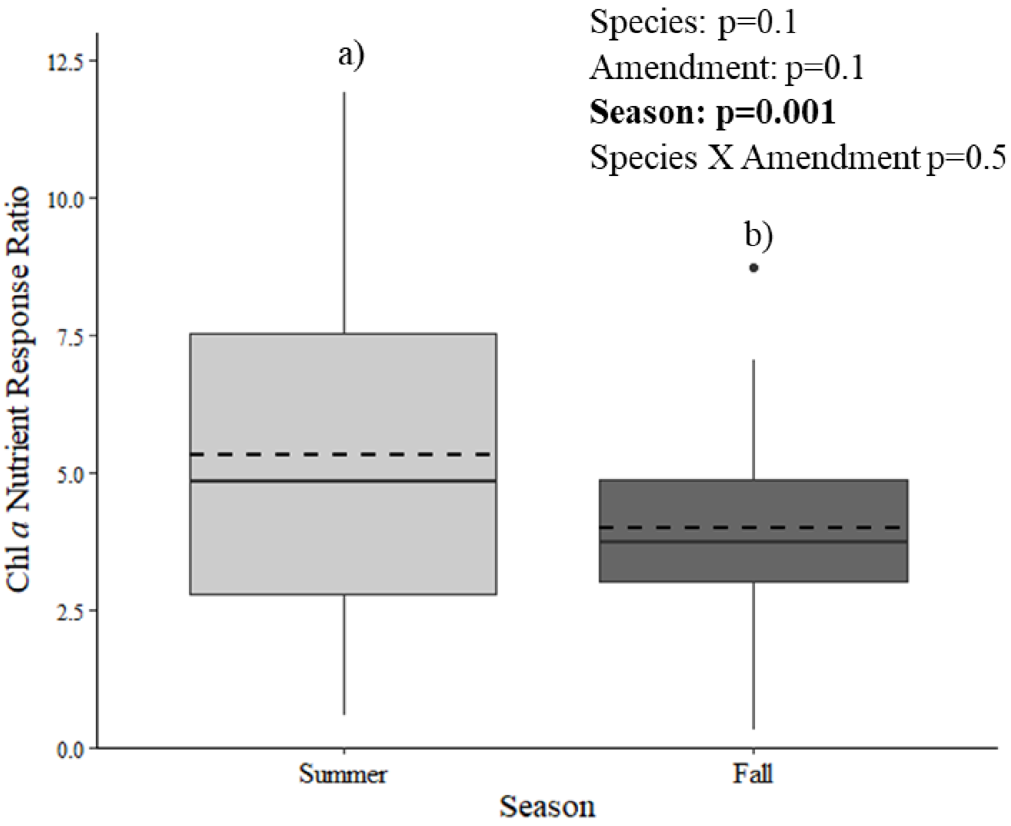

Figure 9 Seasonal nutrient response ratio (NRR) of Chlorophyll *a* to different fish treatments (lamprey and salmon) and amendment type (tissue in agar and tissue in nylon) blocked by season (summer and fall). Means indicated by dashed line. Bolded p-values indicate significance at $\alpha = 0.05$.

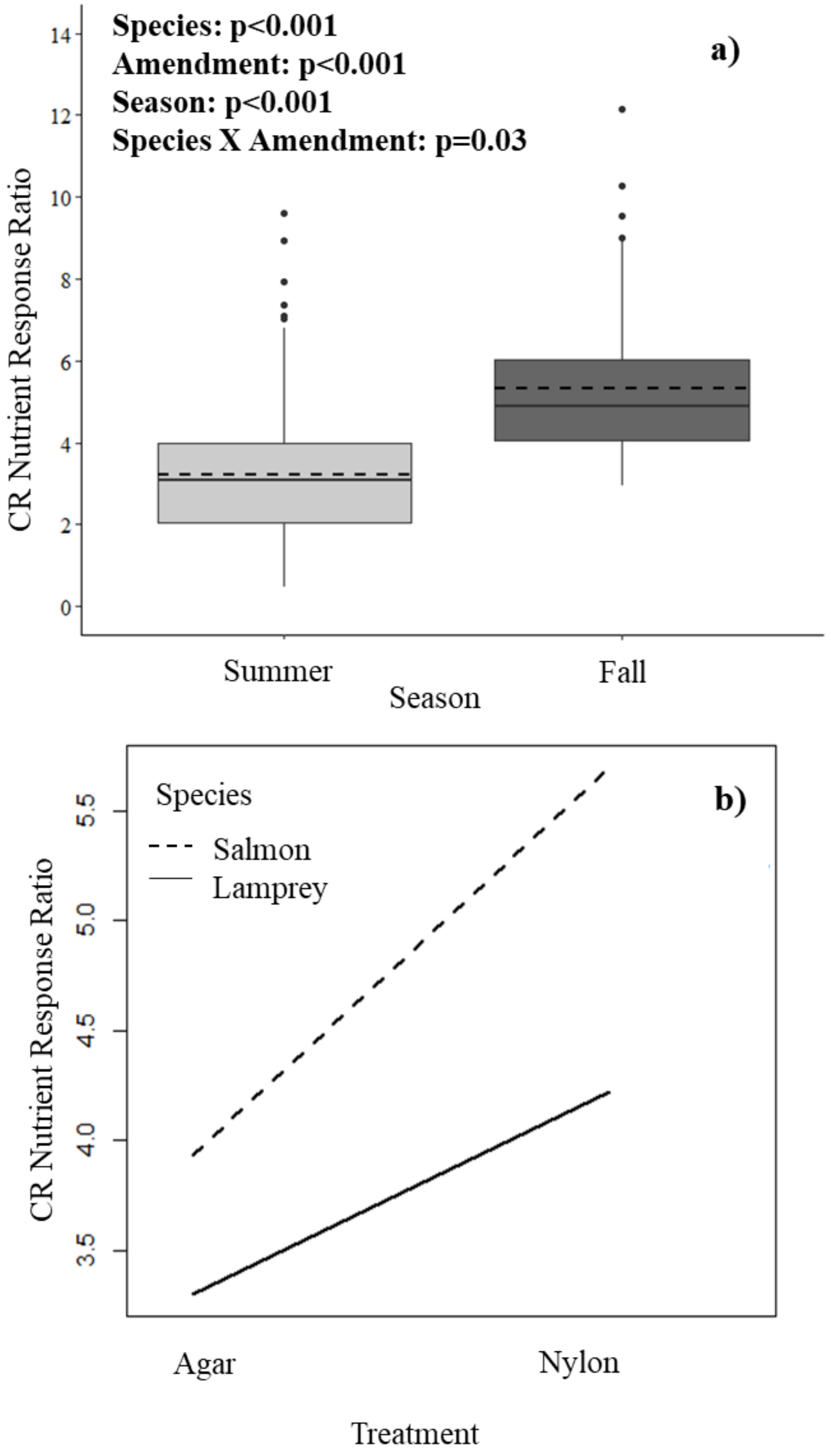

Figure 10 Seasonal response of community respiration (CR) nutrient response ratio (NRR) to different fish treatments (lamprey and salmon) and amendment type (tissue in agar and tissue in nylon) blocked by season. Bolded p-values indicate significance at $\alpha = 0.05$. a) boxplot showing CR response to seasons; means indicated by dashed line; b) interaction plot showing CR response to tissue type and amendment.

Although upstream dam passage may not result in high lamprey mortality, pre-spawn mortality can still occur in river systems prior to spawning (Keefer et al. 2020), therefore it is possible that stream maturing lamprey elemental composition could differ from the time of fresh water re-entry to the time they spawn, potentially and influencing the biofilm response. To test this, I included fresh migrant lamprey tissue in the Swauk summer NDS deployment to determine if the nutrients in the different migration stages (fresh migrant versus sexually mature) influenced the ecosystem response. However, this comparison revealed no difference in autotrophic response (ANOVA, $p_{GPP} = 0.3$, $p_{\text{chl } a} = 0.1$) to sexually mature or fresh migrant lamprey, and no difference in tissue in agar or tissue in nylon (Figure 11). Moreover, there was no significant difference in CR response between fresh migrant tissue or sexually mature tissue (Figure 11), but CR was significantly higher in fresh migrant in agar compared to fresh migrant in tissue (ANOVA, p = 0.02, Figure 11).

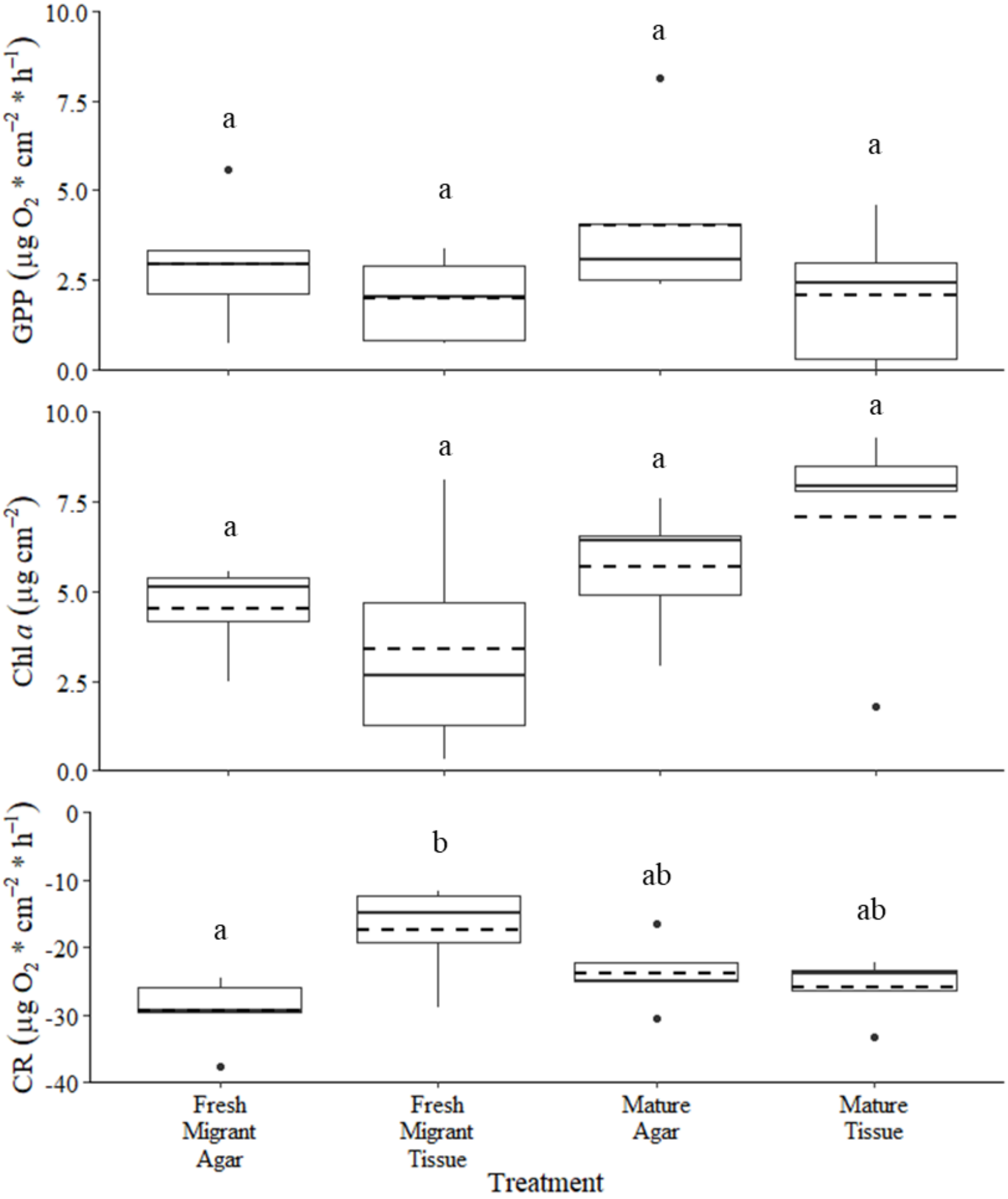

Figure 11 Gross primary production (GPP), chlorophyll *a* (Chl *a*), and community respiration (CR) response to fresh migrant and sexually mature lamprey tissue in Swauk Creek in the summer nutrient diffusing substrate deployment. Dashed lines indicate mean; tukey letters indicate significant differences.

Elemental Composition and Stable Isotopes

Salmon tissue was composed of 2.0-2.5% P, significantly more than mature lamprey which ranged from 0.4-1.0% P (ANOVA, $p < 0.001$, Table 4). Lamprey eggs were composed of approximately 1.3-1.4% P, however this was not significantly different from sexually mature pre-spawn female lamprey (Kruskal-Wallis, $p = 0.1$). There were no significant differences in salmon and lamprey % C or % N, which ranged from 48.5-54.4% C, and 10.8-14.2% N (Kruskal-Wallis, $p_{carbon} = 0.06$, $p_{nitrogen} = 0.1$). Despite no observed differences in % C and % N between the two species, on average, tule fall Chinook salmon weighed 1774.7 g, whereas a sexually mature lamprey weighed 252.4 g respectively. Therefore, the salmon tissue had 49959.2 mg/kg C, 13025.5 mg/kg N, and 2170.0 mg/kg P, which is approximately 6.6 times more C, 7.7 times more N and 19.2 times more P than the lamprey tissue, due to higher body mass and the presence of bones in salmon (Table 4). Fresh migrant and sexually mature lamprey did not vary in elemental composition. Fresh migrant lamprey was composed of approximately 65.3-66.7% C, 5.3-6.4% N, and 0.3-0.4% P compared to 48.4-59.6% C, 8.8-14.2% N, and 0.4-1.0% P for sexually mature lamprey (Table 4).

Table 4 Sample size, mean (standard error) aggregated mass of fish, mass of carbon (C), nitrogen (N), and phosphorous (P), as well as molar C:N, and molar N:P. "Avg. Mature" is the average of 5 mature male and 5 mature female lamprey, and "Avg. Migrant" is the average of the 3 fresh migrant male and 3 fresh migrant female lamprey.

Tissue Type	n	Mass (g)	C (mg/kg)	N (mg/kg)	P (mg/kg)	C:N	N:P
Salmon	5	1774.7 (109.3)	49959.2 (525.2)	13025.5 (169.5)	2170.0 (93.0)	4.5 (0.1)	13.4 (0.4)
Mature M	5	238.7 (22.2)	51539.6 (2076.2)	12763.5 (1024.1)	694.0 (71.7)	4.9 (0.7)	42.6 (6.2)
Mature F	5	266.1 (40.5)	53097.1 (551.0)	11669.8 (419.4)	867.0 (67.0)	5.3 (0.2)	30.9 (3.7)
Migrant M	3	351.0 (19.6)	66164.6 (386.7)	5831.2 (325.0)	358.3 (19.6)	12.8 (0.5)	30.5 (0.7)
Migrant F	3	416.3 (48.0)	65958.3 (402.9)	6001.5 (213.5)	435.0 (7.6)	13.3 (0.8)	36.2 (2.7)
Avg. Mature	10	252.4 (22.2)	52318.4 (1045.4)	12216.6 (552.6)	780.5 (54.5)	5.1 (0.4)	36.7 (3.9)
Avg. Migrant	6	383.6 (27.4)	66061.4 (254.0)	5916.3 (178.0)	396.7 (19.6)	13.1 (0.4)	33.4 (1.8)

There was no significant difference in $\delta^{15}N$ (Kruskall-Wallis, p =1.0; Figure 12) enrichment between mature lamprey and salmon, which ranged between 14.7-15.7‰. Salmon displayed the highest $\delta^{13}C$ enrichment with an average of -16.5‰ compared to the lamprey which averaged -18.2‰ (Figure 12). The $\delta^{13}C$ signature differed between salmon and mature lamprey, and between female and male mature lamprey (ANOVA, $p_{female} < 0.001$, $p_{male} < 0.001$; Figure 12). There was no significant difference in $\delta^{13}C$ enrichment between male and female mature lamprey (ANOVA, p = 1.0), Enrichment of $\delta^{13}C$ did not vary between fresh migrant and mature lamprey and ranged from -19.4 to -17.6‰. Fresh migrant female and lamprey eggs were the most heavily enriched with $\delta^{15}N$, with means of 16.2‰ (Figure 13). Fresh migrant male and sexually mature male which were the least enriched with means of 14.8‰, and 15.1‰, respectively (Figure

13). Migrant females were significantly more enriched in ^{15}N than migrant males (Pairwise Wilcoxon Rank Sum, p = 0.046), and lamprey eggs were significantly more enriched than migrant males (Pairwise Wilcoxon Rank Sum, p = 0.01), mature males (Pairwise Wilcoxon Rank Sum, p = 0.04), and mature females (Pairwise Wilcoxon Rank Sum, p = 0.001).

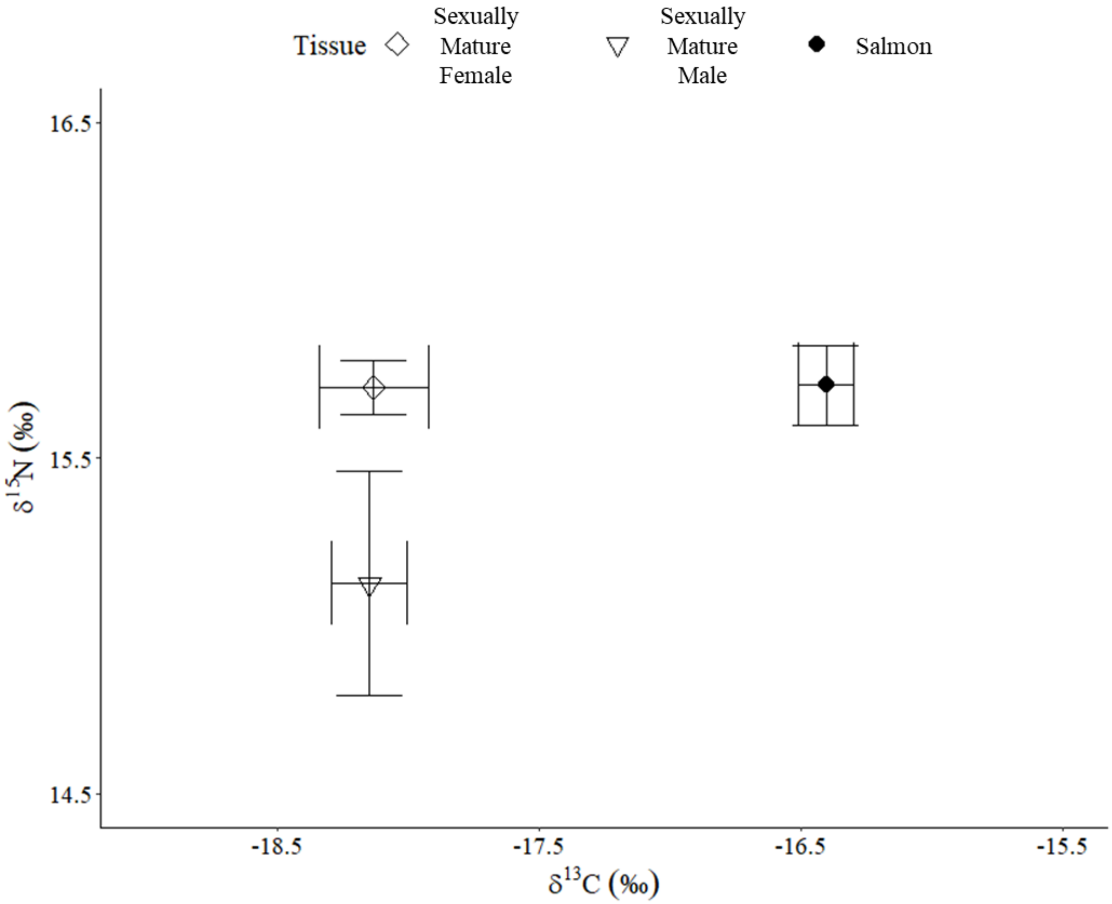

Figure 12 Mean (+/- 1 standard error) of the isotopic relationships between sexually mature male and female Pacific lamprey and salmon.

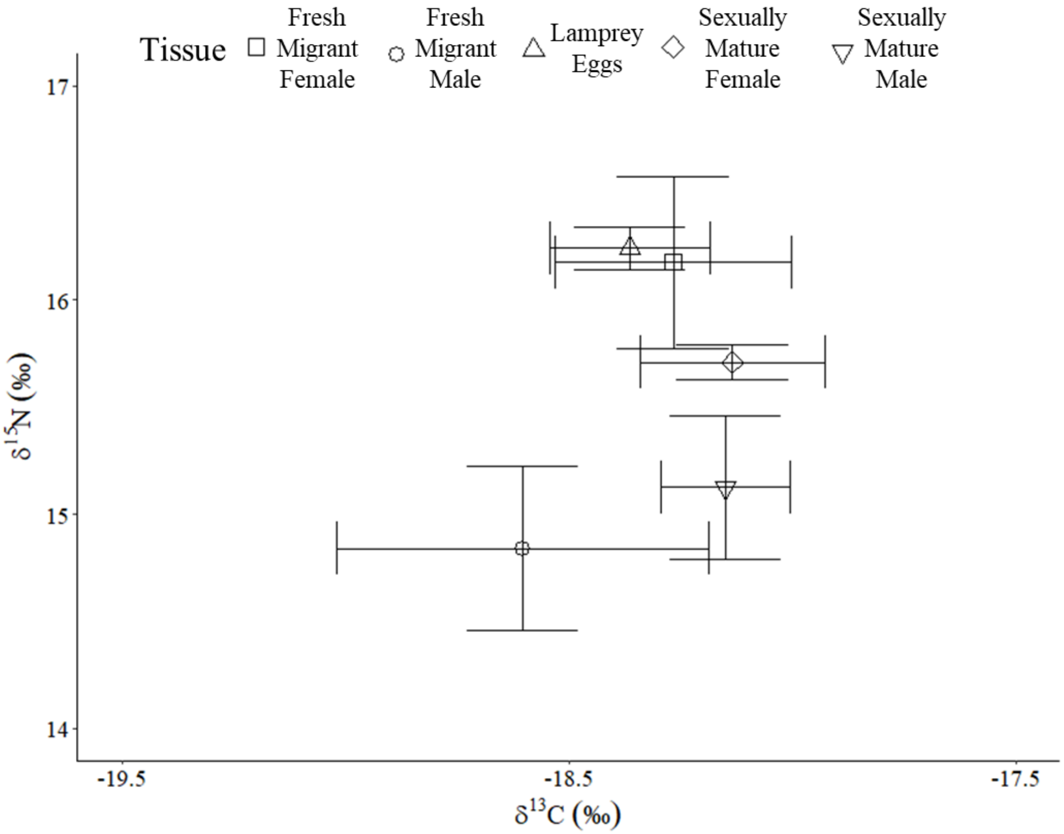

Figure 13 Mean (+/- 1) standard error of the isotopic relationships between lamprey tissue samples.

Factors Influencing Food Web Response

I used linear mixed effects models to understand how environmental factors influenced the autotrophic and heterotrophic response to added nutrients, LA, and SA. Due to low productivity and the high number of instances where GPP ≤ 0 in the fall samples, GPP was not included in the mixed effects modeling. Instead chlorophyll *a* was used as a metric for the autotrophic response, which was consistently explained by seasonal factors. The final mixed effects model for chlorophyll *a* in response to the +N+P treatment indicated that chlorophyll *a* was higher in the summer (lme, $p = 0.002$, Figure 9), and decreased with increasing % open canopy (lme, $p = 0.0002$, data not shown). For the lamprey in agar tissue treatment, the chlorophyll *a* NRR was also higher in the summer (lme, $p = 0.004$, Figure 9). Finally, the chlorophyll *a* NRR response to salmon tissue in agar was higher in the summer (lme, $p = 0.0004$, Figure 9) and increased with increasing molar N:P ratio of dissolved water column nutrients (lme, $p = 0.046$, data not shown).

Community respiration was also best explained by seasonal factors. The final mixed effects model for CR NRR in response to +N+P+C suggested that CR was significantly higher in the fall (lme, $p < 0.001$), increased with increasing discharge (lme, $p < 0.001$, Figure 14) and with decreased % open canopy (lme, $p = 0.007$, data not shown). However, the observed increase in CR associated with increased discharge could be driven by site-specific factors in the Yakima in the summer, and Teanaway in the fall, outliers that drive the significant regression (Figure 14). The final mixed effects model for CR in response to LA included site as a random effect and suggested that CR increased with decreasing temperature (lme, $p < 0.001$, Figure 15). Finally, the CR response to salmon included site as a random effect and suggested that CR was higher in the fall, (lme, $p < 0.001$, Figure 10b) and decreased with increasing molar N:P ratios of dissolved stream nutrients (lme, $p < 0.001$, Figure 16).

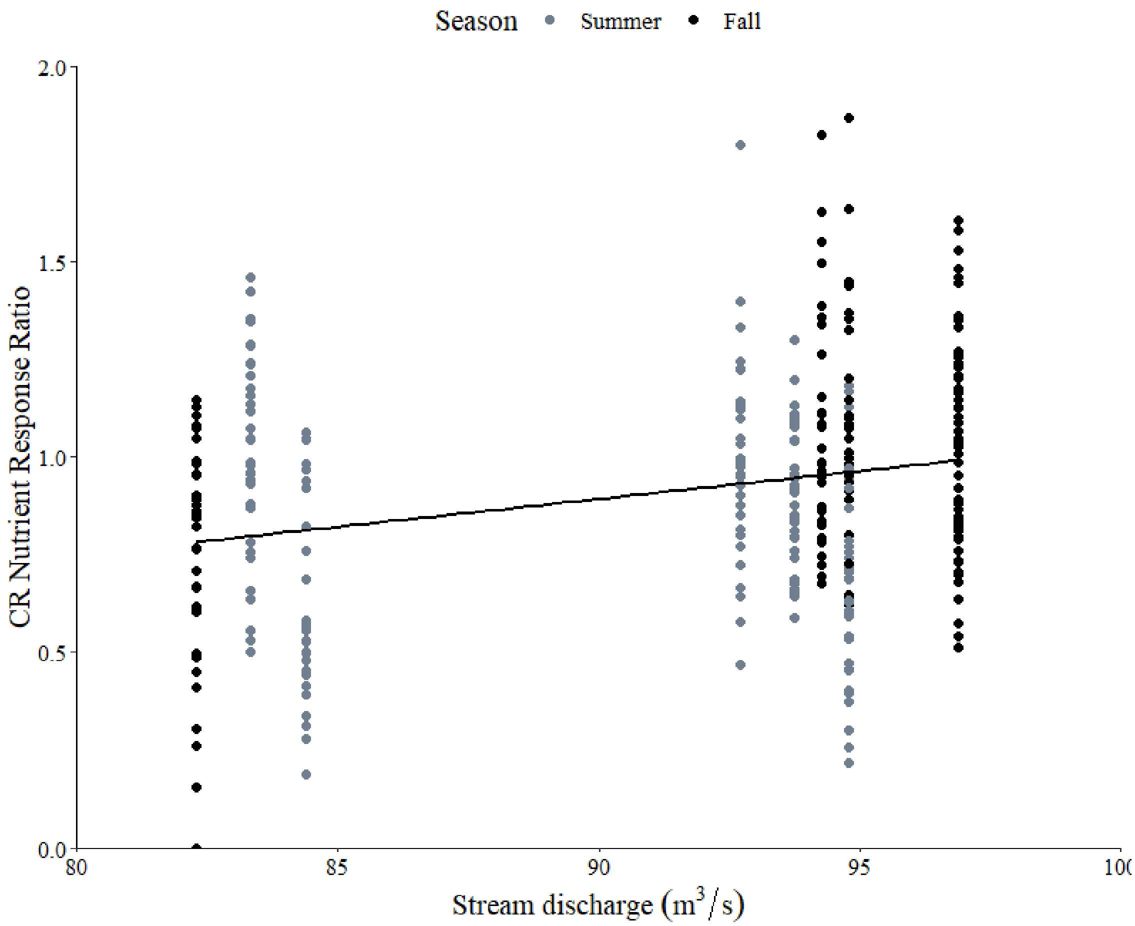

Figure 14 Relationship between community respiration nutrient response ratio (CR NRR) in response to +N+P+C treatment, and stream discharge. Best-fit line shown in black.

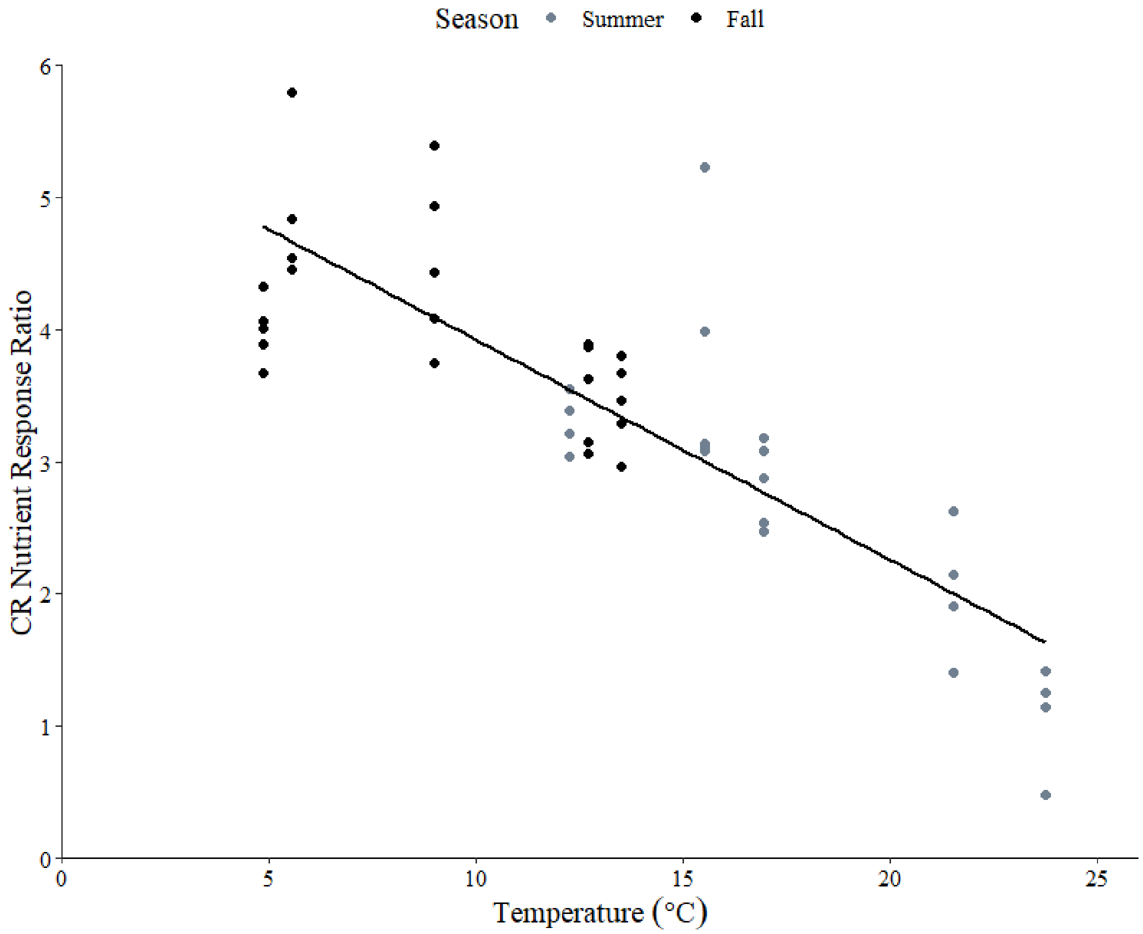

Figure 15 Relationship between community respiration nutrient response ratio (CR NRR) in response to lamprey in agar treatment and temperature ($p < 0.0001$). Temperature was the final main effect, with site treated as a random effect in a mixed-effects model to explain CR NRR for the lamprey treatment. Best-fit line shown in black.

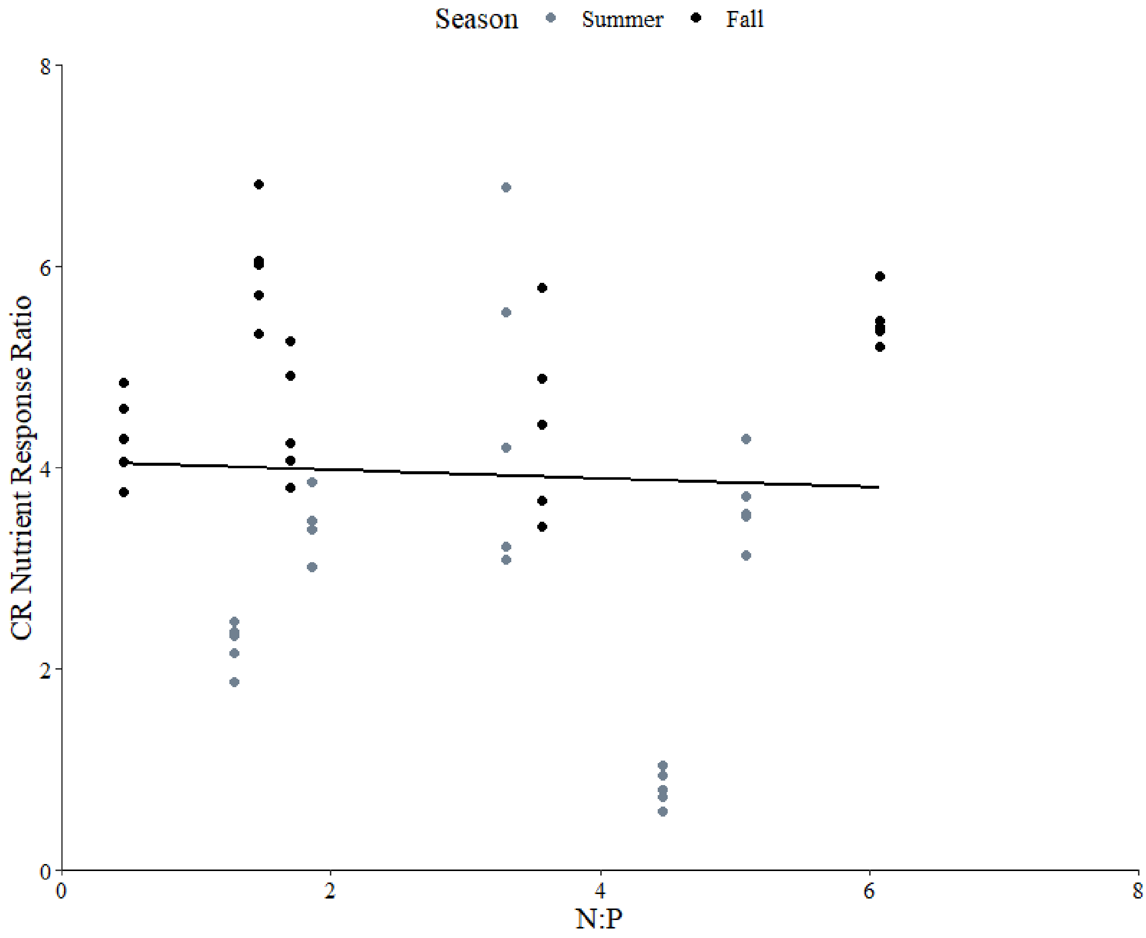

Figure 16 Relationship between community respiration nutrient response ratio (CR NRR) from salmon in agar treatment and water column molar nitrogen to phosphate (N:P) ratio. Best-fit line shown in black.

CHAPTER IV

DISCUSSION

Because salmon are known as important resource subsidies in oligotrophic PNW streams, resource managers commonly use salmon carcass supplementation to increase stream food web productivity to mitigate for declining salmon runs (Kohler et al. 2012). Although studies have demonstrated a positive food web response to the presence of salmon carcasses via increased biofilm biomass and increased macroinvertebrate abundance, reviewed in Janetski et al. (2009), this salmon-centric approach has either ignored or disregarded other anadromous fish species as potential resource subsidies. A side-by-side comparison of the benthic biofilm response to Pacific lamprey, and Chinook salmon tissue revealed that lamprey and salmon tissue alleviated nutrient limitation to a similar or greater degree as added nutrients. Chlorophyll *a* biomass responded similarly to both tissue types and was higher in the summer when light availability was greater. Community respiration had a higher response to salmon than lamprey and was higher in the fall. Although I found no difference in % C or % N between mature lamprey and salmon, or between mature lamprey and fresh migrants, an individual salmon can transport more carbon and nitrogen per fish compared to an individual lamprey due to larger body size. While salmon have higher % P, likely due to bones, lamprey eggs were also relatively high in % P, making them an important P source. In the N-limited streams that I studied, when standardized for body mass, lamprey were an equally important resource subsidy as salmon, particularly for the autotrophic community in the summer when salmon would not be spawning.

Seasonal Patterns in Stream Nutrient Limitation

Nutrient limitation of autotrophic and heterotrophic biofilms shifted seasonally in all streams in my study. Although other studies in streams in the Olympic Peninsula (Morley et al. 2016), Idaho (Marcarelli et al. 2009; Sanderson et al. 2009), Ohio (Olapade and Leff 2005), and northern Michigan (Hoellein et al. 2010) have noted similar seasonal shifts in nutrient limitation, their noted seasonal patterns were not as pronounced as I observed. These prior studies found N and P limiting in both seasons, but that the seasonal change varied including a shift in the primary limiting nutrient (Morley et al. 2016), the seasonal response was not uniform across sites (Marcarelli et al. 2009; Sanderson et al. 2009; Hoellein et al. 2010), or the seasons differed in magnitude but not nutrient treatment (Olapade and Leff 2005). In contrast, I found a remarkable consistency of N limitation in the summer for autotrophic and heterotrophic communities among sites. However, in the fall the occurrence of no-limitation and P co-limitation increased in the autotrophic community, and that the heterotrophic community increased in C limitation or-colimitation.

The frequent N limitation I observed in my study across autotrophic and heterotrophic communities is likely due to the oligotrophic conditions of my study streams (USEPA 2000). Across seasons, molar N:P ratio ranged from 0.46-6.07 (Figure 16), much lower than the 17:1 ratio identified for optimal growing conditions for benthic microalgae (Hillebrand and Sommer 1999), and much lower than the oft-cited Redfield ratio (16:1; Redfield 1958), suggesting overall N limitation. The widespread N limitation can be further explained by landscape factors; the igneous rocks of the Cascade Mountains (McBirney 1978) release P when weathering (Dillon and Kirchner 1975), often making N the limiting nutrient, as seen in many of Washington's surface waters (Thut and Haydu 1971). Although background nutrients did not explain the biofilm response, background N:P and C:P were both collinear with discharge. Therefore, stream discharge outliers, Yakima in the summer and Teanaway in the fall, that were positively related to nutrient limitation may have been conflated with nutrient concentrations, making it likely that background nutrients can be correlated, or predict biofilm response as seen in other studies (Tank and Dodds 2003; Rüegg et al. 2011; Reisinger et al. 2016).

Seasonal changes in light availability in northern latitudes likely explain the low productivity and change in limitation status observed in the fall autotrophic communities at my study sites. Other studies have noted low productivity in the fall (Rüegg et al. 2011) and no nutrient limitation of GPP (Johnson et al. 2009). Although I did find instances of nutrient limitation for chlorophyll *a* in the fall, the overall low rate of productivity suggests that light availability primarily controlled autotrophic metabolism (Ambrose et al. 2004), as PNW streams have less light in the fall (Morley et al. 2016) due to shorter daylight hours and lower sun angle. Other studies have noted the increasing importance of P in both autotrophic and heterotrophic communities in the fall (Marcarelli et al. 2009; Morley et al. 2016) or an increase in N+P co-limitation for chlorophyll *a* (Tank and Dodds 2003; Marcarelli et al. 2009; Sanderson et al. 2009; Hoellein et al. 2010), also observed in my study streams. Some studies have attributed the increased importance of P due to the coupled relationship of nutrients (Morley et al. 2016), where the addition of one causes limitation by another (Elser et al. 1996; Schade et al. 2011). Although this could be the case in my study as well, the lack of seasonal change in background nutrients suggests that shifting nutrient limitation pattern between seasons is likely driven by different stoichiometric demands driven by a shift in biofilm species composition (Francoeur 2001; Dodds et al. 2002).

An increase in C limitation in fall heterotrophic communities is likely driven by the decrease in available labile C sources due to the decline in autotrophic activity (Olapade and Leff 2005). Although heterotrophic decomposers receive an influx of allochthonous organic matter from leaf litter input in the fall, this material can be composed of less desirable heavy-weight organic compounds such as lignin and cellulose (Ward 1986), compared to the glucose used in my NDS arrays. For example, heterotrophic communities will select for labile C when available, especially when chlorophyll *a* concentrations are low (Olapade and Leff 2005) consistent with the finding of increased C demand in the fall by heterotrophs in my study streams. Moreover, this could explain why C was generally not seen as a limiting nutrient for heterotrophs in summer, when high algal activity would have produced an abundance of low molecular weight carbon compounds made available by “sloppy feeding” of herbivores (Sterner 1990). While the fall increase in C demand was the most consistent pattern observed in my study streams, I also saw somewhat higher demand for P by heterotrophs in the fall. Other studies have similarly found an increase in P limitation in fall heterotrophic communities (Rüegg et al. 2011) and have attributed this to changing stoichiometric demands between different biofilm communities (Elser et al. 1996).

Lamprey and Salmon Resource Subsidies

In the side-by-side comparison performed here, both Pacific lamprey and Chinook salmon alleviated biofilm nutrient limitation at least as well as nutrient addition. For example, the positive correlation in NRRs from chlorophyll *a* biomass in response to the fish tissue in agar treatments and the added nutrients indicate that either tissue type can stimulate algal production in the summer. Furthermore, heterotrophic activity had a higher response to both tissue types compared to the added nutrients. These patterns were similarly seen by Rüegg et al. (2011) in a fall study based in southeast Alaska using nutrient diffusing substrata amended with pink salmon tissue, and were interpreted to suggest that salmon can alleviate nutrient limitation. In contrast to chlorophyll *a* and CR patterns, I did not see a consistent GPP response to nutrients and LA or SA which could be due to scouring of algae (Olapade and Leff 2005) or insect grazing (Marcarelli et al. 2012) in the summer, and in the fall could be due to overall low productivity. Suppressed autotrophic metabolism in the fall could be due to the fact that although benthic biofilms are mutualistic communities composed of diverse constituents, autotrophic and heterotrophic components simultaneously compete for necessary nutrients (Daufresne and Loreau 2001; Marcarelli et al. 2009) and heterotrophs could be more competitive in lower light conditions. Regardless, my results show that either lamprey or salmon MDN can produce a high autotrophic and heterotrophic response.

Stoichiometric differences in lamprey and salmon tissue coupled with differing stoichiometric demands of biofilm communities (Elser et al. 1996) and seasonal environmental controls (Morley et al. 2016) likely facilitate how anadromous resource subsidies would be received in the upper Yakima basin. Overall, I found that chlorophyll *a* biomass was approximately 2 times higher in the summer, whereas CR was approximately 2 times higher in the fall. It is worth noting that several studies have found that riparian canopy can prevent an autotrophic response to added nutrients (Ambrose et al. 2004; Weaver et al. 2016), however much of the interior Columbia River basin is considered shrub-steppe (Benson et al. 2011) with streams having limited riparian cover. Community respiration had a higher response to SA compared to LA suggesting that the timing of nutrient availability from spawning lamprey and salmon may influence the biofilm response depending on shifting stoichiometric demands in the receiving ecosystem among seasons. Stoichiometric demands, where organisms require certain C:N:P ratios to facilitate proper growth and function (Elser et al. 1996), can explain differences in receiving ecosystems (Sterner et al. 1992). For example, the instances where the +N+P treatment elicited a higher response than LA and SA in conjunction with the uniformly higher CR response to LA and SA is likely due to stochiometric demands of biofilms and C:N:P ratios of the treatments (Elser et al. 1996). I found that lamprey and salmon had molar C:N:P ratios of approximately 187:37:1 and 60:13:1 respectively, whereas the nutrient treatments were all 1:1:1. Therefore, LA and SA treatments likely stimulated productivity to the point where N limitation was relieved and P became limiting (Schade et al. 2011), whereas the +N+P treatment met that demand, allowing higher algal growth. Similarly, the higher C and P demand by fall heterotrophic communities was likely met by the presence of more labile C in the tissue treatments (Rüegg et al. 2011; Hoellein et al. 2010), and the higher P content of salmon due to bones and scales (DaCosta and Stern 1958; Hendrixson et al. 2007) compared to lamprey. Furthermore, the higher autotrophic response in the summer, and higher heterotrophic response in the fall is likely due to competition between biofilm communities (Daufresne and Loreau 2001; Marcarelli et al. 2009), where greater light availability in the summer can provide autotrophs the advantage over heterotrophs (Ambrose et al. 2004), thus determining the limitation status of biofilm communities. Therefore, depending on the seasonal demand by different biofilm community constituents and the nutrients delivered by the specific resource subsidy, the stream ecosystem response will likely differ.

The influx of nutrients from Pacific lamprey has the potential to stimulate indirect trophic transfers of energy as documented in anadromous sea lamprey (Weaver et al. 2016; Weaver et al. 2018b) and salmon (Bilby et al. 1996; Naiman et al. 2002). The timing of anadromous lamprey spawning in the spring and early summer can stimulate autotrophic production while simultaneously extending the MDN signature into the food web and increasing stream production for longer periods of time. Spring and early summer can be characterized by high in-stream nutrient demand due to increased algal activity (Hoellein et al. 2010). Given the autotrophic nutrient limitation seen in my study and by others in the region (Morley et al. 2016; Reisingeret al. 2016), nutrients provided from spawning and post-spawn Pacific lamprey may arrive at an ecologically critical time when they can alleviate benthic biofilm nutrient limitation. Furthermore, the addition of MDN from spawning Pacific lamprey likely extends the temporal availability of MDN to be incorporated into a food web. Given that I did not find any difference in the ^{15}N signature of lamprey and salmon (Minagawa and Wada 1984), some studies that have attributed historic MDN signatures to the presence of salmon may have inadvertently underrepresented anadromous spawning Pacific lamprey. This is especially true where studies have found extended spring MDN signatures along with the presence of larval Pacific lamprey within the study reach (Bilby et al. 1996) or when stable isotopes were used to reconstruct consumer diets (Hilderbrand et al. 1996). Lastly, fresh migrant and mature lamprey elicit the same food web response, suggesting they can promote indirect food web productivity at any migratory stage in addition to acting as a direct resource.

Therefore, during their spawning period, Pacific lamprey provide the necessary nutrients to alleviate benthic biofilms in the Yakima River basin, and other similarly N-limited basins, thus stimulating bottom up food web productivity.

Although tule fall Chinook salmon would not spawn in the Yakima basin, they were the only carcasses available at the start of this study. Their N:P elemental composition appears to be somewhat lower compared to other Pacific salmon species. The C:N ratio of salmon used in this study was 4.5:1, comparable to a range of 3.7:1-5.9:1 depending on species (Lyle and Elliott 1998; Johnston et al. 2004; Rüegg et al. 2011). Although I did not include the head of the salmon in my study, which is likely a substantial source of P (DaCosta and Stern 1958), I found a lower N:P ratio of 13.4:1 compared to 18.7:1 for other Chinook salmon (Larkin and Slaney 1997), or 24:1 for coho salmon (Rüegg et al. 2011). This difference is likely due to a lower N content as opposed to a higher P content in the salmon used in my study, as tule fall Chinook do not need as many stored reserves compared to their long-distance migrating counterparts because tule fall Chinook salmon do not migrate far prior to spawning (Wyndoski and Whitney 2003). A study based on Columbia River migrating Chinook salmon found that along a 920 km migration, male Chinook salmon utilized 82% of somatic energy reserves and began metabolizing proteins to develop secondary sexual characteristics (Hendry and Berg 1999; Bowerman et al. 2017). Given that spring and summer Chinook in the Yakima River migrate approximately 744.9 km to Roza Dam (roughly 60.7-76.1 km downstream of my upper sites), it is possible that by the time they metabolize energy and protein reserves, they might have a lower N:P ratio similar to the tule fall Chinook used in my study. Regardless of the elemental composition of the salmon I used, the only other salmonid species spawning during the summer deployments of my study would be steelhead (*O. mykiss*) which do not have obligate semelparous life histories in the Yakima basin (Yakama Nation 2019) and would not provide the same post-spawn resource subsidy as Pacific salmon or Pacific lamprey. Therefore, my findings that Pacific lamprey can stimulate autotrophic activity in the summer are relevant given that Pacific lamprey would be the only anadromous fish providing this kind of resource subsidy in these streams at that time.

Management Implications

Anthropogenic interference and prevention of resource flows from anadromous fish (i.e., dam construction, water diversions, overfishing), likely have far-reaching consequences (Larsen et al. 2016) for Pacific lamprey, salmon, and other species that have co-evolved (Close et al. 2002; Miller 2012) to rely on the annual, regular supply of MDN. In fact, low amounts of MDN entering PNW streams (Gresh et al. 2000) resulting from reduced anadromous fish runs have likely decreased in-stream productivity and affected subsequent adult returns (Naiman et al. 2002). For example, decreasing numbers of returning adult salmon reduce overall stream productivity, thus reducing juvenile survival, which results in fewer adult returns, ultimately decreasing a stream’s ability to support healthy fish populations (Bilby et al. 1996). Conversly, restoration efforts that increase spawner abundance can create a positive feedback loop, whereby decomposition of spawned out adult carcasses benefit emerging fish via increased stream productivity, which increases the chance of juvenile survival and ultimately leads to increased spawner abundance (Bilby et al. 1996; Naiman et al. 2002; Weaver et al. 2018b). Given that the upper Yakima River basin has oligotrophic nutrient levels (USEPA 2000) and mostly N-limited biofilm activity, even small amounts of N are likely to stimulate food web productivity (Bilby et al. 1996). Therefore, successful Pacific lamprey restoration efforts could result in substantial increases in food web productivity in the upper Yakima basin. As seen in this study, Pacific lamprey resource subsidies can alleviate nutrient limitation and increase biofilm productivity, which should result in more energy transferred to higher consumers via indirect, bottom-up mechanisms (Bilby et al. 1996; Naiman et al. 2002). Although I did not examine direct pathways, others have observed consumption of lamprey eggs and carcasses by stream consumers demonstrating their importance (Close et al. 2002; Arakawa and Lampman 2020), and both pathways would ultimately stimulate the positive feedback loop to increase stream productivity.

If Pacific lamprey populations recover to the target goal of 28,000-35,000 within the Yakima River basin (Ralph Lampman, unpublished data), this would equate to approximately 3700-4600 kg of C, 800-1050 kg of N and 5.5-6.9 kg of P added to the basin from carcasses alone. Spawner densities would determine if this amount of lamprey-MDN would contribute to a reach-scale effect, however sea lamprey studies on the east coast suggest that that densities of approximately 50 carcasses km^{-1} (Hogg et al. 2013) could increase algal biomass and macroinvertebrate MDN enrichment directly downstream of the carcasses via indirect, bottom-up trophic transfers (Weaver et al. 2016). Although anadromous sea lamprey are larger than Pacific lamprey (Clemens et al. 2010) and can therefore transport more MDN per fish, target population goals of 28,000-35,000 Pacific lamprey equate to an average of 91.6 adults per km throughout the mainstem Yakima River. This density is theoretically possible, given that Brumo and

Markle (2006) reported 48 adult Pacific lamprey/km in a coastal stream in Oregon, and traditional ecological knowledge suggests that lamprey may have been the dominant biomass in some streams (Petersen 2006; Miller 2012), especially where waterfalls were a barrier to salmon. Therefore larger Pacific lamprey populations that result from sustained restoration efforts could then elicit a similar indirect effect as seen in salmon studies (Zhang et al. 2003; Hood et al. 2019; Kaylor et al. 2020). Moreover, if post-spawn Pacific lamprey carcasses accumulate in depositional areas in conjunction with increased in-stream habitat complexity (Dunkle et al. 2020), then their subsidy effect may be more concentrated in those areas creating a hot spot (McClain et al. 2003; Dunkle 2017) of productivity.

Fortunately salmon and lamprey have similar distributions (Wicks-Arshack et al. 2018) and face similar conservation challenges, therefore, inclusive restoration efforts such as habitat restoration have the potential to benefit both species (Clemens et al. 2017). Unfortunately, some conservation efforts specifically geared toward salmon (i.e., fish passage structures, water diversion bypass screens) have likely unwittingly contributed to lamprey declines. Ironically, salmon ladders built to facilitate salmon passage at mainstem dams have created passage barriers for lamprey and have been identified as one of the most immediate threats faced by Pacific lamprey populations (Clemens et al. 2017, CRITFC 2011). Poor lamprey passage likely caused the local extirpation of Pacific lamprey in the upper Yakima basin as Pacific lamprey had not been documented above Roza Dam until the Yakama Nation translocated adults in 2015. Although there have been minor passage improvement projects, telemetry studies by the

Yakama Nation have determined that Roza Dam continues to act as a passage barrier for lamprey and will be the focus of future restoration work (Lampman 2017a).

Although Pacific lamprey populations in the PNW are at historically low levels, there are several reasons to celebrate. For example, adult translocation efforts have been successful, as Yakama Nation biologists and staff found larval Pacific lamprey above Roza Dam 1 year after adult translocation efforts began (Lampman et al. 2016). Although lamprey passage at Roza Dam still requires lamprey passage structures, the presence of larval lamprey will likely support lamprey recolonization due to the presence of larval pheromones which attract spawning adults (Sorensen et al. 2005; Close et al. 2009; Yun et al. 2011). Furthermore, there have been several success stories where the removal of dams that had previously been a passage barrier for lamprey have almost immediately resulted in lamprey recolonization (Jolley et al. 2018; Hess et al. 2021), suggesting that improved lamprey passage significantly increase lamprey spawner abundance.

It is likely that the health and future of lamprey and salmon populations are intertwined through direct and indirect relationships. As a direct relationship, Chinook salmon and other marine fish populations and Pacific lamprey returns are positively correlated, likely due to higher marine food sources for both (Murauskas et al. 2013). Salmon eat dead larval lamprey (Arakawa and Lampman 2020), migrating lamprey act as salmon predation buffers, and spawning lamprey provide carcass and egg material available for direct consumption (Close et al. 2002; Kaylor et al. 2020). Indirectly, lamprey and salmon likely contribute to the increased growth of larval lamprey and juvenile salmon via a reciprocally beneficial positive feedback loop. For example, salmon stimulate stream food web activity in the fall (Bilby et al. 1996; Wipfli et al. 1998;

Chaloner et al. 2002; Zhang et al. 2003), increasing autochthonous production which is then available for larval lamprey (Evans and Bauer 2016). Similarly I have demonstrated that Pacific lamprey can stimulate autochthonous production, which can then increase available food sources for juvenile salmon via indirect trophic transfers (Verspoor et al. 2011; Weaver et al. 2016). Overall, my study demonstrates that reintroducing Pacific lamprey to the upper Yakima River basin, and possibly other basins with similar nutrient limitation patterns, will likely increase productivity in stream food webs that ultimately support larval lamprey and juvenile salmon as well as resident aquatic species and terrestrial species that utilize stream food webs.

Future Studies

Future studies that attempt to estimate how stream food webs will respond to an anadromous resource subsidy at the basal level (biofilm response) via an NDS approach should be able to use the methods outlined by Ruegg et al. (2011) and implemented in this study. Prior to my study, Rüegg et al. (2011) had added salmon tissue in agar as an NDS amendment, whereas my study added to this method by including a treatment of homogenized fish tissue in nylon, which more closely mimics a fish carcass in a stream. Based on my findings, there was no significant difference in the chlorophyll *a* response to tissue in agar or nylon, therefore 10% *w/v* for fish tissue in agar can measure the autotrophic response as well as tissue in nylon. However, I found that the use of fish tissue in nylon elicited a significantly higher heterotrophic response than tissue in agar. This suggests that using 10% *w/v* for fish tissue in agar may be a conservative estimate of the heterotrophic response compared to fish tissue in a stream. This methodological information is useful when there may not be enough carcasses available to perform stream carcass subsidy studies as seen in salmon research (see Janetski et al. 2009), but where researchers are still interested in estimating how low population fish carcasses, such as Pacific lamprey, could influence stream food webs.

Given that PNW rivers historically received reliable pulses of anadromous resource subsidies throughout the year, the high amount of carcass material and nutrients this provided likely drove both direct and indirect pathways. This is important as resource subsidies may not be received equally even when available to species in similar trophic levels. For example, Kaylor et al. (2020) found that salmon carcasses contributed to stream food webs directly via juvenile salmonid feeding, however non-salmonid native fish benefitted via an indirect food web pathway, suggesting that the addition of a well-known subsidy may not directly impact different species in the same way. Similarly, Arakawa and Lampman (2020) found that different piscivorous fish species have different rates of predation on larval lamprey. Therefore, although my study determined how the basal food web responds to lamprey carcasses, how indirect food web effects benefit other species remains poorly understood. If future studies utilized lamprey carcasses in similar methods as salmon carcass subsidy studies (Wipfli et al. 1998; Morley et al. 2016; Kaylor et al. 2020) to track the trophic transfer of energy via stable isotopes, this would fill a large knowledge gap in our understanding of the nuanced pathways that lamprey can act as a resource subsidy.

Furthermore, as restoration efforts increase the possibility for bigger lamprey and salmon populations, it is important to understand how each species will affect the other. For example, while we know that increased salmon (Wipfli et al. 1998; Naiman et al. 2002) and lamprey (Weaver et al. 2018b) spawner abundance can initiate a positive feedback loop to support future spawners, few studies have researched how a lamprey-initiated positive feedback can impact salmon, and vice-versa. Therefore, future studies should focus on how the presence of adult salmon might influence larval lamprey, and how adult lamprey might influence juvenile salmon. This information could contribute to a better understanding of the relationship between lamprey and salmon, and help to guide future management decision making.

Conclusion

Pacific salmon have long been recognized for their important role in linking marine systems to oligotrophic river systems via MDN transport, thus stimulating food web activity through indirect (bottom-up) and direct pathways that benefit the receiving stream ecosystem, the riparian corridor, and upland species that depend on stream ecosystems. This dogma is so well known that resource managers actively add salmon carcasses and salmon carcass analogs to streams to compensate for diminished salmon returns (Kohler et al. 2012; Marcarelli et al. 2014). This salmon-centric view disregards the importance of other anadromous species such as Pacific lamprey, which once dominated anadromous returns in some streams (Petersen 2006; Miller 2012). By performing a side-by-side comparison of autotrophic and heterotrophic biofilm response to nutrients transported by Pacific lamprey and Pacific salmon in the upper Yakima River basin, I demonstrated that lamprey elicit the same autotrophic response as salmon. Although salmon are larger than lamprey and can therefore transport more nutrients on an individual basis, the stoichiometric composition of Pacific lamprey is in the correct proportion to alleviate biofilm nutrient limitation during Pacific lamprey spawning months in late spring through early summer. This suggests that lamprey may be able to facilitate an autotrophic response in other regions where N is a limiting nutrient as it is in many PNW streams (Thut and Haydu 1971). Cumulatively, my results suggest that lamprey may provide important MDN at a time when autotrophic and heterotrophic pathways experience nutrient limitation. Overall, the results of this study demonstrate that lamprey are an equally important subsidy of MDN as salmon, and restoration of lamprey populations should achieve similar ecological benefits as salmon population restoration.

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