Resource Subsidies from Spawning Pacific Lamprey: Spatial Dynamics of Carcass Fate and Entry into Stream Food Webs

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Matthew R. Dunkle

Major Professor: Christopher C. Caudill, Ph.D.

Committee Members: Alexander K. Fremier, Ph.D.; Brian P. Kennedy, Ph.D.

Department Administrator: Lisette P. Waits, Ph.D.

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Authorization to Submit Thesis

This thesis of Matthew R. Dunkle, submitted for the degree of Master of Science with a Major in Natural Resources and titled "**Resource Subsidies from Spawning Pacific Lamprey: Spatial Dynamics of Carcass Fate and Entry into Stream Food Webs**," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: _____   Date: _____
Christopher C. Caudill, Ph.D.

_____   Date: _____
Alexander K. Fremier, Ph.D.

_____   Date: _____
Brian P. Kennedy, Ph.D.

Department Administrator: _____   Date: _____
Lisette P. Waits, Ph.D.

General Abstract

Marine-derived nutrients (MDN) from spawning anadromous fish have received significant attention recently and are a model for understanding how migratory species transport resources across ecotones. Few studies report the role of species other than Pacific salmonids, despite evidence that watersheds were subsidized by resource pulses from multiple species. We explored the role of Pacific lamprey on stream food-webs using a stream productivity model, an evaluation of carcass fate in spawning ecosystems, and an experimental mesocosm to evaluate the response of juvenile salmon to carcass resources. We found that lampreys are unlikely to affect system-scale primary-productivity, but that carcasses may be local-scale resources to which juvenile stream fish may express a fine-scale behavioral response. These findings contribute to understandings of pulsed resources in streams and the role they play on consumers, with implications for restoration of migratory fish and ecosystems.

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Finally, this project would not have been possible without the fruitful collaboration with and support from the Columbia River Intertribal Fish Commission, the Confederated Tribes and Bands of the Yakama Nation, and the Confederated Tribes of the Umatilla Indian Reservation. In particular, I would like to thank Brian McIlraith, who helped guide and fund these studies, Ralph Lampman, whose enthusiasm for lamprey is contagious, and Aaron Jackson, who has been working to conserve lamprey longer than anyone I've met.

Dedication

To my friends and family, especially Danielle Berardi, whose support and encouragement has made even the most stressful parts of grad school fun and exciting, and to Salix and Django who assume I'm going to the river every day I leave them home. This is also dedicated to the Pacific Lamprey, the scientists who work to understand them, and the native peoples fighting to save them.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

Food webs are a central interest in ecosystem science. Food webs are dynamic, complex systems comprised of, and influenced by, the movement of species, materials, and energy at varying scales. Species and materials often move across boundaries and influence dynamics outside of the system they were produced in. Stated eloquently in a foundational paper by Polis and colleagues (1997), "The basic components of food webs—nutrients, detritus, and organisms -- all cross spatial boundaries." Trans-boundary resource subsidies come in many forms and influence temporal and spatial dynamics in both source and sink ecosystems.

Long-distance migratory species can increase productivity of temporally heterogeneous ecosystems and are central to meta-ecosystem functioning (Loreau et al. 2003). Migration, as a special case of animal movement, is defined as highly directional and seasonal movement between distinct spatial zones. Because migration is often tightly coupled with phenological changes and seasonal dynamics, it can represent a predictable component of both producing and recipient ecosystems. Lundberg and Moberg (2003) characterized migratory species as 'mobile-link organisms,' which may be classified as trophic or transport subsidies depending on their active or passive role in recipient ecosystems. The strength of the influence of migratory species depends on the scale and timing of the migratory subsidy, as well as the background conditions of the recipient system (Marczak et al. 2007). The greatest influence of migratory subsidies should occur where that subsidy is large relative to similar *in-situ* resources, when that subsidy is rendered at an ecologically relevant time, and in places where background conditions facilitate efficient utilization of that subsidy.

Stream food webs in temperate habitats are often oligotrophic and particularly shaped by subsidies produced in headwaters, terrestrial zones, and the marine environment (Wipfli and Baxter 2010). The spawning behavior and distribution of anadromous fish influences the uptake of marine-derived nutrients into recipient food webs. Chronic declines in wild anadromous fish returns to spawning tributaries have resulted in a significant reduction in many areas (Cederholm et al. 1999, Gresh et al. 2000, Limburg and Waldman 2009). This deficit has been identified as a potential driver of a downward spiral in juvenile salmon production in systems which otherwise remain somewhat pristine in terms of physical habitat

features (Naiman et al. 2012, Walters et al. 2013, ISAB 2015). Anthropogenic barriers to the passage of anadromous fish limit the resources and processes they provide to spawning streams (Gresh et al. 2000).

Various aspects of salmon-delivered MDN have been studied in detail (Janetski et al. 2009). Although relatively few studies have evaluated the fate and transport of post-spawn salmon carcasses, two have reported that carcasses move only a short distance downstream despite high flow events and that woody debris and slack water retain carcasses in spawning streams (Cederholm et al. 1989, Strobel et al. 2011). Controlled experiments with the addition of carcass material have shown biological responses in periphyton, aquatic invertebrate, and fish communities (Bilby et al. 1998, Wipfli et al. 1998, 2010, Chaloner et al. 2002). Other studies have used stable isotope analysis to confirm uptake of marine nutrients into various aspects of stream food webs (Reimchen et al. 2003, Yanai and Kochi 2005, Claeson et al. 2006) and a growing literature has evaluated salmon subsidies on riparian food webs (Naiman et al. 2002, Schindler et al. 2013, Deacy et al. 2016, Schindler and Smits 2016). These findings have spurred efforts to restore MDN as part of ecosystem restoration projects to recover endangered wild Pacific salmon (Griswold et al. 2003, Nislow et al. 2010).

Recent studies have shown that despite decades and millions of dollars invested in restoration efforts for wild Pacific salmon populations in the Columbia River Basin, juvenile salmon production has been limited to a fraction of historic estimates (ISAB 2011, 2015, Walters et al. 2013) due to lack of historic food web complexity and resource-limited density dependence in juvenile salmon rearing streams. Basic food web dynamics suggest productivity will increase when nutrients are added to a nutrient limited system, barring other limiting factors. It has long been understood that small-order headwater streams are often dependent on allochthonous nutrient subsidies for the majority of primary and secondary production (Vannote et al. 1980). In the Pacific Northwest, many small order streams may also contain spawning habitat for anadromous fish, of which many are semelparous and can deliver a significant pulse of marine-derived nutrients on a seasonal basis (Wipfli and Baxter 2010).

Diadromous species are ecologically important worldwide (Mcdowall 1995, Kappel 2014), though the role of non-salmonid anadromous species in spawning stream food webs

has received significantly less attention. A Web of Science search using the terms *marine-derived nutrients* and *anadromous*, but excluding results with the topic salmon result in only eight papers studying nutrient contributions from non-salmonid anadromous fishes compared with over 70 with an explicit focus on salmon-derived nutrients. While this is certainly an underestimate of the total work on non-salmonid nutrients, the study of anadromous fish-derived nutrient subsidies has missed many potentially ecologically important species, which may comprise other crests in a system's resource waves (*sensu* Armstrong et al. 2016).

Pacific lamprey, unlike most Pacific salmonids, spawn in the late-spring to early summer across their range. Carcasses become available at the beginning of a seasonal bottleneck period in stream productivity and may contribute to stream food webs via several potential pathways: through direct consumption by aquatic invertebrates or fish, by uptake of mobile nutrients released from decomposing carcasses by microbes or periphyton, and/or through indirect pathways transferred through riparian consumers. Because lamprey runs are at low densities throughout much of their range, it is likely that these nutrient subsidies may be too small to induce a measurable response in productivity at the ecosystem-scale. Instead, carcasses of low-density spawning fish may provide a fine-scale, spatially-restricted 'trophic hotspot.' It has been recognized that many ecosystems are a dynamic and are characterized by a shifting mosaic of resources and that distribution of resource patches within a riverscape that can induce measureable responses in primary and secondary productivity in aquatic and riparian habitats (Pringle et al. 1988, Fausch et al. 2002). For example, Payne and Moore (2006) reported that salmon carcasses induce a 10-fold greater in algal production in small lakes adjacent to gull nesting sites than lakes without gulls, despite little evidence for landscape scale effects of salmon on nutrient dynamics. Rather, they conclude that gull-transported resources are deposited in specific locations near nesting sites and create an aggregated resource hotspot.

Like Pacific salmon, anadromous lampreys obtain most their adult body mass during their ocean phase and are semelparous. These nutrients are delivered as a subsidy to spawning streams and represent a potentially significant proportion of available nutrients in streams under certain conditions. Thus, spawning Pacific lamprey, while comprising a small component of the marine biomass subsidy into many systems, may be a driver of early summer ecosystem productivity in spawning streams. Pacific lamprey returns have

dramatically declined in the Pacific Northwest over the last century due to overharvesting, anthropogenic barriers, and habitat degradation. Close and colleagues (2002) estimated a >99% reduction in Pacific lamprey populations entering certain inland watersheds in the period 1966-2002 and numbers reaching interior watersheds (e.g., Snake River) remains low. Though Pacific lamprey is an important cultural resource for the Native American tribes of the Columbia River Basin, conservation of this species has been limited compared with other native anadromous species.

To evaluate the relative role of resource subsidies from spawning Pacific lamprey, we pursued two lines of inquiry: "*what is the spatial distribution of post-spawn fish carcasses in a coupled stream-riparian ecosystem?*" and *"how food webs respond to summer-timed carcasses from Pacific lamprey at these sites?*" The following three chapters address these two motivating questions.

Thesis Structure

This thesis is divided into six chapters. This first chapter contains a general abstract and introduction. The second chapter presents the results of a review and meta-analysis of studies reporting the growth response of juvenile and resident salmonids to the addition of marine-derived nutrient subsidies. The third chapter provides a short summary of results from a mechanistic food-web model simulating varying scales of Pacific lamprey run sizes on primary production in typical spawning reaches. The fourth chapter assesses the spatial dynamics of Pacific lamprey carcass deposition in two spawning streams. The fifth chapter explores the response of juvenile salmon density, growth, and behavior to a high-quality resource subsidy in a controlled mesocosm experiment. The final chapter is a review of the previous chapters and a general discussion of how each relates to the study of resource subsidy dynamics and stream food web ecology.

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Chapter 2: Conceptual and Quantitative Review of Juvenile and Resident Salmonid Responses to Marine-Derived Nutrient Subsidies

Matthew R. Dunkle and Christopher C. Caudill

Department of Fish and Wildlife Sciences, University of Idaho

Moscow, Idaho 83844 USA

Abstract

Marine-derived nutrients from spawning adult salmon have received significant attention in the literature recently. Studies focusing on the impact of nutrients on ecosystem-wide stream productivity have found mixed results, with some finding large net-increases in productivity and others finding small positive, neutral, or negative effects. Direct and indirect uptake by juvenile salmonids has been suggested as an important pathway, though relatively few studies have quantified the effect of direct uptake on juvenile salmon growth, body condition, and overall survival. Spawning salmon disturb stream systems and may limit potential primary production responses to their carcasses. We pooled the available literature on juvenile and resident salmonid growth responses to marine nutrient additions and conducted a quantitative meta-analysis to assess responses to similar subsidy additions. While whole-system production responses in the literature have been varied, all but one study on juvenile or resident salmonid responses to salmon carcass material reported a positive effect. We pooled studies which reported some metric of juvenile fish growth response compared with a control (e.g. individual specific growth, change in mean weight, change in mean length) and calculated a unit-less response ratio of individuals in treatment conditions (i.e. had access to carcass materials) to those in control conditions. The strength of response varied by region, species, timing of addition, and by the type of salmon carcass material added. Strong responses were reported in Alaska, with intermediate responses in the Pacific Northwest and Inland Northwest, and relatively weak responses in the North Atlantic. Coho and Chinook had strong, but varied responses to nutrient additions, whereas Atlantic salmon had consistently low responses to nutrient subsidies. Resident salmonids had intermediate to strong responses to salmon carcass material addition. Additionally, there was evidence of a

seasonal trend, with higher summer and fall responses and low winter responses, and a trend of higher responses with carcasses versus salmon carcass analog pellets. With these findings, we discuss potential mechanisms for variance in published results and recommend future directions for research.

Introduction

The role of marine-derived nutrients (MDN) delivered to streams by anadromous fish has received substantial attention in the ecological literature over the last two decades (Naiman et al. 2002, Janetski et al. 2009). Basic food web dynamics suggest productivity will increase when nutrients are added to a nutrient limited system, barring other limiting factors. It has long been understood that small-order headwater streams are often dependent on allochthonous nutrient subsidies for the majority of primary and secondary production (Vannote et al. 1980). In the Northern Hemisphere, many small order streams may also contain spawning habitat for anadromous fish, of which many are semelparous and can deliver a significant pulse of marine-derived nutrients on a seasonal basis (Wipfli and Baxter 2010).

In the Pacific Northwest, chronic declines in adult salmon returns have been suggested as a cause of cultural oligotrophication, defined as anthropogenic limitation of a natural source of nutrients to a system (Stockner et al. 2000), which can create a positive feedback loop whereby limited adult returns provide a smaller subsidy of MDN, leading to reduced stream productivity (Wipfli et al. 1998, Naiman et al. 2002). Limited stream productivity is a potential mechanism for resource-driven density-dependence and lower overall body condition for juvenile salmon, which may, in turn, limit overwintering survival and out-migrant population (Walters, Copeland, & Venditti, 2013). Restoration of MDN subsidies through greater natural adult returns, artificial addition of carcasses, and addition of artificial carcass analog pellets have all been suggested as possible solutions (Pearsons et al. 2011).

The relative importance of these nutrients on the recipient system likely depends on many abiotic variables, including the background nutrient context, the environmental and hydrogeomorphic conditions at time of delivery, and the seasonal timing of nutrient subsidies (Wipfli and Baxter 2010). While marine-nutrient subsidies have been shown to increase primary and secondary production in some cases (Wipfli et al. 1998, Yanai and Kochi 2005, Kohler and Taki 2010), other studies have shown either no response (Harvey and Wilzbach 2010, Cram et al. 2011) or have shown negative effects of spawning on periphyton and macroinvertebrate communities (Moore et al. 2004, Holtgrieve and Schindler 2011, Tiegs et al. 2011). Direct uptake by fish consumers is an understudied pathway, as many studies have

not directly assessed changes in juvenile salmon growth, body condition, or biomass, despite most management paradigms citing increased growth rate as a central goal (Janetski et al. 2009). Juvenile salmon growth is also affected by biotic variables, including density-dependent interactions, variability in size-specific growth rate, feeding behavior, and habitat complexity (Chapman 1966, Metcalfe et al. 1990, Zabel and Achord 2004).

Using the technique of quantitative meta-analysis, we reviewed the results of studies that assessed some metric of growth in the juvenile salmonid community. Our goal was to partition the variation in effect size among potential drivers of ecosystem response to salmon MDN. The strength of juvenile salmon response to MDN additions likely depends on many, potentially confounding factors, including degree of nutrient limitation, hydrogeomorphic context, environmental conditions, and seasonal timing of MDN subsidy. My driving hypotheses are that 1) response will vary by region, with more inland systems in the Inland Northwest eliciting a stronger response than coastal systems due to lower background nutrient availability and greater current nutrient deficit due to declines in wild salmon returns and a trend for more snow and rain/snow dominated systems which maintain stable, low flows throughout much of the year; 2) that resident and 'stream-type' species which spend multiple years in streams will have a stronger growth response than 'ocean-type' species which smolt after 3-4 months; 3) that spring and summer MDN subsidies will drive a stronger response than fall and winter additions, due to lower system metabolism caused by stream temperature and light conditions; and 4) that there will be a stronger response with natural spawning and additions of carcass versus additions of salmon carcass analog pellets due to differences in direct consumption by aquatic insects and fish and rates of stream retention. We predict the strongest responses would be in the Inland Northwest per weight of nutrient addition due to the level of current salmon nutrient deficit and oligotrophication as well as the more snow and snow/rain dominated hyrdogeomorphic conditions in these systems. Southeast Alaska, the Pacific Northwest, and the North Atlantic were expected to have more variable flow regimes throughout the years, leading to flashier systems that have the potential to export carcass material before it could be incorporated into the food web. Conversely, snow and snow/rain dominated systems typically have low and consistent flows throughout much of the year, with predictable peaks in the hydrograph in the early spring, before natural additions of MDN would occur.

Methods

We restricted the literature search to papers reporting a change in juvenile salmonid growth or biomass. We searched the database Web of Science for relevant key words: marine-derived nutrient, MDN, marine nutrient and juvenile. Studies were only included if they assessed some metric of juvenile or resident salmonid growth. We also included studies that reported juvenile growth response a previous meta-analysis by Janetski et al. (2009) and metrics were extracted from the supplementary materials provided by the authors. These criteria resulted in a group of 11 comparable studies. Where the results of multiple separate field experiments were presented, their outcomes were treated as independent samples, resulting in an overall sample size of n=21, spanning four distinct geographical regions: Southeast Alaska (SEAK), comprising systems which drain to the Gulf of Alaska; Pacific Northwest (PANW), comprising rain-dominated systems on the west slope of the Cascade Range; the Inland Northwest (INNW), comprising the interior Columbia and Snake River basins; and the North Atlantic (NOATL), comprising streams in either New England or Northern Europe (Figure 2.1). These distinctions were made to address regional differences in species assemblages, meteorological patterns, and background environmental conditions.

Following the methods used by Janetski et al. (2009) and another ecological meta-analysis (Marczak et al. 2007b) we calculated the effect size (L) by taking the natural logarithm of the ratio of mean response of treatment groups receiving salmon MDN to the mean response of the control groups, which did not receive salmon MDN. This measure of effect size was chosen because it provides a clear and biologically meaningful metric that can be compared readily across studies and systems. Although the review by Janetski and colleagues (2009) included many of the same studies used in this review, we were explicitly interested in the role of timing of resources and variation by region.

Studies with a positive juvenile salmon growth response to MDN have an L>0 and studies with a negative response have an L<0. A response ratio close to L=0 suggests no response. Studies reported various metrics of change in the juvenile salmon community, but the most common metrics were related to specific growth rate or percent change in mass at the individual or community level. Response species were limited to juvenile salmon and char, which were the most common in the literature. Resident and anadromous species were

both included under the assumption of broadly similar foraging behavior at similar size classes. A summary of the included studies is provided in Tables 2.1 and 2.2.

Results

We analyzed a spatially broad set of 11 papers reporting results of either experimental or natural manipulations of marine-derived nutrient subsidies into recipient streams on the growth or change in biomass of juvenile salmonids. Where salmon MDN was experimentally added, it was either as post-spawn hatchery-origin carcass material or in the form of salmon carcass analog pellets (Pearsons et al. 2011). Observation of natural spawning effects were also compared with control reaches where salmon MDN was excluded. These studies represent the effect of MDN subsidies in watersheds of both the North Atlantic and North Pacific on 8 juvenile salmonid species.

Contrary to hypothesis 1), the strongest effects were observed in Southeast Alaska, with the lowest in the North Atlantic and intermediate in the Inland Northwest (Fig. 2.2). This finding may be due to many factors, including the most stable hydrograph of the regions assessed, a somewhat complete historic consumer assemblage, and strong wild salmon returns relative to other regions. Studies in the Pacific Northwest ranged from low to intermediate. Mean effect size by region varied from 0.25 in the North Atlantic to >2.50 in Southeast Alaska, suggesting potential regional differences (Table 2.2, Fig. 2.2). Of the 21 samples included, half were conducted in Southeast Alaska and one quarter of the studies were from the Pacific Northwest. Studies from the Inland Northwest and the North Atlantic were also included, though there were relatively few in the published literature (Fig. 2.1).

We also predicted with hypothesis 2) that the response size would vary by species, with resident species showing the greatest response to salmon carcass material and the weakest response by 'ocean type' species, which migrate out of freshwater at < 6 months of age. We expected that 'stream type' species, which rear for 1+ years in freshwater, should express an intermediate response. Mean effect size by species also varied considerably, though very few studies reported the response of species other than Coho or Chinook salmon (Fig 2.3), which can express both stream-type and ocean-type life histories. The largest mean response ratio was reported with Coho salmon and the lowest reported for Atlantic salmon, with resident species ranging from intermediate to high response ratios. Interestingly, Atlantic salmon, which typically remain in freshwaters for 2-3 years, had the smallest response, whereas Coho salmon, which are typically more 'ocean type' juveniles in coastal

systems, had the largest response. Small sample sizes for most species other than Chinook and Coho salmon limits further analysis, but there is evidence for moderate to strong responses in resident salmonid communities.

In hypothesis 3), we predicted the strongest responses would occur in the early and late summer, due to abiotic conditions conducive for primary and secondary production responses including higher water temperatures, more photosynthetically active radiation (PAR), and moderate to low stream flows. Response by timing showed covariance between timing and region, preventing rigorous assessment of timing effects and imbalance in reporting across seasons with fewer studies reporting additions during winter, spring, and summer (Fig. 2.4). The strongest mean seasonal responses were observed in fall additions, with the lowest in early summer, with late summer and winter showing intermediate mean responses. This was contrary to our predictions and the strong winter response reported by two studies was unexpected. More early summer and winter studies are necessary to conclude there is an underlying seasonal bias for juvenile salmon response.

Our final hypothesis 4) was that natural carcasses would have a more consistently positive effect on juvenile salmon growth than salmon carcass analogs, due to preferential tissue utilization by aquatic insects and fish and because carcasses represent both a substrate and a subsidy to the benthic community. Effects also varied by MDN addition type, with many strong effects shown with natural carcass material and moderate effects reported with SCA material (Fig 2.5). Surprisingly, studies observing MDN addition through natural spawning of wild salmonids had the smallest mean effect, potentially due to physical disturbance by live salmon or a mismatch of loading rates between artificial and natural nutrient additions.

Discussion

This analysis provides a quantitative summary of recent studies on the response of juvenile salmonids to additions of salmon carcass. We expected a wide variation in responses by region, response species, timing (relative to both instream flow conditions, ambient resources, and consumer life history), and the form resources are provided in. We expected the strongest effects would be found summer additions, in inland, snow-dominated systems, with 'stream type' or resident species, and with carcass additions versus carcass analogs. Surprisingly, there was little evidence to support our first three hypotheses and the only prediction strongly supported by the literature was that the form of MDN resources have strong effect on consumer response. It is likely that regional, species, temporal, and material differences in response rates are driven by several biotic and abiotic factors which limit direct uptake by juvenile salmonids as well as indirect uptake through food web incorporation of salmon MDN, but relatively few studies have explicitly explored the system-wide response to MDN across regions or spawning seasons.

Our first hypothesis was that response would vary by region because implicit in broad regions is the flow conditions, season length, and, in the case of Southeast Alaska, integrity of the freshwater community. We expected the strongest response would be found in the Inland Northwest due to severity of nutrient limitation (Sanderson et al. 2009) and declines in spawning returns to these systems (Gresh et al. 2000) resulting in a disproportionately large impact of any MDN addition. Instead, the greatest effects sizes were found in studies in Southeast Alaska, suggesting that nutrient limitation in these streams may significantly greater than nutrient limitation in lower latitudes. Studies of primary productivity response to added nutrients in Southeast Alaska and in British Columbia report strong nutrient limitation in these systems (Tank and Dodds 2003, Karlsson et al. 2011). Alternatively, relatively intact Alaskan streams may contain biotic or abiotic processes necessary to more efficiently utilize salmon MDN subsidies than other areas. These results could also suggest that juvenile salmon responses outside Alaska are limited by something other than nutrients (i.e. density, degraded habitat, aquatic contaminants).

Our second hypothesis was that the greatest response would be found with stream-type fish, which remain in freshwater for 1+ years. This was somewhat supported, as the

strongest responses were reported in Coho and Chinook salmon, which often exhibit stream-type life histories, although one study reported a strong response in resident Dolly Varden trout (*Salvelinus malma*). It is possible, however, that Chinook included in these studies migrated as subyearlings, as this is found in some coastal populations. No studies reported the response of strongly ocean-type juveniles, such as Pink salmon (*Oncorhynchus gorbuscha*) or Chum salmon (*Oncorhynchus keta*). Responses by rainbow trout/steelhead *(Oncorhynchus* myskiss) were only reported in one study and expressed a relatively weak response.

Our third hypothesis was that seasonality could influence the response of fish consumers to MDN, with the greatest effects seen in spring and summer and the lowest in fall and winter, due to metabolism and food availability. The seasonal impact of carcass material on juvenile growth response (Fig 2.4) stratifies the response-by-rate relationship by the season in which carcass material was added. Contrary to our expectations, fall-timed subsidies drove the strongest responses with the weakest responses observed in winter and summer. Few studies have evaluated spring-timed MDN and one reported a relatively strong response and one reported a generally weak response. This could be important, because iteroparity rates in steelhead are low in the Inland Northwest (<3%; Keefer et al. 2017) and could represent a vector for spring-timed MDN to these watersheds. It is essential that future studies qualify the seasonal dynamics of flow in their study system, as well as information about the bed structure, heterogeneity, and presence of large woody debris, as these factors likely shape the amount of time carcass material remains in each stream reach.

Our fourth hypothesis was that the strongest responses would be reported by studies observing natural spawning populations or carcass additions, as these resources are more complex and representative of historic conditions, and that these carcasses would be distributed into traditional habitat patches within a spawning stream. This expectation held for carcass addition studies (of which most included studies reported), with a moderate response reported by studies of salmon carcass analogs, and the weakest response by observing natural spawning populations. These results suggest that the indirect pathways of MDN in spawning streams may be important, because natural spawners have been shown to

limit the primary production response through bed disturbance (Tiegs et al. 2011, Bellmore et al. 2014)

Because scientists and managers have sought to mimic natural timing of salmon spawning for nutrient addition studies, the influence of MDN on food webs have been understudied during spring and early summer periods. Only two of the included studies measured nutrient additions in early summer and only three studies were conducted during winter months. A further search into the literature will undoubtedly reveal examples of nutrient additions in other forms, such as soluble reactive phosphorous, nitrate, or nitrite into stream systems from agricultural settings and could provide a rough idea of the nutrient need during those periods, but such studies would not likely represent stream responses to natural carcass additions.

Future research should account for the temperature and light conditions at the time of nutrient addition as well as the seasonal changes in juvenile salmon growth. Ideal studies would include a longer-term study window that captures the initial response of juvenile salmon and follows those fish over the winter months to assess potential increases in winter survival, out-migration success, and return as adults. Another potentially important, yet understudied facet of MDN effects on stream ecosystems is the importance of timing in the addition of nutrient resources as it relates to non-salmonid species. While this analysis included studies from 9 of the 12 months in a year, there is a clear focus in the literature on late summer and early fall additions to correspond with historic imports of MDN via spawning salmon. One of the studies from the North Atlantic region assessed the response of juvenile Atlantic salmon to carcass material introduced to mimic the timing to mimic the spawning of a sympatric species of lamprey (Guyette et al. 2013).

While juvenile fish have a positive response in most conditions, there is clear variation in the scale of the effect size by region, timing, species, and the form in which salmon carcass material is added. Marine-derived nutrients and carcass material may be incorporated into ecosystems through multiple direct and indirect pathways, each of with is likely mediated by separate factors (Fig. 2.6). Depending on the combination of factors unique to each stream in each system, the relative strength and efficiency of each pathway may be dramatically different than superficially similar systems. Lotic systems are inherently

dynamic and spatial distribution of material resources in dynamic systems can lead to 'hot spots' of biological activity. Because spatial distribution of carcass material in a stream is not uniform and utilization by juvenile salmonids, primary producers, or food web dynamics may be dramatically different in reaches of close proximity. Because of this propensity for nutrient 'hot pots,' even a small response ratio could yield ecologically important results of nutrient additions and may be missed in large-scale or manipulative studies.

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Tables and Figures

Table 2.1. Number of studies, sample size, and mean effect size for the Inland Northwest (INNW), North Atlantic (NOATL), Pacific Northwest (PANW) and Southeast Alaska

Region	Number of Studies	Sample Size	Mean Effect Size (L)
INNW	1	3	1.51
NOATL	2	2	.255
PANW	3	8	.459
SEAK	5	12	2.58

(SEAK).

Table 2.2. Studies included in the analysis. Those with multiple entries presented results of multiple distinct studies. Study designs were classified as side-by-side (SBS), upstream-downstream (U/D), natural observation (OBS), or before-after control-impact (BACI).

Study	Metric	L	Region	Study	Type	Rate	Species	Season
Wipfli et al. 2004 (Mesocosm)	Percent Change in Mass	1.674	SEAK	SBS	CARC	6.8	CHNK	Fall
Wipfli et al. 2004 (Bridget Cove Cr.)	Percent Change in Mass	2.971	SEAK	U/D	CARC	0.54	CHNK	Fall
Wipfli et al. 2003 (Art. 2)	Percent Change in Mass	2.546	SEAK	SBS	CARC	3.72	Coho	Fall
Wipfli et al. 2003 (Art. 1)	Percent Change in Mass	2.42	SEAK	SBS	CARC	1.86	Coho	Fall
Wipfli et al. 2003 (Cedar Cr. 1998)	Percent Change in Mass	3.163	SEAK	U/D	CARC	0.82	Coho	Fall
Wipfli et al. 2003 (Art. 4)	Percent Change in Mass	2.813	SEAK	SBS	CARC	7.44	Coho	Fall
Wipfli et al. 2003 (Art. 3)	Percent Change in Mass	2.783	SEAK	SBS	CARC	5.58	Coho	Fall
Bentley et al. (2012) Lynx Cr	Specific Growth	0.5596	SEAK	OBS	NAT	4.5	Grayling	Summer

	Rate							
Bentley et al. (2012) Hidden Cr	Specific Growth Rate	0.3448	SEAK	OBS	NAT	4.5	Mykiss	Summer
Bentley et al. (2012) Hidden Cr.	Specific Growth Rate	0.4054	SEAK	OBS	NAT	4.5	Grayling	Summer
Denton et al. (2011)	Instantaneous Growth Rate	2.302	SEAK	OBS	NAT	1	Dolly Varden	Fall
Wipfli et al (2010	Percent Change in Mass	0.2623	SEAK	MESO COSM	CARC	9.06	Coho	Summer
Wilzbach et al. 2005 (All Streams)	Specific Growth Rate	1.157	PANW	SBS	SCA	0.94	CHNK	Winter
Bilby et al. 1998 (A400 Cr.)	Growth Factor	0.091	PANW	U/D+SBS	CARC	0.71	Coho	Winter
Bilby et al. 1998 (Salmon Cr.)	Growth Factor	0.095	PANW	U/D+SBS	CARC	0.56	Coho	Winter
Harvey and Wilzbach 2011	Specific Growth Rate	-0.1053	PANW	U/D+SBS	CARC	0.94	CHNK	Winter
Guyette et al. 2013	Specific Growth Rate	0.1294	NOATL	U/D+SBS	SCA	0.1	ATS	Spring
Williams et al. (2009)	Total Juvenile	0.3814	NOATL	U/D+SBS	CARC	0.15	ATS	Fall

	Biomass							
Kiffney et al. 2014	Percent Change in Mass	1.929	PAN W	SBS	SCA	0.01 2	Coho	Spring
Kohler et al. (2012)	Least Square Difference	1.098	INNW	BACI+S BS	SCA	0.2	Salmon (gen)	Fall
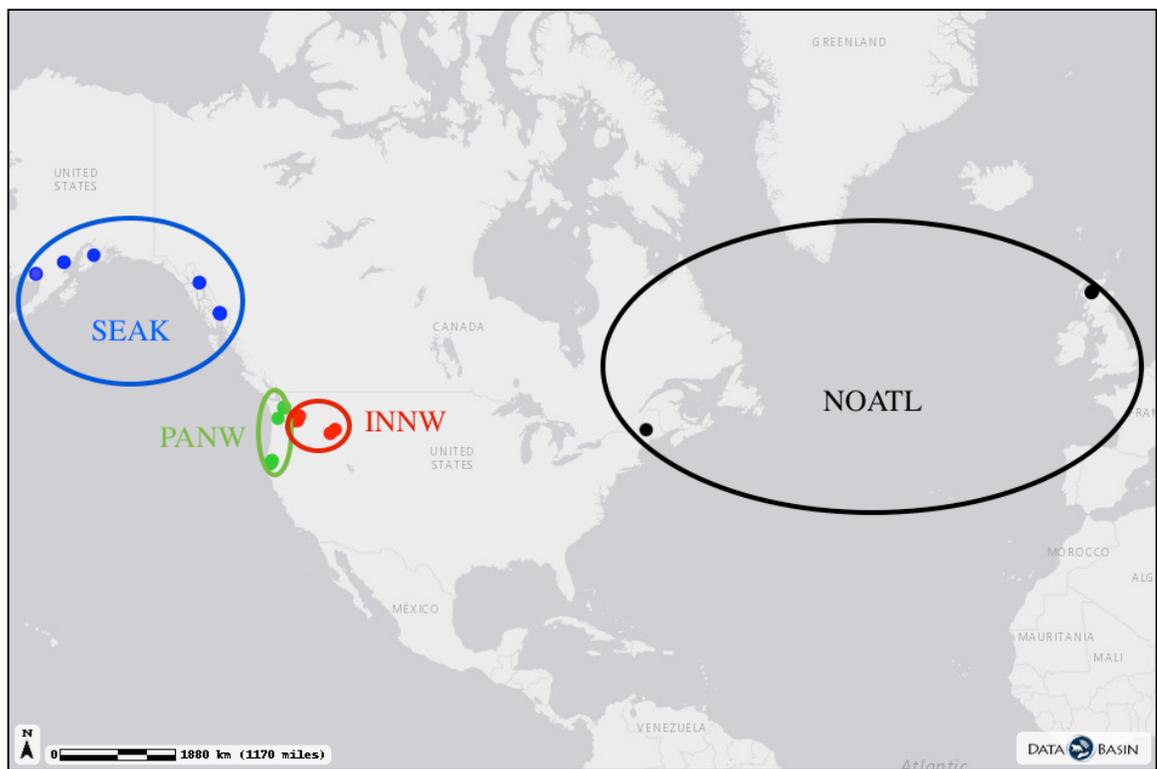
Figure 2.1. Map of study locations included in meta-analysis. Locations were stratified by region: Southeast Alaska (SEAK), Pacific Northwest (PANW), Inland Northwest (INNW), and North Atlantic (NOATL).
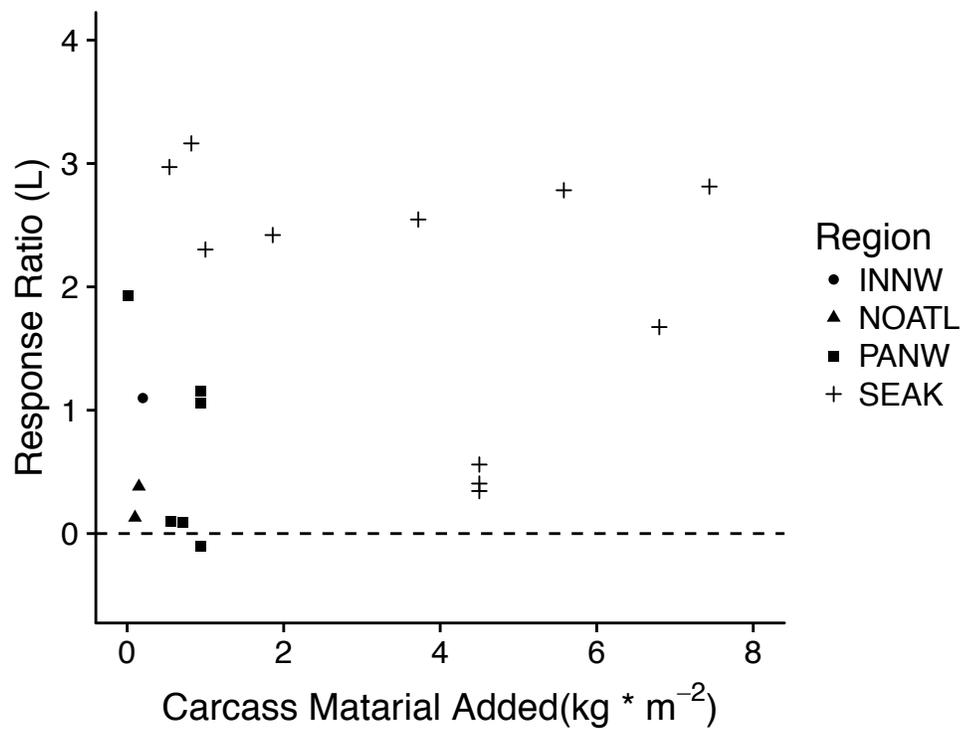
Figure 2.2. Response ratio across carcass material loading rates. Region of study location is noted by shape. The line at L=0 reflects no effect.
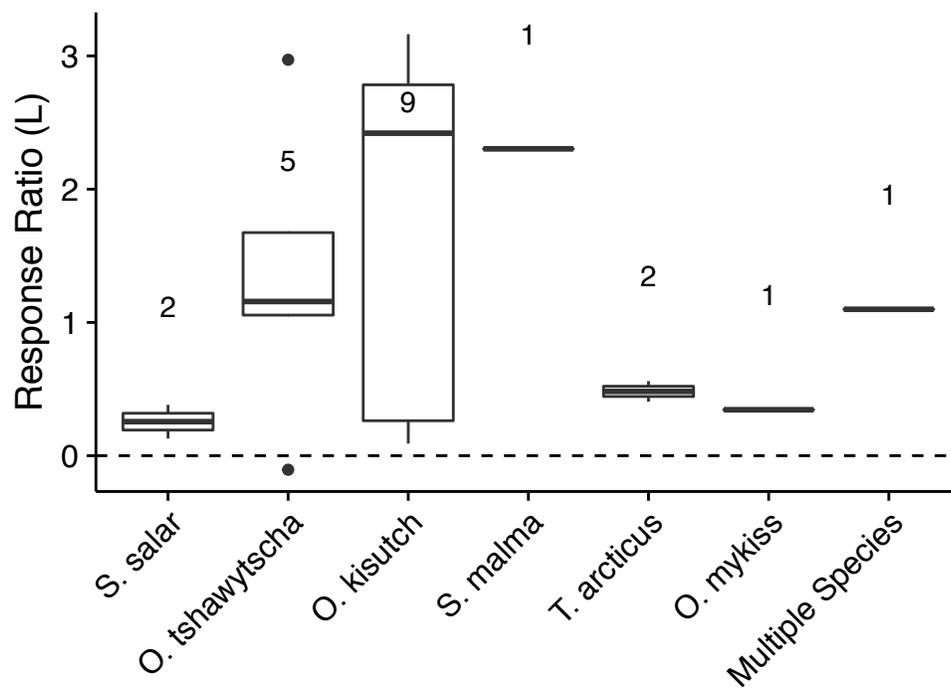
Figure 2.3. Response ratios reported from studies separated by response species. Numbers reflect sample sizes.
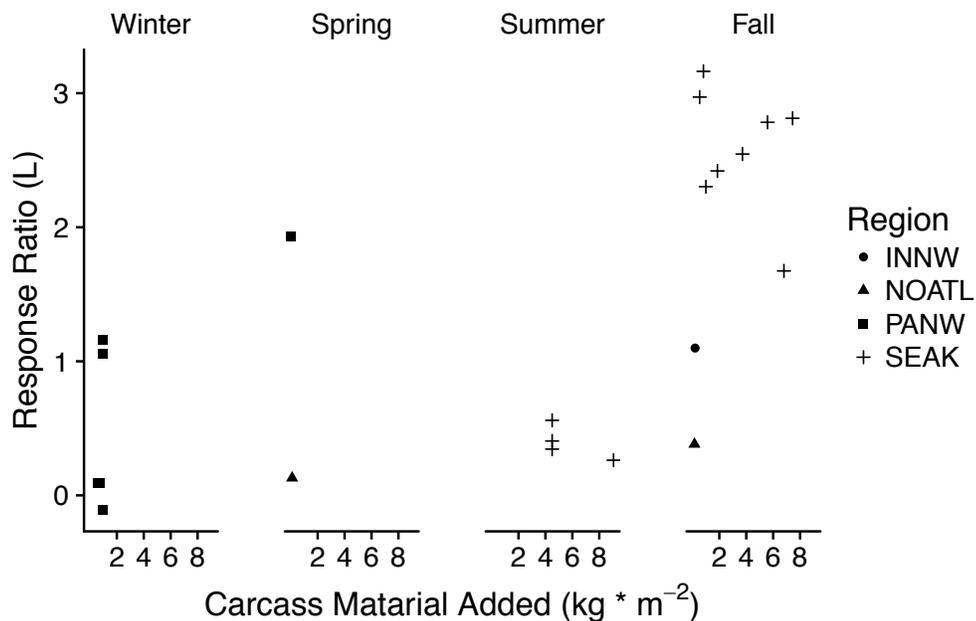
Figure 2.4. Response ratio stratified by season and region of study location. Seasons were broken into three month periods: summer (July-Sept), fall (Oct-Nov), winter (Dec-Feb), and spring (Mar-Jun).
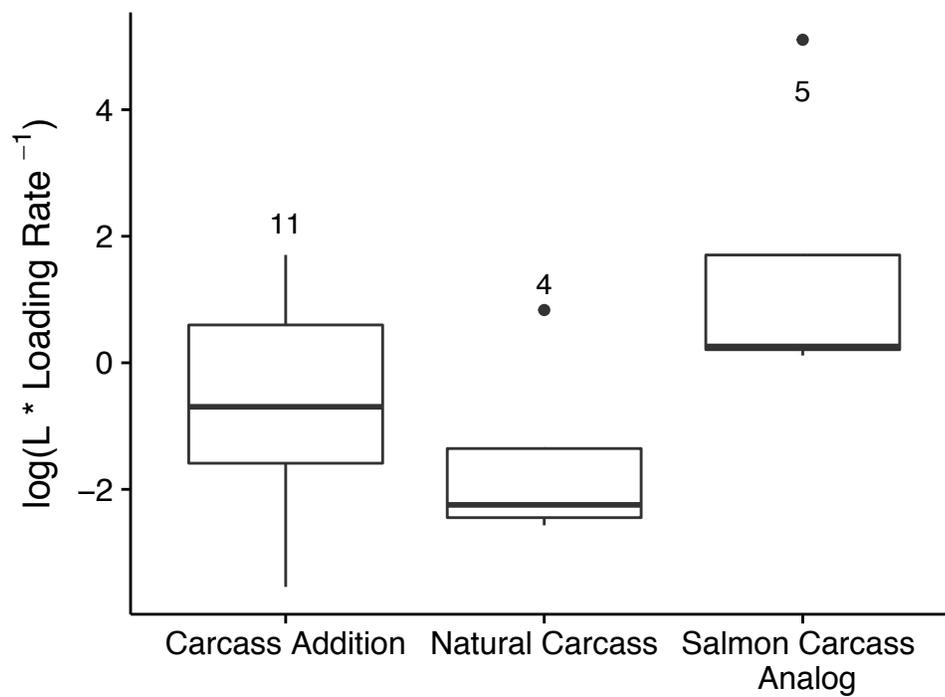
Figure 2.5. Response ratio by carcass addition type while controlling for loading rate. Sample sizes are shown above.
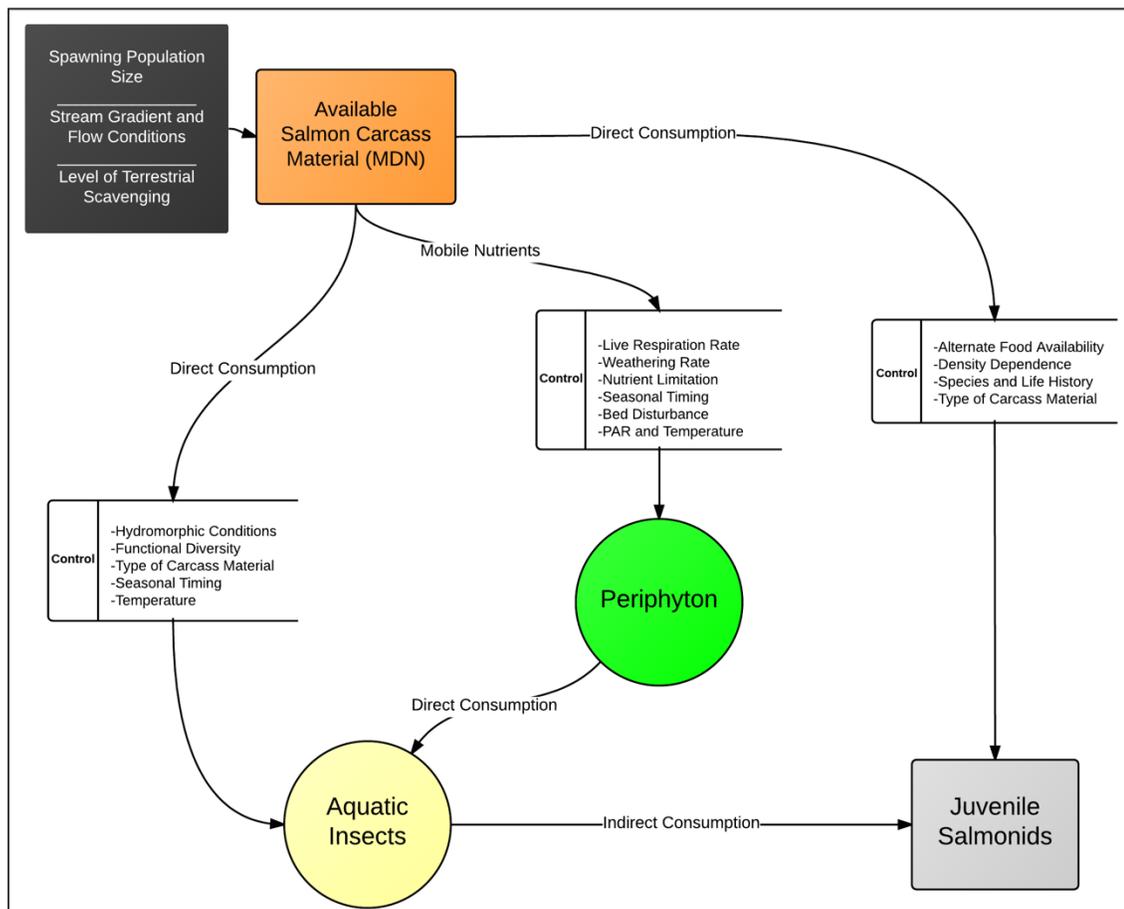
Figure 2.6. Conceptual diagram of factors influencing juvenile fish response to carcass additions.

Chapter 3: Do Nutrient Subsidies from Early Summer Carcass Subsidies Increase Reach-Scale Periphyton Production? Simulations Using a Mechanistic Food-Web Model

(From a poster presented at 145th Annual Meeting of the American Fisheries Society, Portland, OR, USA)

Matthew R. Dunkle[1], Christopher C. Caudill[1], J. Ryan Bellmore[2], Alexander K. Fremier[3]

[1]Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Dr. MS 1136, Moscow, Idaho, 83844, USA
[2]Pacific Northwest Research Station, US Forest Service, Juneau Alaska
[3]School of the Environment, Washington State University, Pullman, Washington, USA

Abstract

Food web dynamics in spatially complex habitats are affected both by local nutrient conditions and the transport of nutrients and energy across ecological boundaries. Both terrestrial- and marine-derived nutrients (MDN) subsidize streams in the inland Northwest, where many systems are naturally low in nutrients or culturally oligotrophic. Further, streams are seasonally dynamic, yet most MDN studies have focused solely on contributions in autumn from spawning salmonids, a time of deciduous litterfall and declining biological activity that may limit community response to MDNs. No studies to date have measured the impact of MDN from Pacific Lampreys spawning in late spring. Here, we expand an existing model of salmon nutrient-driven periphyton growth and biomass to explore the role of MDN subsidies from lamprey. Model scenarios assess the relative effect of current and historic lamprey and salmon densities on periphyton under flow and background nutrient conditions representative of lamprey spawning reaches in the inland Northwest. We found that primary production responds strongly to environmental baselines of discharge and background nutrients, but predict that lamprey have a generally weak effect on reach-scale primary productivity. Thus, we conclude MDN resources from low-density spawning populations of Pacific lamprey are more likely to contribute to resource patch dynamics than

system nutrient status and to effect secondary production through alternative food web pathways.

Introduction

Resource subsidies can have significant ecosystem scale effects on donor communities, particularly when resource conditions are constrained and temporally variable. Streams in the Pacific Northwest are seasonally dynamic and often nutrient limited. These ecosystems receive much of their energy from terrestrial and marine resource subsidies, which vary seasonally with stream flows, riparian inputs, and anadromous fish runs.

Most studies of marine subsides have focused on contributions in autumn from spawning Pacific salmon (Janetski et al. 2009; Chapter 2), a time of deciduous litterfall and declining biological activity that may limit community response to marine nutrients. Currently, no studies have analytically considered the impact of marine subsides from spring spawning species, including Pacific lamprey (*Entosphenus tridentatus)* spawning in late spring to early summer throughout their range (Mesa and Copeland 2009). Like salmon, lamprey may affect primary productivity positively through the addition of biologically available nitrogen and phosphorous through excretion and decomposition and negatively through bed disturbance during nest creation (Fig. 3.1). Compared to salmon, lamprey body size is smaller, respiration and excretion rates are thought to be very low, nutrient density of lamprey carcasses may be higher and lamprey nutrients become available at the onset of the growing season. To evaluate the potential system-level effects of lamprey marine-derived nutrients on primary production, we adapted a mechanism-based model of aquatic ecosystem production to include spring-spawning Pacific lamprey and then used the model to assess periphyton production dynamics across a range of current and plausible historic lamprey spawner densities and background physical, nutrient, and salmon spawning conditions.

Methods

We adapted the mechanistic periphyton biomass model created by Bellmore et al. (2014) to include the spring-timed entry and spawning of semelparous Pacific Lamprey in the Interior Columbia River Basin using a systems dynamics approach using Stella software v 10.1 (ISEE Systems, Lebanon, NH, U.S.A.; Fig. 3.1). Physical and biological parameters were chosen from the literature to represent typical conditions in snow-dominated inland Northwest spawning streams. Simulations of lamprey spawning were assessed at four densities: *none (0.0 lamprey m^{-2}), low (0.01 lamprey m^{-2}), medium (0.05 lamprey m^{-2}), and high (0.1 lamprey^{-2}).*

Salmon run size was chosen to reflect possible scales of salmon run size in a similar fashion to lamprey, with a low density of (0.01 salmon *m^{-2}),* a medium density of (0.05 salmon *m^{-2}),* and a high density (0.1 salmon *m^{-2}).* Data on background nutrients were not widely available, so values were chosen from a range of possibilities. Like salmon and lamprey, both nitrogen and phosphorous loads represented extremely low to reasonable moderate and high levels for a typical stream in the Inland Columbia basin. Because gradient influences water velocity and bed scouring effects on periphyton, we chose to vary the gradient from a low level, similar to the spawning reach of Satus Creek (Chapter 4) and the conditions we later mimicked using an artificial stream system (Chapter 5) at 1% slope. Moderate and high levels reflect conditions upstream of the spawning reach on Satus, where spawning habitat is likely limited.

The patterns of temperature and flow were drawn from conditions measured in Boulder Creek, WA, a small tributary of the Chewuch River in the Methow River basin, but actual values for discharge and temperature in the model were scaled to reflect a low water year (warmer than average and less discharge than average), a normal year (reported conditions in 2014), and a high-water year (colder and less discharge on average). Because slope, bankfull width, depth, floodplain width, and bank angles were fixed at constant values, actual simulated conditions do not represent Boulder Creek.

We chose to assess biomass rather than production to account for the bed disturbance effects of spawning fish. Biomass also represents the available standing stock for

consumers in the stream food web and were assumed to be the most biologically important result. Because lamprey build much smaller nests than salmon and their bed disturbance levels reflect this.

Following the methods used by Harper et al. (2011), a global sensitivity analysis of 2000 simulations of annual periphyton biomass was conducted to assess relative importance of eight potentially important stream and spawner density characteristics. The most important factors were combined into four simulation scenarios with three levels and assessed under four levels of lamprey spawning density (Fig. 3.4).

Results

Lamprey run size had a generally weak influence on periphyton biomass (Fig. 3.2). Greatest effects of varying lamprey spawner density were seen under low water year and low gradient simulations, but these effects were more than an order of magnitude smaller in comparison to scenarios of varying background nutrient concentrations. Under most scenarios, differences in primary production due to lamprey run size were undetectable at the system level, except for low-nutrient, low-water conditions where model predicted biomass in the high-density lamprey scenario was nearly double that in the low and no lamprey density model scenarios, and this difference persisted for an approximately a month in early summer (Figure 3.3, middle panel).

A global sensitivity analysis revealed that temperature had the strongest influence on model output. Discharge, background nutrients, and salmon and lamprey spawner density all produced similar variation model output. Lamprey run timing was also included in the initial sensitivity analysis, but had only marginal influence on model output and was dropped from subsequent simulations.

Discussion

Simulations suggest that Pacific Lamprey may have limited potential to influence bottom-up food web dynamics at the ecosystem scale except under low nutrient and low water conditions. We emphasize the model results apply to lamprey effects on primary production and that lamprey-derived nutrients may nonetheless have effects through direct consumption by invertebrate and vertebrate predators (Objectives 2 and 3).

These results reflect the fact that lamprey, even at relatively high spawner densities, represent a small vector for marine-derived nutrients due to their small body size. Additionally, our model assesses the role of lamprey spawning in late spring. Field studies conducted in two Inland Northwest streams (Chapter 4) suggest that our model had peak lamprey spawning much earlier in the season than we assumed. Earlier spawning in the model places lamprey carcasses in the stream near peak discharge and under colder conditions than we observed in the field. Follow-up simulations could alter spawn timing and physical conditions in the stream to reflect spawning occurring at or near base-flow and warm (15-25 °C) conditions.

Additionally, our simulations emphasize that the greatest effect of MDN is likely to occur under extremely low background nutrient concentrations. It is possible that many watersheds considered oligotrophic may still be at a high enough nutrient status that lamprey MDN would not elicit a measurable primary production response. Rather, it seems plausible that lamprey carcasses may represent a localized nutrient hotspot within spawning streams and responses by primary and secondary consumers should not be considered at the reach scale, as the model considers, but instead at the micro-site specific scale.

Anecdotal field analyses have revealed that microbial and periphyton on or around lamprey carcasses may be largely driven by the water velocity and light conditions at the site of decomposition. For example, we observed higher abundances of filter-feeding *Chironomidae* adjacent to carcasses in slack water areas compared with higher-velocity open channel areas, which could be due in part to periphyton and microbial growth in these areas. Further research should evaluate the response of periphyton at fine scales adjacent to carcasses and under varying temperature and light regimes.

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Tables and Figures

Table 3.1 – Parameter conditions used for model simulations. Bolded values were held as background conditions while running simulations of other factors.

Factor	Low	Moderate	High
Background Nutrients	***DIP= .001 mg/l*** ***DN= .005 mg/l***	DIP= .01 mg/l DN= .05 mg/l	DIP= .1 mg/l DN= .5 mg/l
Salmon Run	.01/m²	***.05/m²***	.1/m²
Gradient	***1%***	5%	10%
Water Year	TempScalar=2 FlowScalar=.5	***TempScalar=1*** ***FlowScalar=1***	TempScalar=.5 FlowScalar=2
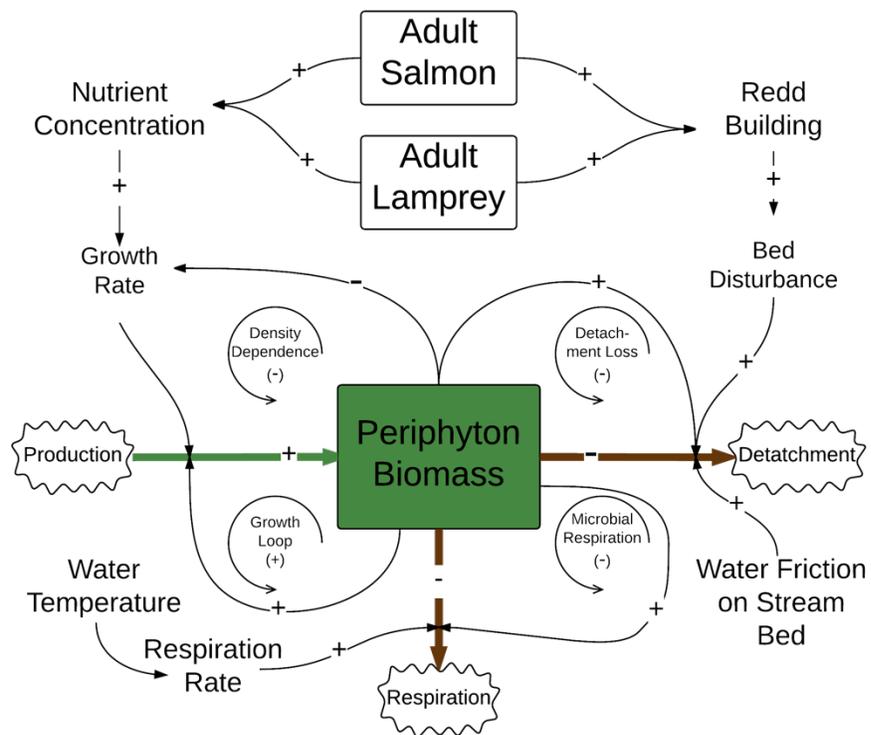
Figure 3.1 – Conceptual causal diagram of periphyton community dynamics used as a framework for model structure (adapted from Bellmore et al., 2014).
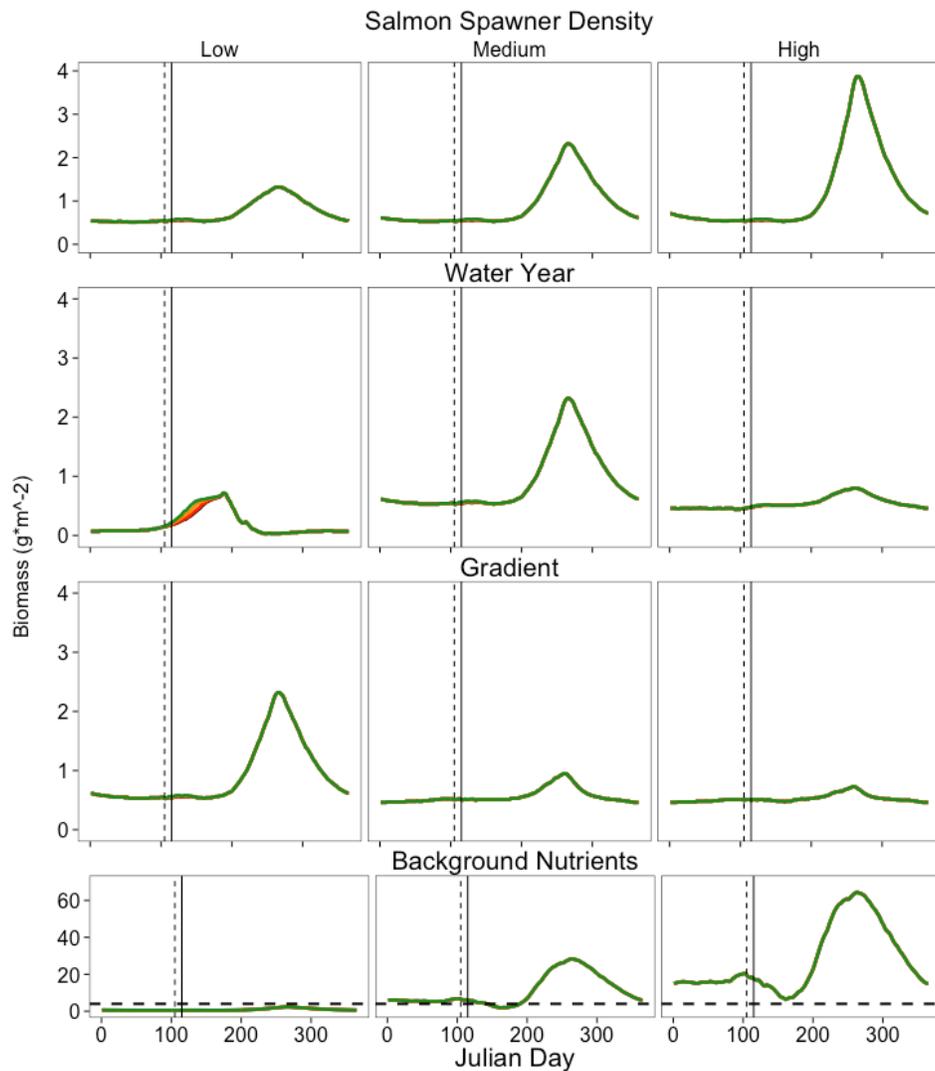
Figure 3.2 – Daily periphyton biomass in response to simulation scenarios for a period of 365 days after model stabilization under four simulation scenarios at low, medium, and high conditions for each factor. Lamprey density are marked as follows: black = no lamprey; red = low; yellow = medium; green = high. Note the change in scale for background nutrient simulations.
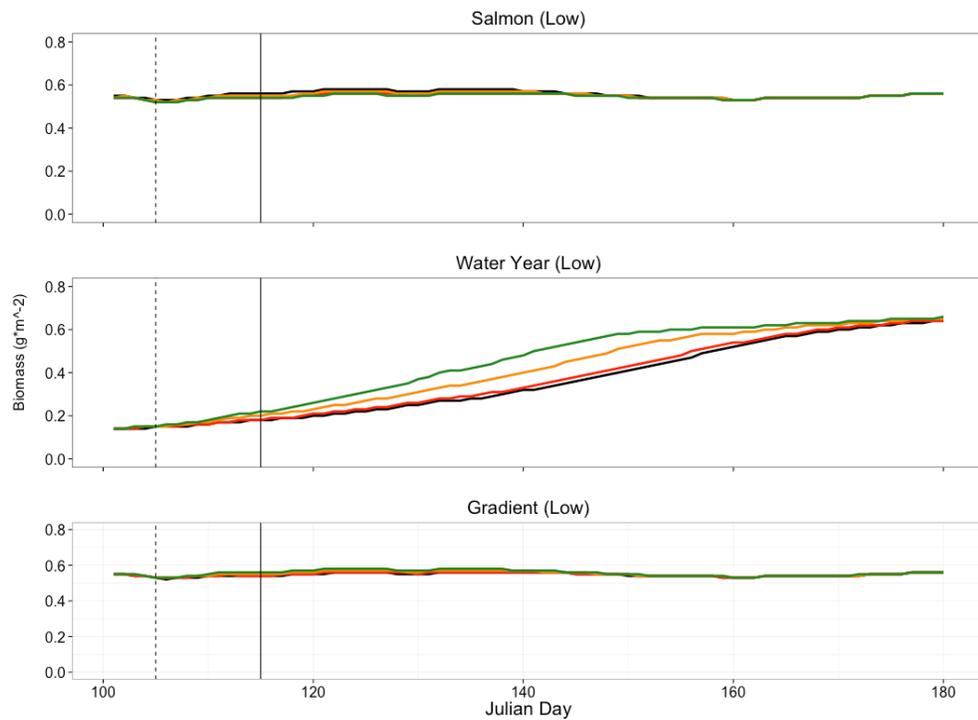
Figure 3.3 -- Periphyton biomass response during the proximate period of lamprey spawning under low scenarios for salmon run size, water year, and gradient. Dashed and solid lines represent mean time of lamprey entry to system and spawning respectively. Density: Black = no lamprey; red = low; yellow = medium; green = high.
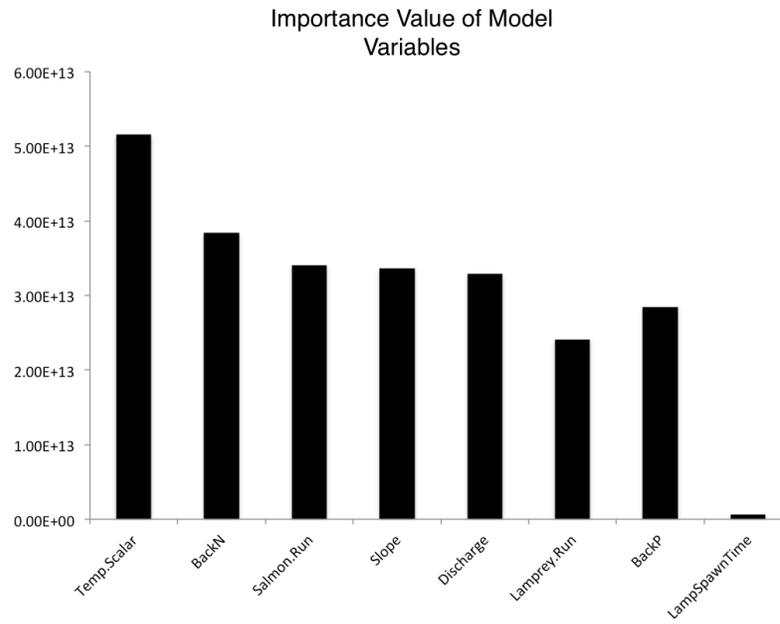
Figure 3.4 – Results of a global sensitivity analysis of model parameters. Scale on y-axis is arbitrary.

Chapter 4: Spatial Dynamics of the Post-Spawn Fate of an Anadromous Fish and Implications for Stream and Riparian Food Webs

Matthew R. Dunkle[1], Christopher C. Caudill[1], Ralph T. Lampman[2], Aaron Jackson[3], Brian J. McIlraith[4]

[1]Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho 83844

[2]Pacific Lamprey Project, Yakama Nation Fisheries, Toppenish, Washington 98948

[3]Department of Natural Resources, Confederated Tribes of the Umatilla Indian Reservation, Pendleton, Oregon 97801

[4]Pacific Lamprey Project, Columbia River Intertribal Fish Commission, Portland, Oregon 97232

Abstract

Anadromous fish import marine-derived nutrients (MDN) to relatively low productivity freshwaters during spawning migrations. Many studies have explored the role of post-spawn fish in stream food webs, but few have explored how carcasses are naturally distributed within stream channels and none have quantified the distribution of post-spawn Pacific lamprey carcasses in streams or the rates of transport into the riparian zone. We radio-tagged and released 144 mature Pacific lampreys as part of a restoration translocation program and tracked their spawning and post-spawn movements in two streams within the historical spawning range of the species. Carcass fates were determined by identifying macrohabitat type at the point of final radio-tag detection during the post-spawn period. Between 25-50% of carcasses were removed to the riparian zone immediately adjacent to spawning streams, but most remained within the wetted width to decompose. We used logistic regression models to evaluate the relative importance of habitat variables associated with carcasses fate and found depth was positively associated with carcasses remaining in stream to decompose, whereas higher water velocity, shallower water, and larger bed substrate were associated with carcasses being removed to the riparian zone. These patterns likely reflect the ability of riparian scavengers (e.g. great blue herons, *Ardea herodius*; raccoons, *Pyrocon lotor*) to detect and remove carcasses from streams. These results

demonstrate that the spatial distribution of post-spawn carcasses mediates how resources enter and are processed by stream and riparian food webs and suggests the influence of seasonal pulses of MDN from spawning anadromous fishes on biota is dependent on ecological and geomorphological contexts. Knowledge of the fate and resource distribution of MDN within riversacapes is needed to guide future restoration decisions and to restore the natural timing and spatial distribution of marine-derived resources to anadromous streams.

Introduction

Food webs are complex and variable in space and time (Polis and Strong, 1996). Aquatic food webs in temperate latitudes are particularly dynamic due to seasonal fluctuations in community assemblage, temperature, and productivity, meaning that both consumers and resources may be present with specific phenologies (Shurin et al. 2006). Migratory species within these systems can be drivers of food web processes as consumers, resources, or both, and may provide predictable pulses of energy or disturbance across ecotones (Lundberg and Moberg 2003). Human effects on riverscape connectivity, animal migration, and species' life history expressions have altered and often simplified resource pulses in form, scale, and timing.

Long-distance migratory species may connect distant ecosystems with distinctly different community assembly and productivity through the transport of resource subsidies (Polis et al. 1997). A premier example of such a subsidy is the carcasses of post-spawn anadromous fish, which link low-productivity freshwaters with relatively high-productivity marine environments (Naiman et al. 2002, Janetski et al. 2009). Carcasses have been found to increase food web productivity through direct consumption by fishes or invertebrates (Collins et al. 2016) or through assimilation of nutrients by benthic periphyton or microbes (Bilby et al. 1998).

The community response to subsidies is context-dependent because only certain species may access a resource under specific conditions and the system response may be limited by resources already in the system (Marczak et al. 2007 Chapter 3). Contexts mediating efficient resource use include the form of the resource (e.g. dissolved nutrients or fish tissue; Tiegs et al. 2011; Chapter 2), the phenology of the resource relative to consumer life history (e.g. gape limitation in salmon egg consumption; Armstrong et al. 2010), and the fate of the resource (e.g. drifting in open channel, settling in slack water, or stranding on bank, or transport to riparian/terrestrial habitats).

The role of anadromous fish carcasses in stream food webs will, by necessity, depend on the location of carcass decomposition. Physical fate of post-spawn carcasses is likely controlled by an interplay between hydraulic conditions and the presence and ability of riparian scavengers to detect and remove carcasses from the stream (Willson and Halupka

1995). For carcasses that remain instream to decompose, the rate of decomposition and pathways for energetic uptake will depend on both physical conditions and consumers present at the location of decomposition. Importantly, responses may differ across trophic levels depending on the entry pathway(s) of the subsidy to the recipient food web. Higher trophic levels (i.e. 'tertiary' consumers such as most fishes) may be affected by increased primary productivity, increased secondary productivity via direct consumption of carcasses, and/or MDN recycling. Thus, the phenologic, hydrologic, thermal, and habitat context at the site of decomposition are expected to have strong effects on uptake pathway and local- and system-scale responses.

Twelve species of anadromous fish are found in Western North America. Many are semelparous salmonids (*Oncorhynchus sp.*) that undergo spawning migrations throughout the year, but spawn in the autumn or winter months. Salmon subsidies may be large in biomass, but largely spawn at a time when stream metabolic activity is declining in the fall and well before winter and spring periods of high discharge, both of which may limit uptake and retention of resources. Many of these systems also support spawning of anadromous Pacific lampreys (*Entosphenus tridentatus*), which undergo similar migrations, but spawn in early summer, when discharge is decreasing and metabolic activity is increasing. Distribution and abundance of Pacific lamprey adult returns has declined throughout much of their historic range due largely to human constraints on migration (Close et al. 2002). An adaptation of an ecosystem productivity model suggested that lamprey subsidies are unlikely to have strong general effects on primary productivity in spawning streams, further emphasizing the need to understand uptake pathway and local-scale distribution and fate of carcasses (Chapter 3).

While many studies have evaluated the role of post-spawn salmon carcasses on riparian scavengers or how carcass-derived nutrients influence stream food web productivity, few have explicitly quantified the rate of removal of post-spawn carcasses of anadromous fish by riparian scavengers or used radio telemetry of spawning-phase fish to evaluate the final fate of carcasses in stream systems (see Cederholm et al. 1989, Garman 1992, Strobel et al. 2011). No studies to date have evaluated the fate of post-spawn Pacific lamprey in spawning streams. We chose to evaluate carcass fates in systems with few to zero natural returns and which receive fish translocated from lower in the basin to simultaneously

evaluate potential impacts of carcasses and to evaluate the effectiveness of the translocation protocols.

The spawning range of Pacific lamprey was likely similar to anadromous salmonids, but carcasses become available late-spring or early-summer. Biotic and abiotic conditions during this spawning window could result in relatively large proportions of carcasses remaining instream to decompose and those carcasses may have a relatively larger impact than salmon due to their potentially ecologically relevant timing. Throughout their historic range, lamprey run sizes have been limited, which reduces the scale of this subsidy, but provides a potential for restoration or management to recover lamprey-timed MDN in these systems, which could lead to greater system productivity with benefits for sympatric endangered salmonids.

The specific objectives of this study were to (1) monitor the distribution of post-spawn Pacific lamprey carcasses within two streams in the historical spawning range of the species using radio telemetry, (2) observe the rate of carcass removal from the wetted stream channel by downstream drift or riparian scavengers, and (3) to estimate specific physical context where carcasses decompose in stream versus conditions associated with removal to the riparian zone. We hypothesized that (1) lamprey carcasses would be distributed in specific microhabitats within a stream channel due to spawning site preference, post-spawn movements, hydrologic conditions, and the ability of riparian scavengers to detect and remove carcasses; (2) that a similar portion of lamprey carcasses would be removed by riparian scavengers in both streams because both locations had low lamprey density and relatively intact riparian communities expected to support similar scavenger communities; and (3) that instream carcasses would be retained in high-complexity areas due to pre-death behavioral decisions or post-death impingement of carcasses and the limitation of scavengers' ability to detect or access carcasses in these locations.

Methods

Study Sites

We studied spawning movements and post-spawn carcass fate in two streams representing spawning habitat in the Middle Columbia and Snake river basins of the interior Columbia River Basin (Fig. 4.1). Satus Creek (Washington, U.S.A.) is a third order stream (mean elevation of study reach: ~300 m, catchment area: 1585 km^2) that flows into the lower Yakima River. The watershed is predominantly sage-steppe dominated by sagebrush (*Artemesia* spp.) and grasses, with headwaters in a forest community composed of predominantly Ponderosa pine (*Pinus ponderosa*). Average precipitation (ca 20cm) occurs largely as snowfall in winter. The upper basin is undeveloped, but has a history of grazing and is entirely within the boundaries of the Yakama Indian Reservation. Headwaters are on the eastern slope of the Cascade Range and a portion of the watershed drains Mt. Adams, the second highest peak in Washington State. The lower valley is agricultural and is used for grazing, cultivation of hops (*Humulus lupulus*), and other row crops. The watershed above the main study reach experienced a small grassfire in July of 2015 ~1km from stream, but no ash or sediment runoff was observed in the creek during the sampling period.

Catherine Creek (Oregon, U.S.A.) is a second order tributary (mean elevation of study reach: 966m, catchment area: 813 km^2) of the upper Grande Ronde River and has its headwaters in the Southwestern Wallowa Mountain Range. The watershed is dominated by open grasslands and pine woodlands in the lower elevations and by dense pine forest in higher elevations. Average precipitation (ca 66 cm) also occurs largely as snowfall in winter months. The headwaters are protected by the Eagle Cap Wilderness Area in the Wallowa-Whitman National Forest. Active habitat restoration was conducted during the spawning window in a ~1km reach in the lower portions of Catherine Creek during the study.

Both Satus and Catherine Creeks are historic lamprey spawning streams as informed by traditional ecological knowledge and systems sites were chosen by the Yakama and CTUIR fisheries programs respectively for adult Pacific lamprey restoration in recent years based on the presence of suitable spawning and rearing habitat (R. Lampman and A. Jackson, unpub.). Daily discharge and temperature data for Satus Creek was obtained from the Yakama Nation Department of Natural Resources Hydrology Program and data for Catherine

Creek was obtained from Oregon Department of Water Resources and CTUIR Fisheries (Fig. 4.2, 4.3).

Lamprey Capture and Tagging

Lampreys used in this study were collected as part of a restoration translocation program conducted by the Yakama Nation and CTUIR Pacific lamprey projects. In both years, lampreys were collected during upstream migration as they passed through large hydroelectric facilities on the lower Columbia River (Bonneville, The Dalles, and John Day dams) in July and August using a combination of box and tube traps (Ward et al., 2012). After collection, adults were transported to either the Yakama Tribal Fish Hatchery in Prosser, WA (2015) or Threemile Dam and, subsequently, the Minthorn Springs Fish Facility, Umatilla Co., OR (2016), where they were held in fiberglass or plastic flow-through holding tanks until maturation in late spring (ca 9 mo.) the following year. Lampreys bound for Satus Creek were tagged on April 19th-20th, 2015 and those bound for Catherine Creek were tagged on May 12th-13th, 2016.

We anesthetized lampreys using a buffered eugenol solution (est. 10 ppm), determined sex, measured length, girth, and dorsal distance, weighed to the nearest gram, and surgically implanted with a uniquely coded radio transponder (21mm x 6mm, Lotek Wireless, Newmarket, Canada) using methods approved by the University of Idaho Animal Care and Use Committee (Protocol 2015-17) and described in detail by Johnson and colleagues (2012). In 2015, lampreys were held under observation for 4 weeks prior to release. On May 25, 2015, lampreys were released into Satus Creek at rkm 30 (Fig 4.1) and tracked for 10 weeks. In 2016, only male lampreys were tagged to limit potential for female mortality and loss of eggs in the translocation sample. Fish were allowed to recover for 4-6 hrs prior to release on the same day into Catherine Creek at rkm ~50 at Catherine Creek State Park, OR. Measurements of tagged lamprey are described in table 4.1.

Fixed-site and Mobile Tracking

Radio-tagged lampreys were tracked using two methods: 1) using weekly mobile radio telemetry surveys; and 2) using an array of fixed-site radio telemetry receivers. On Satus Creek, six fixed-site radio telemetry receivers were established at 5-10km intervals

encompassing the release location, the presumed spawning reach, the upstream extent of likely spawning habitat, and the downstream confluence with the Yakima River. In 2016, three fixed-site radio telemetry receivers were established on Catherine Creek encompassing the release location, the upstream extent of presumed spawning habitat, and downstream at the beginning of a heavily agricultural, low-gradient, lower valley section. Each receiver was connected to a three-element Yagi-type antenna oriented 90° to the stream. Fixed-sites were downloaded on a weekly basis.

Mobile surveys were conducted weekly from time of release until no new movements were detected (~July 1, 2015; ~July 15, 2016). Observers would move along the stream margin and visually inspect for spawning activity, nests, or living lamprey or carcasses. Observers carried a GPS-capable wireless VHF radio receiver with a low-range whip antenna (SRX600, Lotek Wireless, Newmarket, Canada). In both years, final carcass fates were determined by thoroughly surveying the reach containing active tags by two observers on foot after the window of peak spawning. In 2015, no new movements were detected by early July and final carcass fates were determined during a final survey July 8-9. On July 19-21, 2016, all spawning activity in Catherine Creek was assumed to be concluded and an extensive mobile survey was conducted to determine final fates of radio-tagged carcasses.

When a tag was detected, we lowered receiver gain and moved parallel and perpendicular to flow until the point of highest tag strength could be determined. If the highest tag strength was detected within the stream channel, we estimated the approximate tag location and assess whether a fish or carcass could be observed in that location with confidence and measured habitat conditions (Table 4.2). If the highest detection was on the bank, we used similar movements to identify the approximate tag location, measure the shortest distance to the wetted margin and created a transect perpendicular to stream flow. At each transect, we recorded the stream width, average depth (n = 3 in each location), measured substrate size (n = 3 randomly selected samples), and identified the dominant macrohabitat type.

Modeling Carcass Fate

We modeled carcass fate as a function of habitat covariates using binomial logistic regression, where final detection locations of tagged carcasses were treated as a binary response (*instream* = 1, *bank* = 0) in relation to four continuous variables: mean water velocity at 5 cm above the substrate, mean depth, mean substrate diameter, and, if present, mean wood diameter. This model used the following structure:

General Linear Model:

$$logit[p(instream)] = \beta_0 + \beta_1(Depth) + \beta_2(Wood) + \beta_3(Vel.) + \beta_4(Sub.) + \varepsilon$$

Where β_0 is the intercept and β_1 - β_4 are the coefficients for the main effects of standardized mean values of depth, wood diameter, velocity, and substrate diameter respectively. ε is the error term. Because we were most interested in the relative influence of all factors, predictor variables were converted to standard scores by subtracting the mean for each predictor divided by the standard deviation of that predictor from the observed value. Parameter estimates were obtained by weighted model-averaging of all subsets using the R package "MuMIn" (Bartoń 2015), whereby parameter estimates from each of the candidate models are multiplied by the model weight and summed. Parameter estimates are based on all models, not just models in which a given variable is found (Table 4.5).

Results

Tag Detections and Final Locations

Of the 65 tagged lampreys released in Satus Creek in 2015, 12% were not detected by mobile tracking or fixed site receivers (Table 4.3) and were assumed to be either defective tags or tags removed from a detectible range by avian or other scavengers prior to an initial detection. Conservatively excluding the undetectable tags, the remaining 57 (88%) were detected at least one time and 35 (54%) had a final fate determined, whereas 22 (34%) were assumed living at last detection because they were last detected before or during the spawning period. Of tagged lamprey with a final detection location determined, 40% of were in the riparian zone and 60% remained within the wetted stream channel. Of the tags last detected on the bank, all but two (one in Satus Creek, one in Catherine Creek) were found with no carcass material remaining.

Of the 79 tagged lampreys released into Catherine Creek in 2016, 4 (5%) were not detected by mobile tracking or fixed site receivers (Table 4.3) and were assumed to be either defective tags or carcasses removed from a detectible range by avian scavengers. An additional 4 (5%) tags were detected only at the lowermost fixed site in the first week after release and assumed to have left the system without spawning. The remaining 90% of tags were detected on at least one mobile survey, though the detection rate in weekly surveys declined from a high of 68%-72% in the first three weeks to a low of 44-45% in the last three weeks as carcasses left the system, were removed from detectable range, or tags ceased to function. Final surveys determined a fate of 30 (38%) of tagged fish, whereas 41 (52%) were assumed to be living at last detection. Eight radio-tagged lamprey were known to have been removed from the stream based on final tag detections and 22 were classified as remained in-river.

Carcass Distribution

For tagged lampreys with final tag fates determined, 60% and 73% were recovered within the wetted stream channel in Satus and Catherine Creeks, respectively. In both years, instream fates were associated with either physically complex macrohabitats containing debris dams, cutbanks, or boulders, or in depositional pools (Table 4.4; Fig. 4.4). At least 40% and 27% of tags in Satus and Catherine Creeks were removed to the riparian zone and were generally detected within 3m of the wetted margin adjacent to relatively low-complexity riffle and run macrohabitats. On average, instream tags were found in deeper water than the conditions adjacent to bank tags (Fig 4.5).

Modelling of Likelihood of Remaining Instream to Decompose

All-subsets from the global logistic model resulted in a suite of 15 candidate models. Model-averaging of the full suite of candidate models revealed that depth and substrate diameter have the strongest association with fate (Table 4.5). Mean depth had a positive effect on instream fate and was found in half of the suite of models and in all top models (Fig. 4.6). Mean substrate diameter was found in two of three top models and had a negative effect on fate. Mean velocity was found in one of three top models and had a negative effect on carcass fate. Mean wood diameter was a weakly positive predictor of carcass fate and was not found in any of the top models.

Discussion

We documented the spatial distribution of post-spawn Pacific lamprey carcasses in spawning streams and found that between 30-50% of carcasses were removed to the terrestrial zone by riparian scavengers, whereas more than half remained instream to decompose. Carcasses remaining within the wetted stream width were predominantly found in areas associated with deeper, slower, and more complex areas, whereas carcasses removed to the bank were adjacent to relatively shallower, faster, and lower complexity areas. These findings show that the distribution of resource subsidies from spawning anadromous fish in streams are non-randomly distributed within streams or riparian areas and suggest MDN pathways and ecosystem roles are mediated by both fine-scale features, such as depth and velocity which distribute carcasses, as well as larger-scale features such as macrohabitat type, which influence transport across the stream-riparian boundary.

The study of Pacific lamprey MDN presents a unique challenge for observing carcass decomposition because lamprey returns to much of their range are at a fraction of historic estimates (Close et al. 2002), and because carcasses rapidly decompose or are removed by scavengers. Scavenging rates presented here represent those for a rare species at translocation densities. Our estimation of scavenging rates are biased conservatively, as carcasses with no final detection location resulted from either an uncommon tag malfunction or the removal of the carcass from a detectable range in the terrestrial zone. In 2015, measurements were not taken on a small number (~6) tags detected early in the spawning period that were not detected again. In 2016, higher flows limited our ability to conduct extensive on-foot surveys during the early weeks of spawning.

As we hypothesized, post-spawn carcasses remaining instream were distributed in specific macrohabitats and were found under certain specific conditions. Carcasses were found in a diversity of habitat types, but predominantly in either depositional pools or in areas with retaining features. Depositional habitats are defined by fine substrate, low water velocity, and relatively greater depth and represent areas where drifting carcasses may settle out of the water column. Additionally, many lamprey nests were observed either at the head or tail of pools and could reflect post-spawn behavioral decisions of senescent fish. High complexity features observed retaining carcasses included debris dams, which were observed

entangling and potentially camouflaging carcasses, boulders, which impinged carcasses on the upstream side or allowed carcasses to settle in eddies on the downstream side, and cutbanks, which often contained exposed roots. The role of carcasses in stream food webs is likely different depending on the fine-scale conditions at the site of decomposition, as certain taxa may be unable to access a resource in a high-velocity cutbank, but readily able to colonize a carcass in a slack water pool.

To qualitatively assess the scavenger community present in one of our study streams, a small number of carcasses were placed by hand in open riffle and run habitats observed for 48h using motion-triggered cameras. Cameras recorded at least six unique species, including whitetail deer (*Odocoileus virginianus*), common merganser (*Mergus merganser*), river otter (*Lontra canadensis*), and beaver (*Castor canadensis*), but only great blue heron (*Ardea herodias*) and raccoon (*Procyon lotor*) were observed removing or consuming carcasses. We also observed signs of black bears (*Ursus americanus*) and bobcats (*Lynx rufus*) during surveys, but these were not recorded by camera traps. Raccoon events occurred during both day and night; heron events occurred only during the day. Carcasses were removed predominantly within 24h, but one was removed after ~36hs and one was removed after <1h. It is possible that other avian scavengers in the area removed tags beyond a detectable distance and were undetected by camera traps, as one tagged carcass was found in the riparian zone with avian claw marks around the body (M. Dunkle, *personal observation*).

Our instream carcass findings parallel the results of other studies which evaluated artificially placed fish carcasses in streams. Strobel et al., (2011) reported that most radio-tagged salmon carcasses placed in streams in Northwest Oregon were entrained by wood and boulders, or settled in depositional pools. Garman (1992) found that although most radio-tagged herring carcasses released in a river in Virginia were washed out of the system by normal flows, the few which remained in the spawning reach were retained by boulders. Both studies reported that most carcasses moving consistently during decomposition attributed to discharge, but their observations could be due to seasonality. Carcasses in Pacific Northwest rivers during fall and winter may be subject to high discharge events. We saw little evidence of instream carcass movement during our study periods and only 5 fish were detected moving out of the spawning reach in Catherine Creek. Our findings may be specific to carcass

subsidies entering streams near the onset of base-flow conditions, whereas carcasses of other fall-spawning anadromous species may move longer distances downstream after death. Similarly, iteroparous species may largely move out of spawning reaches prior to death and consumption, even in populations with very low iteroparity rates such as steelhead of the interior Columbia Basin where iteroparity rates are <3% (Keefer et al. *In Review*).

We observed that at least 30-50% of carcasses were removed to the terrestrial zone and were found exclusively adjacent to riffle and run habitat types. These areas were defined by relatively low depth, moderate substrate, and faster water velocity, but also were observed to be less physically complex and more open, suggesting that carcasses in these areas are readily detected and accessed by riparian scavengers. Other studies have shown a similar proportion of post-spawn fish carcass removal, even in dense spawning aggregations. For example, Gende et al., (2004) observed that bears removed ~50% of spawning Coho in small streams in Southeast Alaska. Similarly, Cederholm and others (1989) observed the fate of carcasses artificially placed in streams on the Olympic Peninsula and found that between 27-90% of carcasses were removed to the riparian zone. Although these studies did not report stream conditions adjacent to carcass removal, our findings suggest that salmon carcasses removed by bears in those systems may come more from open riffle and run areas than deeper, more complex habitats within spawning streams. Thus, landscape position and physical characteristics of reaches likely render some areas more 'porous' to transport of carcasses to the riparian zone than others. For example, it may be more challenging for scavengers to access carcasses of species spawning in large, deep rivers and lakes than small, shallow streams.

Together, the results of our study suggest that post-spawn carcasses from anadromous fish represent a spatially-explicit resource subsidy in spawning streams and riparian zones and that the carcasses of summer-spawning species may be more efficiently retained by stream ecosystems due to low flow conditions. Spatial distribution of carcasses is likely a strong mediator of carcass decomposition and food web uptake because stream ecosystems are a dynamic mosaic of microhabitats, communities, and resources. While many studies have explored the role of salmon carcasses in stream food webs (Janetski et al. 2009), relatively few have assessed the natural distribution of carcasses in spawning streams despite

a growing popularity of supplementing MDN in historic spawning streams using artificial carcass analogue pellets (Pearsons et al. 2011, Kohler et al. 2012, Collins et al. 2016).

Multiple species historically subsidized Pacific Rim spawning streams, but many have currently have reduced spawning adult run size, life history diversity, or access to historic spawning habitat. Pacific lamprey historically had a spawning distribution similar reaches to anadromous salmonids, but spawn in late-spring/early-summer, which may lead to greater retention in spawning streams as well as result in relatively large food web responses relative to lamprey biomass. Run sizes are now at a fraction of historic estimates, limiting the scale of this resource subsidy and suggesting potential restoration of summer-timed MDN could support greater system productivity and a lessoning of density-dependent growth and mortality of sympatric endangered salmonids. It is critical that future studies of MDN supplementation effects on food webs mimic natural forms, timings, and distributions of resources within a stream network, as these factors may influence how systems will respond and can lead to disparity between observational and experimental studies.

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Tables and Figures

Table 4.1 – Summary table of lamprey tagged and released in 2015-2016.

	Satus Creek 2015	**Catherine Creek 2016**
Length (mm)	603.92 ± 38.55	540.63 ± 66.95
Weight (g)	377.62 ± 59.94	357.85 ± 71.28
Girth (cm)	103.4 ± 5.8	10.38 ± 9.0
Dorsal Distance (cm)	28.6 ± 5.0	55.8 ± 4.1
Sex Ratio (M:F)	(31:36)	(79: 0)
Percent Tagged of Total Fish Released in System For that Year	32%	47%

Table 4.2 – Description of variables measured around highest instream detection or along each transect adjacent to highest bank detection for lamprey recovered in 2015 and 2016.

Variable	Unit	Description
Depth	(cm)	Average of three randomly taken depth measurements around site of highest tag detection (in-stream detections) or of a transect in stream adjacent to detection (bank detections)
Substrate Diameter	(cm)	Average diameter of three randomly selected bed substrates at site of highest tag detection or adjacent stream transect
Flow	(m/s)	Average measurement of water velocity at stream bed
Wood Diameter	(cm)	Average diameter of woody debris at site of highest tag detection or along adjacent transect

Table 4.3 – Summary of tag detections in both study systems. *Note that only males were tagged in 2016.

	Satus Creek 2015	Catherine Creek 2016
	N = 65	**N = 79***
No Detections	8 (~12%)	4 (~5%)
Detected only at lowest fixed-site	0 (0%)	4 (~5%)
Detected at least once	57 (~88%)	71 (~90%)
Assumed living at last detection	*22 (~34%)*	*41 (~52%)*
Final Detection on Bank	*21 (~36.8%)*	*22 (~31.0%)*
Final Detection in Riparian Zone	*14 (~24.5%)*	*8 (~11.3%)*

Table 4.4 – Summary of macrohabitat distribution of carcasses with a final fate determined and measurements taken (excludes fish assumed living at last detection).

| | Satus Creek 2015 *(54% Recovered)* | | | | Catherine Creek 2016 *(38% Recovered)* | | | |
	In Stream		Bank		In Stream		Bank	
Boulder	3	*(14%)*	0	---	6	*(27%)*	0	---
Cutbank	2	*(9%)*	0	---	2	*(9%)*	0	---
Debris Dam	6	*(29%)*	0	---	7	*(32%)*	0	---
Pool	7	*(33%)*	1	*(7%)*	5	*(23%)*	2	*(25%)*
Riffle/Run	3	*(14%)*	13	*(93%)*	2	*(9%)*	6	*(75%)*
Total	21	*(60%)*	14	*(40%)*	22	*(73%)*	8	*(27%)*

Table 4.5 – Coefficient estimation from logistic modeling of carcass fate for the standardized mean values of depth, substrate diameter, velocity, and wood diameter obtained from all-subsets weighted model-averaging. Importance denotes the relative importance of each parameter in determining the probability of a carcass remaining instream.

	(Int.)	MDepth(st)	MSubstrate(st)	MVelocity(st)	MWood(st)
Importance		0.8	0.69	0.46	0.20
Percent of All Models Parameter Found In		47%	47%	40%	27%
Percent of Models with AICc ≤ 2.00		100%	67%	33%	0%
Parameter Estimate	-0.4912	0.2913	-0.2135	0.1133	0.0042
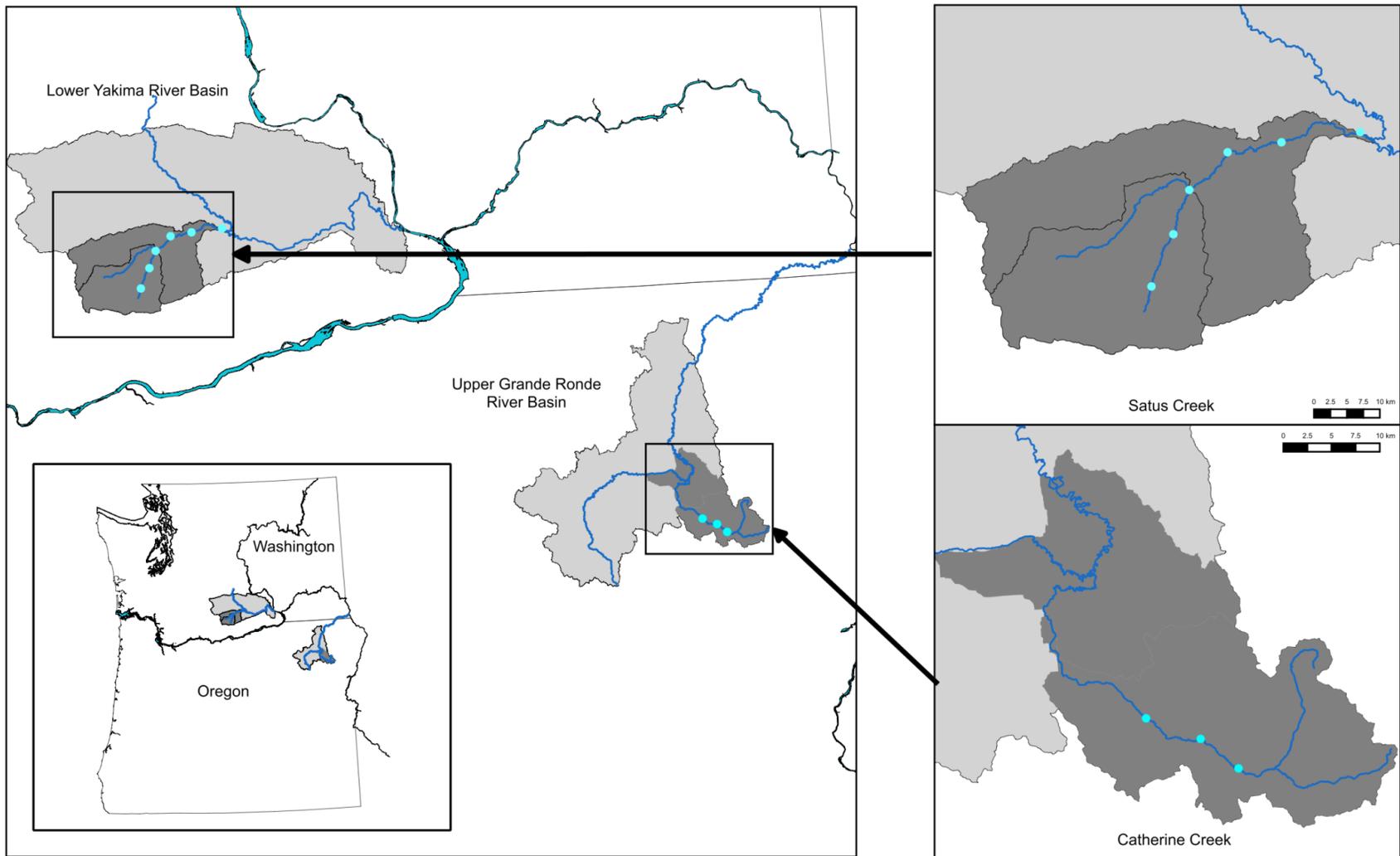
Figure 4.1 – Map of study locations in lower Yakima River Basin (Satus Creek) and upper Grande Ronde Basin (Catherine Creek). Location of fixed-site receivers are noted with points.
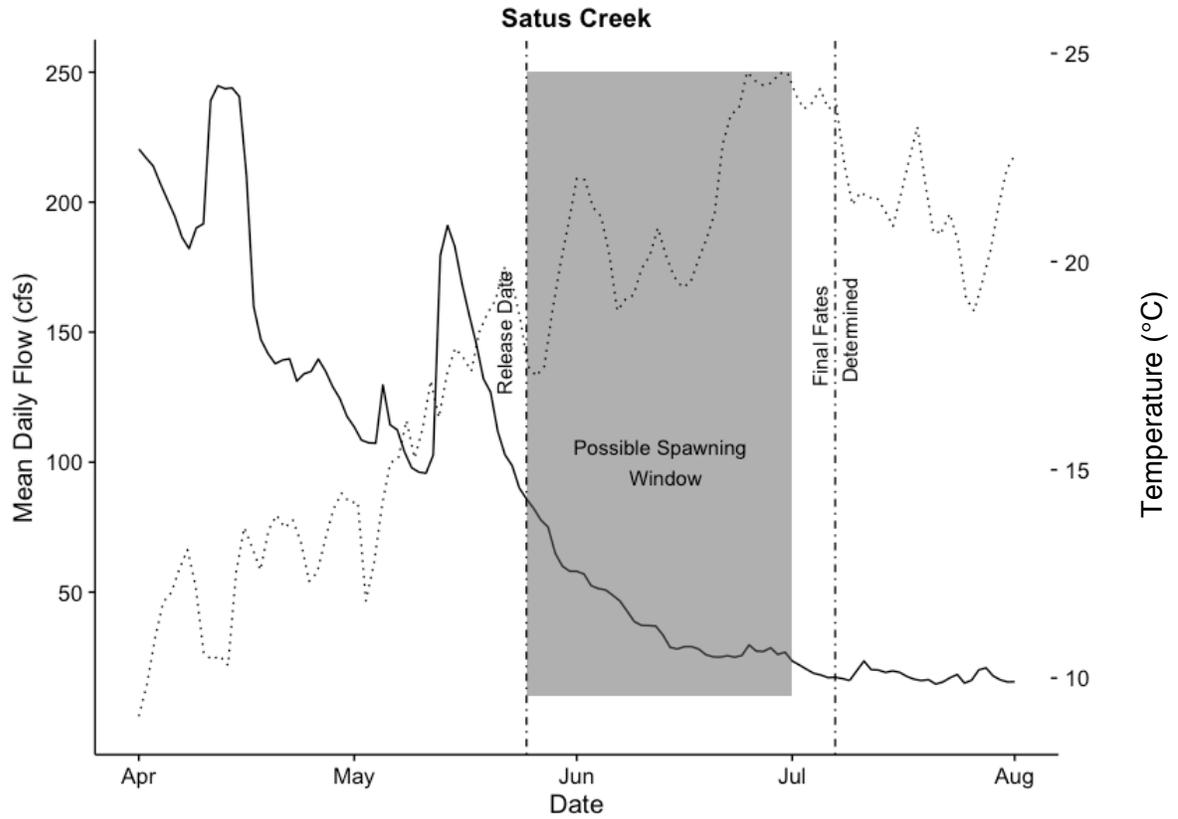
Figure 4.2 – Streamflow (solid line) and temperature (dotted line) of Satus Creek during study period. Release date, period of tag movement, and date of final fate determination are marked.
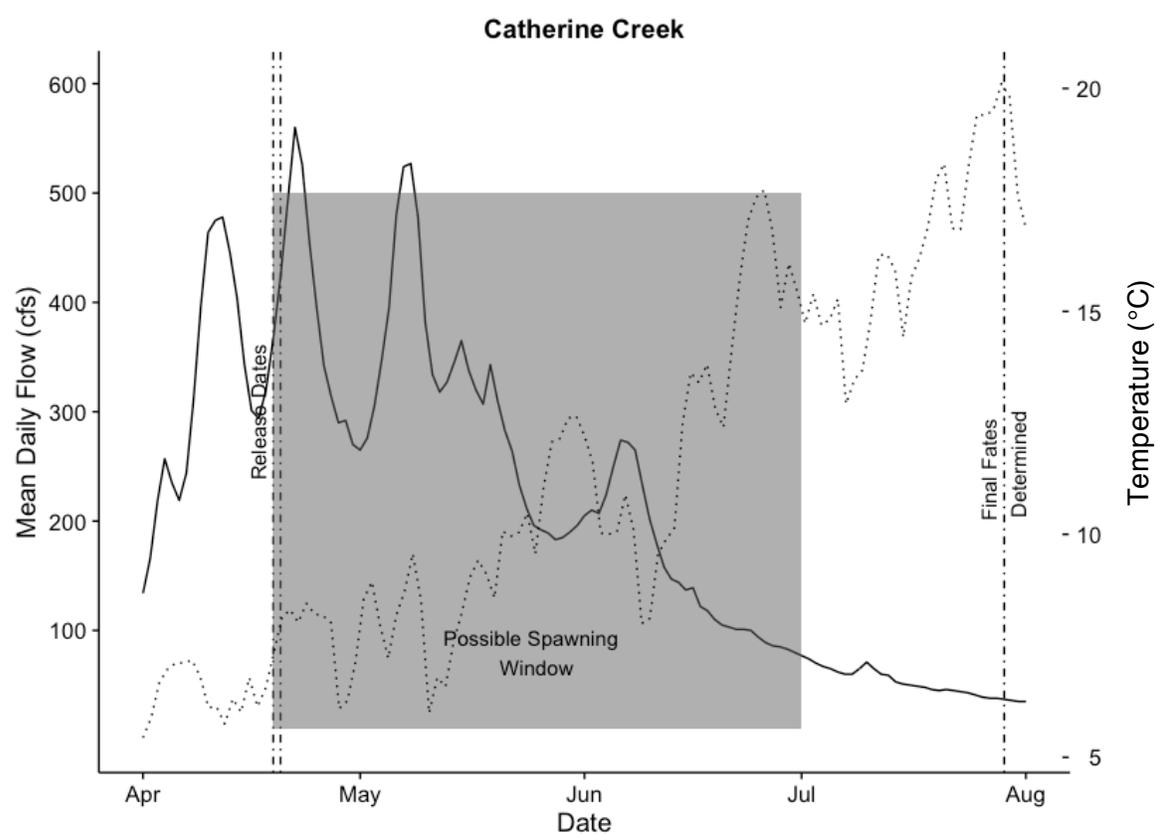
Figure 4.3 – Streamflow (solid line) and temperature (dotted line) of Catherine Creek during study period. Release dates, period of tag movement, and date of final fate determination are marked.
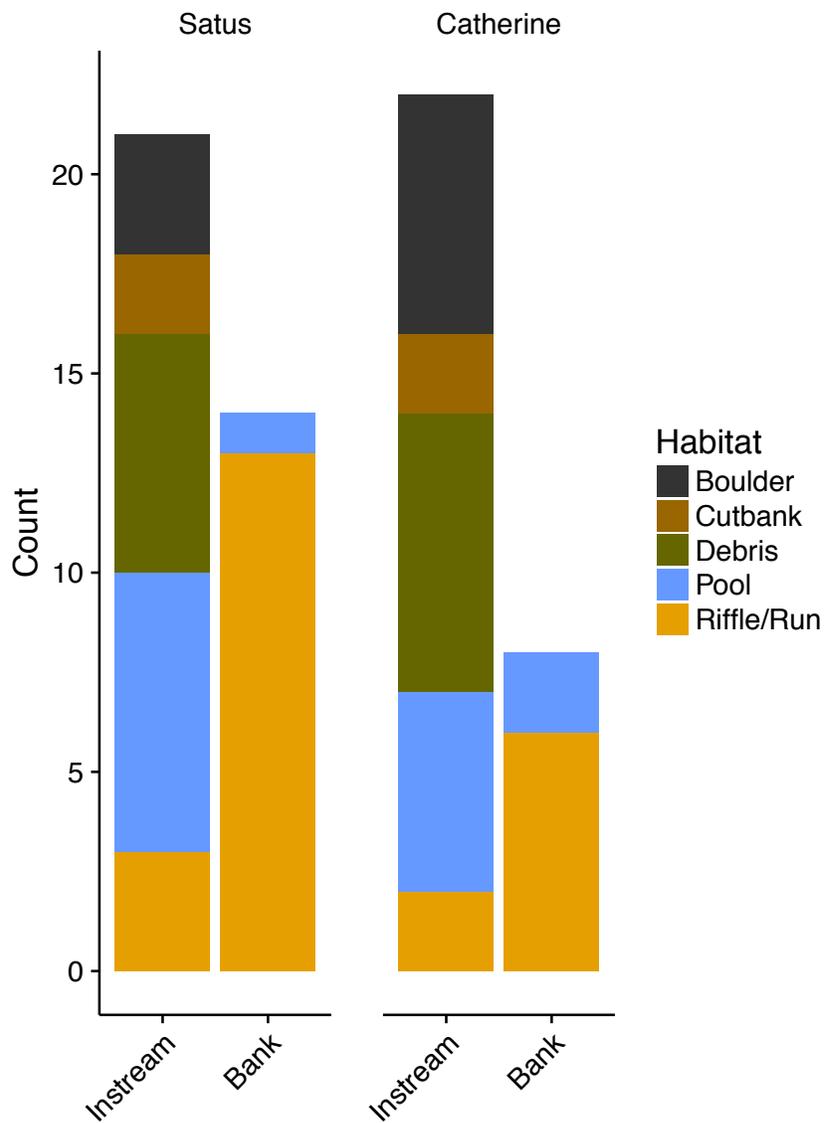
Figure 4.4 – Macrohabitat distribution of carcasses in Satus Creek (2015) and Catherine Creek (2016).
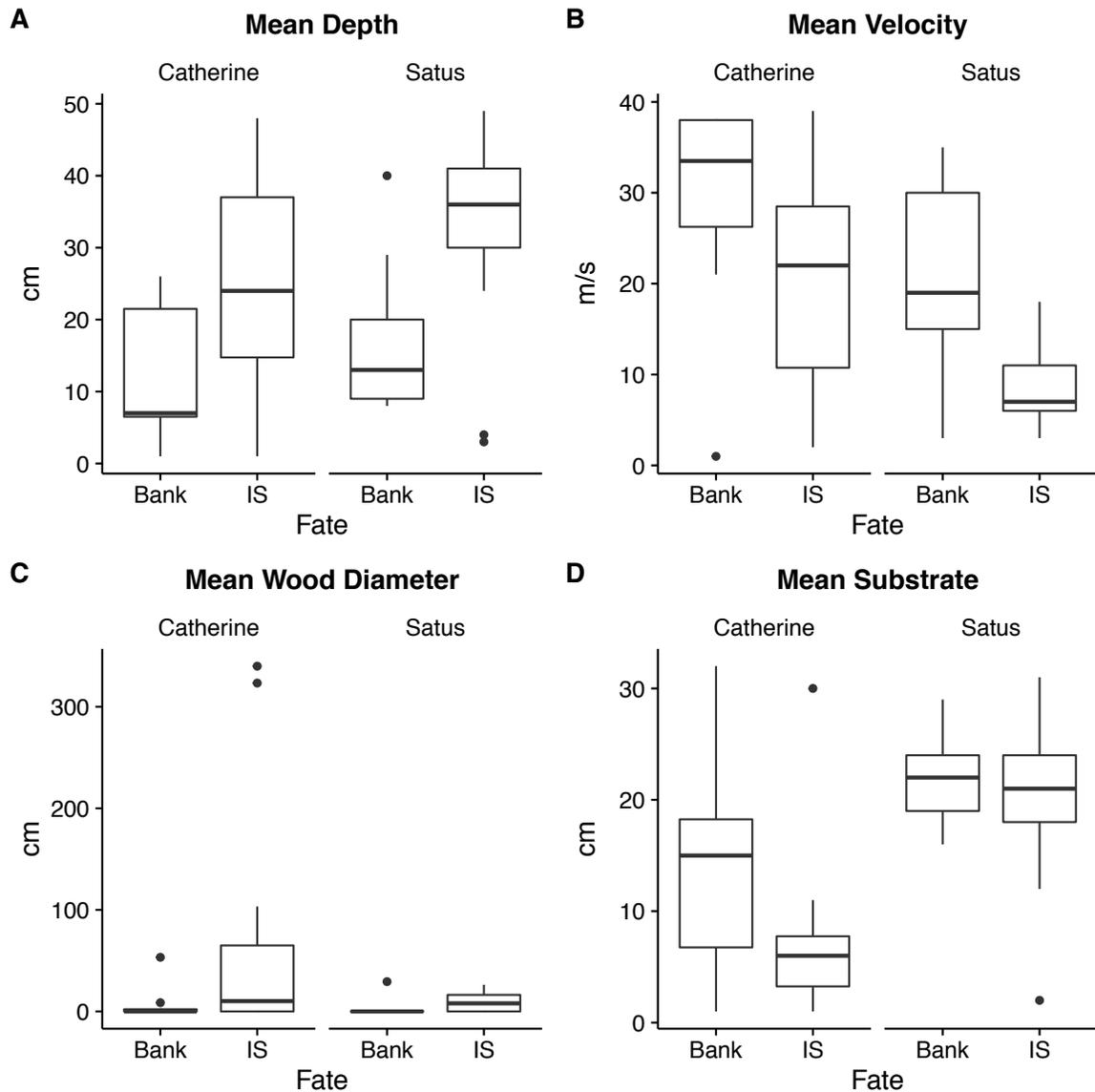
Figure 4.5 – Quantitative habitat variables measured for recovered lamprey carcasses: (A) Mean Depth, (B) Mean Benthic Velocity, (C) Mean Wood Diameter, and (D) Mean Substrate Diameter. Instream (IS) carcass measurements represent conditions at highest detection site; bank carcass measurements represent conditions adjacent to highest tag detection.
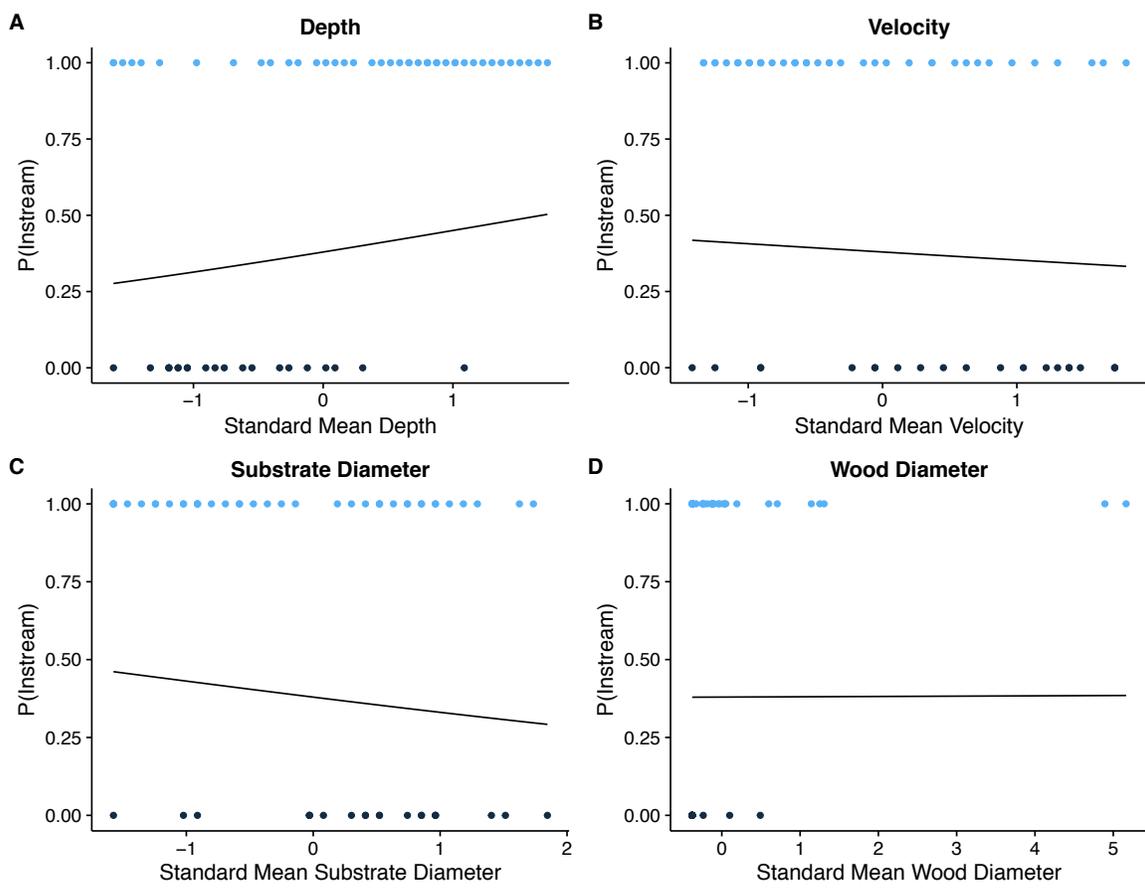
Figure 4.6 – Probability plots for variation in model parameters. For each plot, all other variables were held at their average. P(instream) = 1 suggests all carcasses under those conditions will remain instream to decompose; P(instream) = 0 reflects conditions where all carcasses would be removed to the riparian zone.
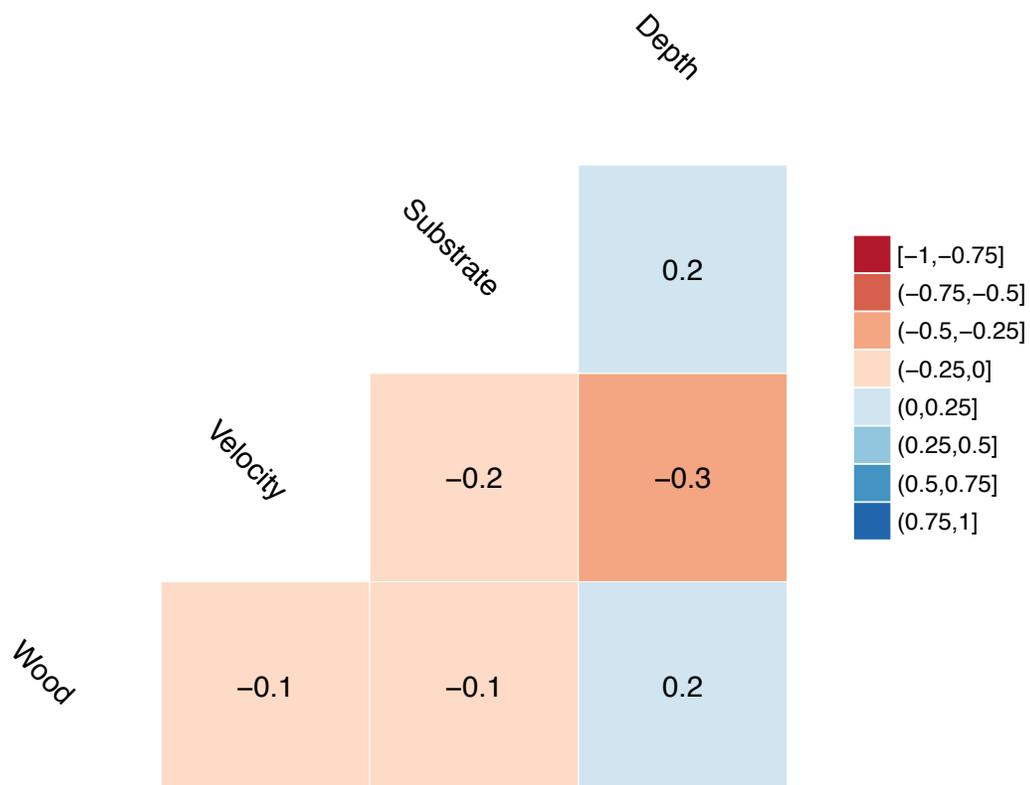
Figure 4.7 – Correlation matrix for variables included in the global model. Note that these variables represent the standardized mean values and that no two variables are more than moderately correlated.

Chapter 5: Addition of An Apparent Resource Hotspot Reduced Movement, but Did Not Increase Growth in a Stream Fish

Matthew R. Dunkle and Christopher C. Caudill

Department of Fish and Wildlife Sciences, University of Idaho

Moscow, Idaho 83844 USA

Abstract

Many species experience growth and survival bottlenecks in early life. Juvenile Pacific salmon (*Oncorhynchus spp.*) in temperate streams face a bottleneck in early summer after emergence due to limitations in space and food resources. Carcasses of semelparous anadromous fish species with predictable spawning phenologies provide direct and indirect resources that may influence juvenile salmon growth, behavior, and movement. We tested whether a carcass subsidy from a historically widespread summer-spawning species, Pacific lamprey (*Entosphenus tridentatus*), could increase sub-yearling chinook salmon (*O. tshawytscha*) growth and density while decreasing intraspecific aggression and emigration in experimental mesocosms representing pool habitats. Pools received one carcass or were held as controls and salmon were stocked at a relatively high initial density. We tracked growth, behavior, and emigration for four weeks and observed little evidence of direct consumption of carcasses. Contrary to our expectations, we found that salmon in the carcass addition treatment did not exhibit a growth response or a strong increase in territoriality, but did express a higher holding density and lower emigration rate. This suggests that indirect responses of consumers to ambient resources may have measurable effects on holding density, even if there are weak responses in growth or body condition. The weak growth response by salmon to an apparent high-quality subsidy we observed does not reflect the findings of previous studies reporting the effect of salmon carcasses and may be related to differences in carcass chemistry, toughness of carcass integument, or alternative food web pathways for lamprey-derived nutrients. Understanding the role of resource form and phenology in fine-scale resource constraints can improve conservation of species experiencing density-dependence in early life history stages.

Introduction

The patterns and processes by which ecosystems support a diversity of species and life histories is of central interest to ecologists. Food web dynamics and movement processes both have strong effects and are mediated by at several scales by resource availability from multiple sources (e.g. terrestrial inputs, headwater subsidies, local production, and subsidies from mobile species). Migratory organisms are defined by predictable movements between disparate ecosystems and transport of nutrients and energy across ecotones may represent a resource pool with specific phenology to which communities may adapt (Lundberg and Moberg 2003). When predictably-timed resource pulses from migratory species are lost, ecosystems may support lower diversity of species and smaller population sizes, prompting conservation challenges. A well-known example is the post-spawn carcasses of salmon and other anadromous fishes, which deliver high-density energy and nutrient resources from marine systems, and affect nutrient dynamics and status of freshwater systems at multiple spatial and temporal scales (Janetski et al. 2009).

Importantly, the response to such inputs also depends on the behavioral and life history traits of consumers in the recipient system. Population dynamics are often mediated by an interplay of extrinsic habitat conditions and intrinsic individual behaviors. The presence of high quality resources in habitat patches can alter individual growth and behavior in the immediate vicinity. Localized patches of high-quality resources may scale up to influence system-wide carrying capacity when consumers are mobile and can track fluctuating resource pools. Early life history consumers, however, may be limited in their ability to track resources in complex landscapes because of limits on movement and ability related to size or social status. Reduced growth, lower survival, or density-dependent emigration may result.

Individual behavior and social dynamics can alter expression of different strategies and influence population trends. In widely dispersing species, plasticity may be expressed in the tendency to emigrate from one habitat patch to another. A prime example of highly mobile species with plastic life histories is found in the genus of Pacific salmonids, *Oncorynchus*, which may express resident, adfluvial, or anadromous life histories throughout

their range in response to, in part, drivers such as resource availability, intraspecific interactions, and individual body condition (Quinn 2005).

Early life history salmonids are often found at high densities following emergence and experience a density dependent bottleneck during this period, resulting in limitations of fine-scale carrying capacity, individual growth rates, and alterations to social hierarchies as feeding territories are established (Quinn 2005). Early summer is also a period of limited resource availability in salmonid rearing streams generally, as spring runoff declines into baseflow and temperature, metabolism, and emergent insects increase. If resource subsidies during this period are limited, juvenile salmonids may experience fine-scale density dependence at stronger-than-historic levels, resulting in population-wide limitations in system carrying capacity and growth rates. Further, movements and growth of subyearling salmonids have been found to respond to density and extrinsic habitat conditions, even during periods of relatively higher food availability in late summer or early fall (Myrvold and Kennedy 2016), and the decision to move downstream from headwater rearing habitats is not necessarily lethal and may in fact be adaptive (Copeland et al. 2014, Bourret et al. 2016).

The carcasses of post-spawn anadromous fishes, particularly semelparous species, have been shown to be an important resource subsidy under certain circumstances (Bilby et al. 1996, Gende et al. 2004). Janetski and colleagues (2009) found that across 37 studies from 79 streams, carcasses from adult salmon have a positive, but variable effect throughout food webs. Carcasses may increase stream productivity and juvenile salmon growth through direct and indirect pathways, but few studies have reported the fine-scale intraspecific social responses of consumers to the presence of a carcass resource or how these resources may indirectly influence consumer densities.

The phenology of resource availability has strong effects on behavior, life history, and population ecology. Relatively little research has evaluated juvenile salmon response to carcasses from species with spawn phenologies outside the fall-spawning period typical of Pacific salmonids. The freshwater distribution of Pacific salmon and steelhead overlaps and was likely influenced carcasses of post-spawn anadromous Pacific lampreys in early summer.

Previous work has found that most lamprey carcasses, even in low run-size conditions, remain instream to decompose and are distributed largely in depositional areas within stream channels (*Chapter 4*). These depositional areas may also be important rearing areas for early-life history juvenile salmonids experiencing a fine-scale density bottleneck during this period (Quinn, 2005). Lamprey abundance in headwater streams has declined throughout their range (Close et al. 2002) and have been extirpated from many areas, particularly in interior streams. The decline or loss may influence juvenile salmonid behavior, emigration, and growth, and population-scale productivity.

We evaluated the role of post-spawn Pacific lamprey carcasses on the fine-scale emigration, behavior, and growth of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in an artificial stream mesocosm experiment. We hypothesized that the presence of lamprey carcasses 1) would decrease emigration rates by weakening resource limitations in habitat patches; 2) would increase aggressive behaviors in holding fish by creating a high-quality resource to be defended; 3) that emigrants would be of lower overall body condition relative to fish holding in channels; and 4) that fish holding in channels with a carcass would increase in both average individual weight and body condition compared with fish holding in channels without a carcass through the interplay of increased resources and aggressive behavior; 5) and/or that the total salmon biomass remaining in each mesocosm would be higher. Additionally, we tracked course changes in productivity within channels via measurement of periphyton standing biomass and the invertebrate community present in the mesocosm at the end of the experiment. We expected carcasses to increase periphyton biomass and invertebrate density and richness.

Methods

The mesocosms consisted of 10 flow-through aluminum channels 2.25m x .55m filled to a depth of 0.4m and held at a 1% slope (Fig. 5.1). Water was supplied from Minthorn Spring, a first order tributary of the Umatilla River (Oregon, USA), and pumped to a head tank before being gravity-fed to each channel at a constant rate of ~18 l/min. Temperature in the mesocosm tracked conditions in Minthorn Spring and varied between 12.8-15 °C (Fig. 5.2). We placed a bulkhead at the downstream end of each channel to regulate water depth in the channel and to create an "emigration trap" (*sensu* Keeley 2001, Sloat and Reeves 2014). Bulkheads had two 3.25 cm radius half-circle cutouts and emigration traps consisted of a 55 cm x 20 cm box with 10cm of water, maintained by a screened standpipe (Fig. 5.1). Water level in traps was 18 cm in emigration traps to limit movement of fish from the emigration trap back to the main channel. Substrate was added to a depth of ~5 cm and was locally-sourced gravel with an average diameter of 1-3 cm.

Each channel was randomly assigned to a treatment group, which received one post-spawn lamprey carcass, or a control group, which received a weighted and capped ~4.8 cm diameter PCV tube to simulate the physical structure of a lamprey carcass. Lamprey carcasses were obtained from an artificial propagation program conducted by the Yakama Nation Fisheries Pacific Lamprey Project. Lamprey were artificially spawned between April 25th and May 30th, 2016, and frozen until June 25th. Carcasses were thawed overnight in water sourced from Minthorn Spring prior to the experiment. Immediately before addition, we measured wet weight, noted lamprey sex, and photographed carcasses. Carcasses were gently removed from channels, weighed, photographed, and returned to the channel once per week.

We placed 40 juvenile hatchery-origin spring Chinook to each channel, creating an initial density of 0.03 salmon • m^{-2} (123.10 ± 5.38 g salmon • m^{-2}) on June 24th and allowed all fish to acclimate to the mesocosm for 48 hrs prior to the beginning of the experiment. Fish were sourced from the Oregon Department of Fish and Wildlife Umatilla Hatchery,

Hermiston, Oregon, USA. Chinook were spawned from adult salmon returning to the Umatilla River on August 17th - September 8th, 2015. Juvenile salmon were held in rearing ponds and fed an artificial feed from April 28th-June 23rd, 2016.

We evaluated growth rates through weekly collection, measurement, and photographing of fish holding in the mesocosm on days 6, 14, 21, and 28 of carcass decomposition. Fish that moved into emigration traps were removed each morning, euthanized, measured for length and weight, photographed, and stored in 95% ethanol. Emigration rates were analyzed using a Kaplan-Meier step-wise survival analysis using the packages "rms" and "ggfortify" in R (Harrell 2013, Horikoshi and Tang 2015). Growth was estimated as average weight or length by time and by using the average Fulton's body condition ($100,000 \cdot Mass \cdot Length^{-3}$) using generalized linear mixed models. Because individual fish were not marked, our sampling unit was each channel replicate and channel ID was treated as a random factor. For each response, a model including the effect of treatment, time (day of experiment), and the interaction was evaluated against a null model that only considered the effect of time. We separately evaluated each response variable for fish remaining in channels versus emigrants.

Intraspecific behavior was assessed from video observation obtained via underwater cameras (Sondecam HD, Fishsens Technology, Fairborn, OH, USA). Eight of the ten mesocosm tanks were chosen at random for observation. Cameras were suspended in the mesocosm channel ~10 cm from the substrate. Observations were focused on the upstream half to tank to capture lamprey carcasses and controls in field of view. Video was recorded for ~24hrs per day, but only usable during periods of daylight. Video was recorded from four channels each day and channels were observed every fourth day for a total of seven days of observation per channel over the course of the experiment. In the laboratory, we reviewed a five-minute subsample of each camera-day from 01300 - 01305 hrs, a period of high light and fish activity. We would record the number of fish in view at one minute intervals and score the number of feeding events and six common behaviors described in previous studies (Chapman 1962, Reimers 1968, Symons 1968, Berg and Northcote 1985). Behaviors included: chasing/charging, fin/gill flaring, hiding, nipping, flight, and redirected aggression.

The latter was defined as a subordinate in an aggressive interaction immediately becoming an aggressor in a subsequent act, presumably directed as an individual of lower social status. Data were analyzed using linear mixed effects models using the R package "lme4" (Bates et al. 2014). The role of treatment was assessed by comparing models predicting event rate by treatment, time, and a treatment over time interaction with a null model that only considered time using a Chi-square test at the $\alpha = 0.05$ level. As with growth data, channel ID was treated as a random effect. If a model containing treatment was significantly different than the null, the significance of model predictors was analyzed.

Drifting invertebrates entered the mesocosm at ambient rates. To supplement drifting and benthic invertebrates, samples collected from Minthorn Springs downstream of the mesocosm were added to the channels on days 2, 10, 19, and 25. Supplemental additions consisted of two 1hr drift samples taken at the heads of pools in Minthorn Spring after sunset and a kicknet sample from a roughly $15m^2$ riffle after sunrise. Samples were pooled and diluted to 18L. The pooled sample was swirled and each channel received two 500mL grab samples drawn and distributed in a random order. An additional six 500mL grab samples were taken at random, passed through a 500μ sieve, and stored in 95% ethanol for later analysis. Samples were sorted in the laboratory and identified to the lowest practical taxon. At the end of the experiment, all channels were thoroughly flushed through a 500μ screen and each full-channel sample was stored in 95% ethanol for later analysis.

At the start of the experiment, each channel received four 10cm x 10cm unglazed clay tiles to track biofilm (including periphyton) accrual. Two tiles were placed in the center of the channel and two were placed near the bulkhead at the downstream end of the channel. One mid-channel and one downstream tile was selected at random and removed from each channel on days 14 and 28, wrapped in aluminum foil, placed in a zip-lock bag, and frozen for later analysis. In the laboratory, tiles were scrubbed and passed onto a pre-ashed glass fiber filter and dried at 70°C to constant weight. Samples were then weighed, ashed at 500°C for one hour, and weighed a second time to determine ash-free dry mass. Data were analyzed using one-way ANOVA.

Results

Carcasses (3 female and 2 male) had an average initial wet weight of 197.7 ± 19.5 g. Weekly measurements revealed an initial increase in weight of ~40% after one week as carcasses were colonized by a thick brown fungus before declining in weight to a final average of 187.7 ± 61.1 g (Fig. 5.8). Carcasses became soft over time, but the skin remained intact (Fig. 5.4) and little evidence of consumption of internal tissues was observed on carcasses or in video observations.

Consistent with our predictions, emigration rates were higher from control channels compared with channels containing a carcass (Kaplan-Meier survival model; p = 0.0262). Emigration rates evaluated using a Kaplan-Meier model revealed a significantly decreased rate of emigration by sub-yearling Chinook from patches containing a lamprey carcass versus control conditions (Fig. 5.5). After one week, carcass channels had lost ~5% of initial density, whereas control channels had lost ~10%. This trend began on day 3 and continued until day 23, when the density in carcass patches began to converge with those in control patches.

Treatment effects on traits of emigrants were less clear, with some evidence that salmon of lower condition emigrated at higher rates early in the experiment. For fish which emigrated from channels, models containing treatment were not significantly different than the null model containing for weight or body condition. For length, the model containing treatment was significantly better than the null model ($p = 0.0346$) and there was evidence for a significant main effect of experiment day ($p = 0.0479$) and a slightly insignificant main effect of treatment at alpha = 0.05 ($p = 0.0708$), but no treatment over time interaction ($p = 0.667$). General trends in the data suggest that early in the experiment, emigrating fish were of slightly longer than average length and lower than average weight and body condition (Fig. 5.4). This trend changed over time, with body condition of emigrants either converging with or surpassing that of holding fish by the third week of the experiment.

For fish holding in channels, an average decline in weight of 0.69-0.81 g was observed in carcass and control treatments respectively between initial and final

measurements (Table 5.1). In both carcass and control treatments, average body condition declined by ~0.25. For holding fish, models containing a treatment main effect were not significantly different than the null model for explaining changes in weight or body condition. The model for length containing treatment was significantly different than the null model (p = 0.00265). For this model, there was a significant effect of both treatment (p = 0.0381) and experiment day (p = 0.01249) main effects as well as a strongly significant effect of the treatment over time interaction (p = 0.00059) with the average length of fish in control channels increasing and the average length of fish in carcass channels decreasing. Average length of fish holding in carcass treatments declined in length by 0.52mm, whereas average length of fish holding in control treatments increased by 0.81 mm. In both carcass and control treatments, average body condition declined by 0.234 and 0.256 respectively. One-way ANOVAs at the end of the experiment, however, reveal no significant differences for average weight, length, or condition between treatment for salmon remaining in mesocosm channels at the end of the experiment.

Analysis of intraspecific behaviors in the mesocosm revealed significantly different rates of common behaviors between treatments, when accounting for local density estimated using number of fish in view (Fig 5.9-5.10), but behavioral trends were similar across treatments over time (Fig. 5.11). An average of 82.9 ± 40.7 total events and a mean of 4.08 ± 2.29 individuals were observed per five-minute video sample in carcass channels; 69.7 ± 23.6 total events and 3.83 ± 2.16 individuals were observed per video sample in control channels (Fig. 5.6). The most common events were feeding (~48% carcass, ~42% control), chasing/charging (~32% carcass, ~32% control), and fin/gill flaring (~10% carcass, ~13% control) and flight (~4% carcass, ~7% control; Fig 5.11). Redirected aggression and hiding were observed, but were uncommon (< 3% events) and not analyzed further. Comparison of mixed models revealed no differences in feeding rate by treatment over time (p = 0.106), chasing/charging (p = 0.446), fin/gill flare (p p= 0.652), or flight (p = 0.130). The average number of total events and fish observed remained relatively constant over the course of the experiment, despite declining densities in the channels at large (Fig. 5.10). Feeding events per number of fish observed increased in both control and carcass channels over the course of the experiment, whereas aggressive events declined in both treatments.

Benthic invertebrate samples collected at the end of the experiment were dominated by midges in the family *Chironomidae* (~64.5%), the genus *Prosimulium* (~9.6%), the order *Cladocera* (~8%), and the genus *Gammarus* (~5.5%). No other taxa comprised more than an average of 5% of total abundance in the mesocosm, but all taxa with an average minimum of at least 5 individuals were analyzed and data are presented in Figure 5.12. Differences in abundance of taxa between control and treatment channels assessed using one-way ANOVA revealed no differences by treatment at the $\alpha = .05$ level. Periphyton samples taken at weeks two and four were assessed for differences in ash-free dry-mass (AFDM) using one-way ANOVA, which revealed a marginally significant difference at week 2 and significantly greater biomass in control channels at week 4 (Fig. 5.13). Contrary to expectations, median mass was ~ 80% higher in controls compared to treatments

Discussion

This study showed that an early-life history consumer density bottleneck may be lessened by the presence of a high-quality resource, even if that resource confers little or no direct benefit in terms of individual consumer growth. We tested the response of young-of-the-year salmon to the presence of a historically-widespread marine-derived carcass resource from Pacific lamprey in simulated depositional pool habitat patches. We hypothesized that the presence of a carcass would 1) decrease the rate of emigration or dispersal from habitat patches by creating a trophic 'hot spot', resulting in a higher overall density of fish holding in those areas, 2) that the presence of a carcass would increase aggressive behaviors associated with territory defending as social hierarchies are established, 3) that emigrants would be of lower body condition than fish holding territory in channels due to lower status in social hierarchies, and 4) that fish holding in channels with a carcass would have greater average weight and body condition than fish holding in channels without a carcass due to direct and indirect consumption of carcass material; 5) total biomass of salmon and abundance of invertebrates would be higher in carcass treatments; and 6) that carcasses would stimulate periphyton biomass.

Our first hypothesis was supported, as we documented a measurable, if ephemeral, effect of carcasses on the emigration rates and the density dynamics of early life-history fish. Our data suggest that in depositional patches containing a carcass, juvenile salmon hold territory at a higher overall density, but that this effect dissipates as carcasses decompose. While previous studies using constant additions of artificial food have found that density will stabilize over time (Sloat and Reeves 2014), the density of our channels had a continued downward trend as the resource pulse dissipated. This pattern is consistent with previous work on resource pulses and observations of juvenile salmon in natural streams, where post-emergent salmonids are often found in high densities in depositional patches in late spring, but that density declines rapidly in early summer as metabolic requirements increase and territories are established (Quinn 2005).

We did not find a strong increase in aggressive behaviors as predicted by our second hypothesis, although we did observe a trend of both more feeding events and more chasing

and charging events in carcass channels relative to control channels when accounting for the social context using number of fish in view. Over the course of carcass decomposition, both the number of fish observed in each channel as well as the total number of events observed held relatively constant. Feeding rates increased for both carcass and control channels over time. Behaviors associated with territoriality were high early in the experiment, but declined over time, suggesting that territories and a social hierarchy were established in both treatment conditions.

Previous studies have found that juvenile salmon behavior (Reimers 1968, Symons 1968, Slaney and Northcote 1974, Titus 1990) and emigration (Chapman 1962, 1966, Keeley 2001, Sloat and Reeves 2014) are interrelated and respond to food and space. Using a similar mesocosm system, Chapman (1962) reported that aggression and territoriality in subyearling coho salmon (*Oncorhynchus kisutch*) was a primary driver in emigration rates from simulated habitat patches. Our data suggest weak differences in aggressive behavior between habitat patches with and without carcasses and that the different emigration rate we observed from channels with and without carcasses was not likely solely driven by these social interactions. These differences are also unlikely due to holding density as some previous studies used similar densities to our study (20 Atlantic salmon • m^{-2}, Symons, 1968), some used much higher densities than ours (100 rainbow trout • m^{-2}, Slaney and Northcote, 1974), and some used much lower densities than ours (2.9 Coho salmon • m^{-2}, Chapman, 1962), though Kallenberg (1958) found that aggression was so high among Baltic salmon fry held at 2.48-3.0 fish • m^{-2} that stable territories no longer existed. It is likely that both interspecific and size-depended differences in social interactions elicit different emigration responses as well.

Our third prediction was generally supported for early emigrants. Emigrants were of lower body condition than the average of fish holding territory in habitat patches with and without a carcass. This trend was strongest during the first week of the experiment, where emigrants were longer and lighter than the average fish holding in channels, resulting in much lower body condition. Emigration of lower condition individuals is consistent with the

expression of territoriality by salmon of higher body condition. This trend was similar across treatments and held until the third week of the experiment, after which time differences between emigrants and holders dissipated.

Our fourth hypothesis of increased growth and condition of fish in carcass patches was not supported. Although previous studies have shown that juvenile salmon growth rates increase when they have access to post-spawn carcasses of anadromous fish, we observed a weak or slightly negative growth response to lamprey carcasses. This result was observed, despite carcasses being added to channels at a similar marine-derived biomass loading rate (137-178 g m^{-2}) to studies reporting strong juvenile fish responses (110-270 g • m^{-2}, Wipfli et al. 2003; 100 g • m^{-2}, Guyette et al. 2013; 24-340 g • m^{-2}, Collins, et al. 2016). Wipfli et al., (2003) used a similar mesocosm system to observe the response of a low density of young-of-the-year Coho salmon to pink salmon carcass and observed between 14-20% mean growth in fork length over the course of two months compared with fish in carcass-free control channels. We observed a 1% loss in average fork length for fish in carcass channels and a 2% increase in average fork length of fish in control channels. In a study with parallel spring phenology and focus on lamprey MDN, Guyette and colleagues observed a 33-48% greater mass and 9-15% greater standard length in juvenile Atlantic salmon with access to lamprey-timed MDN. The differences between our result and others, including Guyette et al. (2013), may be related in part to properties of lamprey carcasses and to our knowledge, ours is the first study to evaluate fish growth using intact lampreys. Specific factors rendering lamprey carcasses as relatively refractory include potential chemical properties that render carcasses relatively unpalatable, a relatively tough integument compared with salmon carcasses and ground carcass analog pellets, and a potential shift in food web pathways for lamprey carcasses relative to marine-nutrients in other forms.

Our fifth hypothesis predicted that fish biomass and invertebrate abundance would be higher in carcass channels relative to controls. Our hypothesis was weakly supported for juvenile salmon, as in carcass channels greater juvenile salmon biomasses during the experiment, despite both treatments losing biomass over time. Comparison of models containing treatment and the treatment over time interaction with a null model revealed a

marginally significant difference ($p = 0.095$). Within this model, only time was significant at the $\alpha = .05$ level ($p = 2.8 \cdot 10^{-4}$). Our hypothesis for invertebrates was not supported, however, as no significant differences were detected between treatments (Fig. 5.11).

Our final hypothesis was that periphyton biomass would be higher, due to lamprey MDN supporting increased primary production in carcass channels. Contrary to our expectations, periphyton biomass was higher in control channels at the end of the experiment, despite being similar two weeks in. A two-way ANOVA revealed a significant effect of treatment over time ($p = 0.044$), despite both main effects being insignificant. This could be due to two control channels randomly falling at one end of the mesocosm, which received slightly more sunlight in the evening. This is unlikely, however, because all but one control sample at week four showed higher biomasses than any of the control samples during that period. It is possible that there was weaker top-down pressure from invertebrates, but if this were true, we would expect to see differences in abundance from our final sample. More samples would have improved our estimation of primary production within the mesocosm. Additionally, future samples should be analyzed for chlorophyll A concentration to estimate the autotrophic/heterotrophic balance.

Together, our results suggest of a short-term emigration response to carcass availability, despite little evidence for behavioral or growth differences could result from a few factors. Carcasses in our study broke down slower than others have reported for salmon carcass breakdown in similar mesocosm systems. For example, Chaloner et al. (2002) reported a ~75% loss of initial mass of pink salmon carcasses in 30 days in a mesocosm; we observed an initial increase it wet weight of almost 40% as carcasses were colonized by microbes before a gradually declining to only ~20% of initial carcass mass. Most studies have used either carcasses from Pacific salmon or pasteurized salmon carcass pellets. It is possible that lamprey carcasses are less palatable than carcasses of other species. Further research is needed to elucidate the role of palatability in trophic resource studies in aquatic environments. Mesocosm studies are often limited in their ability to mimic the abundance and diversity of food web components. Here, we found only a moderate abundance of certain taxa of benthic invertebrates and no significant differences in taxon-specific abundance

between carcass and control channels, suggesting that invertebrate consumers may have been constrained in their ability to sense and access carcasses in our mesocosm system. Decreased invertebrate colonization could result in both a limited response of secondary fish consumers as well as a weakening of top-down pressure on microbial decomposers. Regardless, we found little evidence of direct consumption of carcasses, in contrast to past studies observing the breakdown of salmon.

Although studies have explored food web responses to large-scale carcass subsidies from dense spawning aggregations of Pacific salmonids, many anadromous fish populations spawn at low densities throughout their range and express myriad spawn phenologies. Historically, much of the Pacific salmonid rearing range was subsidized by carcasses from various species at specific times. Studies evaluating the distribution of fish carcasses in stream channels have found that the majority have a final fate in high complexity depositional areas and are often associated with woody debris (Cederholm et al. 1989, Strobel et al. 2011), which are often critical rearing habitat for early-life history juvenile salmonids (Quinn 2005). This suggests that density-dynamics of early life-history fish may respond to small-scale subsidies from low-density spawning aggregations. We found evidence that changes in rearing density can result from resource subsidies that are apparently unused. Limitations of spatially-controlled trophic subsidies could limit fine-scale juvenile salmon behavior, dispersal, and growth, which could scale up to effects on population-scale productivity.

Many species experience life-history specific constraints in density-dependent growth and dispersal. In species with plastic life history, dispersal can result in system-wide diversity in growth and behavior. Because population dynamics can be controlled by a combination of internal, intraspecific, interspecific, and environmental factors, parsing out the relative role of resource subsidies can be challenging. These species are supported by resources from many sources and at many scales and indirect effects of trophic resources are likely widespread. Understanding the interplay of behavior, growth, and dispersal of consumers in response to indirect resources is critical in understanding population-wide productivity. The loss of specifically-timed and spatially-explicit resources from migratory species could help explain why density-dependence is observed in many species, despite seemingly intact ecosystems.

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Tables and Figures

Table 5.1 – Measurements and Fulton's body condition (K) ± standard error of fish holding at the beginning and end of experiment as well as emigrants during first 6 days of the experiment (Week 1) and last 7 days of the experiment (Week 4).

Status	Treatment	n	Time	Weight (g)	Length (mm)	K
Holding	Control	200	Initial	3.81 ± 0.67	67.71 ± 3.38	1.218 ± 0.10
Holding	Carcass	200	Initial	3.86 ± 0.54	68.41 ± 3.02	1.201 ± 0.10
Holding	Control	66	Final	3.12 ± 0.58	68.52 ± 3.54	0.962 ± 0.07
Holding	Carcass	82	Final	3.05 ± 0.51	67.89 ± 2.82	0.967 ± 0.07
Emigrant	Control	47	Week1	3.46 ± 0.54	68.49 ± 2.86	1.069 ± 0.08
Emigrant	Carcass	30	Week 1	3.63 ± 0.56	69.78 ± 3.61	1.063 ± 0.10
Emigrant	Control	14	Week 4	3.21 ± 0.76	68.36 ± 2.37	0.994 ± 0.14
Emigrant	Carcass	22	Week 4	3.13 ± 0.53	68.50 ± 3.16	0.966 ± 0.07
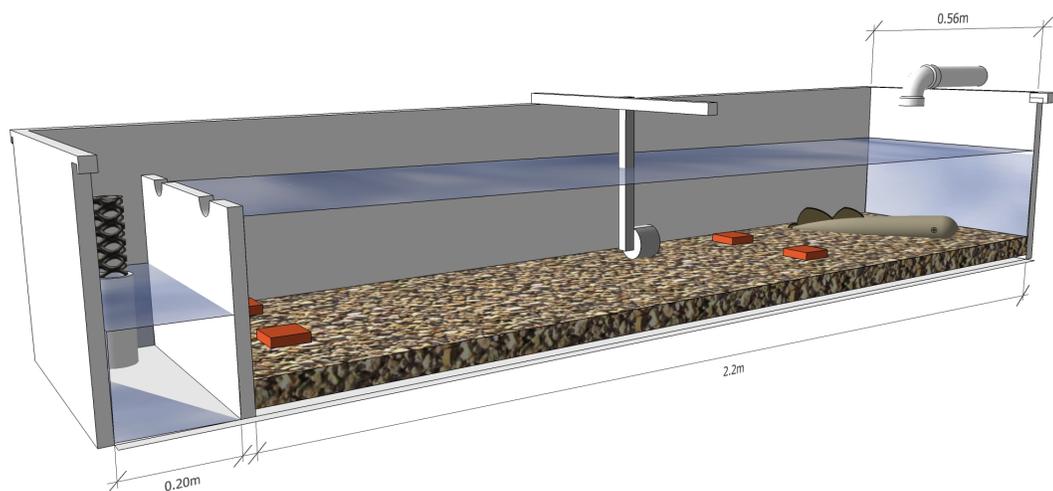
Figure 5.1 – Schematic and photograph of mesocosm along Minthorn Spring, OR, including depiction of camera placement and periphyton sampling tiles.
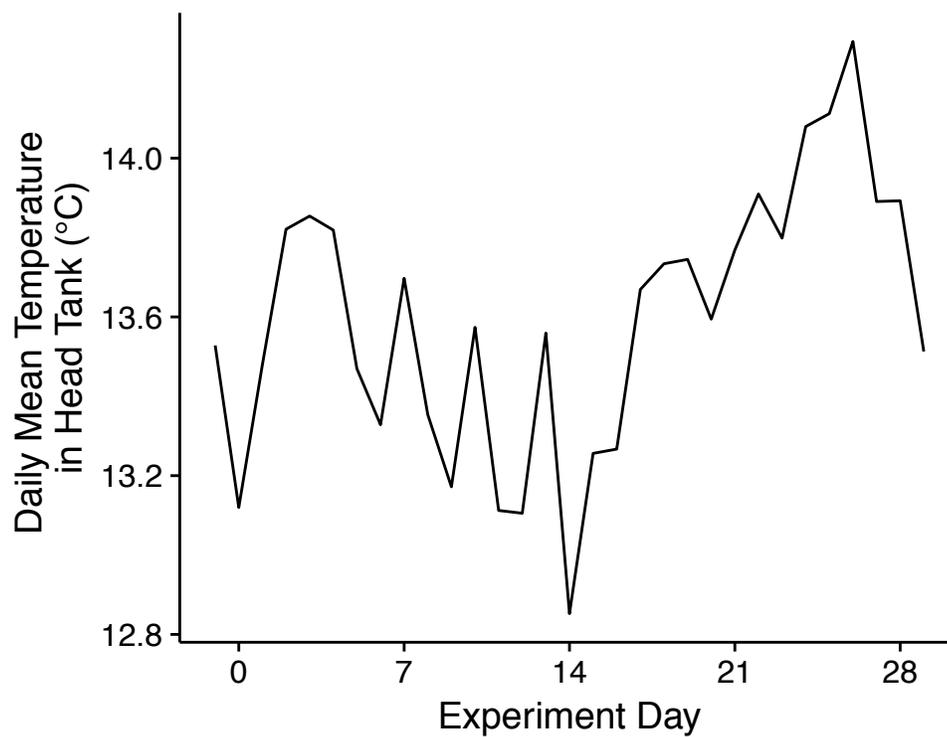
Figure 5.2– Mean daily temperature in head tank over the experiment. A maximum daily mean temperature was recorded on July 22 (14.29° C) and a minimum daily mean temperature was recorded on July 10 (12.85° C).
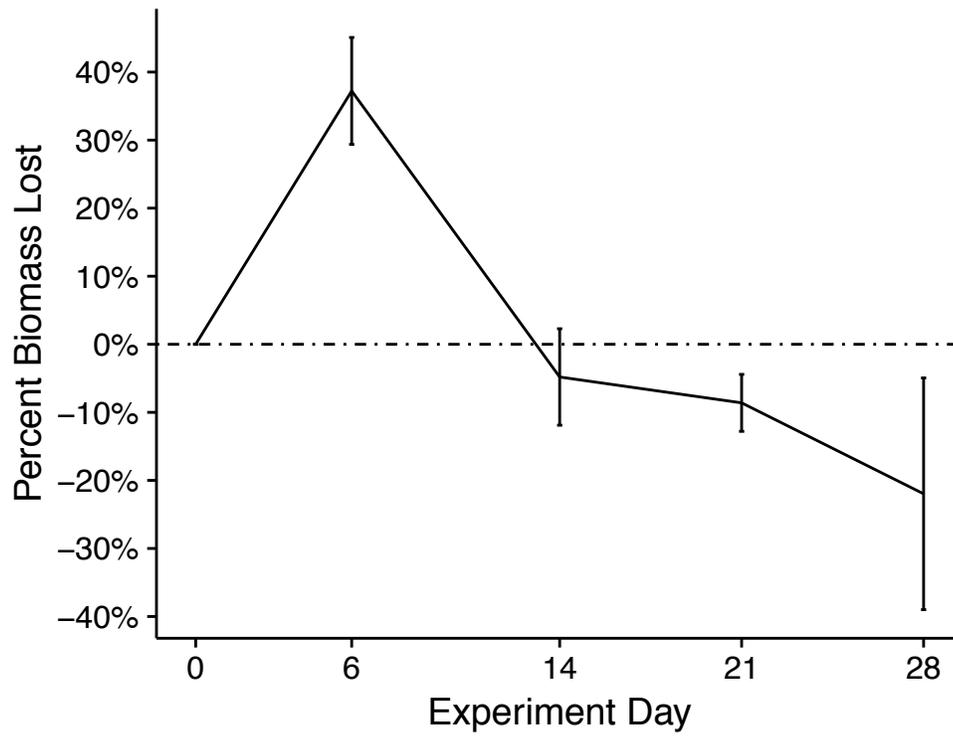
Figure 5.3 – Percent biomass lost from lamprey carcasses (n = 5) used in study over the course of four weeks.

Figure 5.4 – Carcass decomposition in mesocosm over course of experiment. Photos pulled from underwater video and show relative proximity of carcass in view on days 2, 8, 16, and 24.
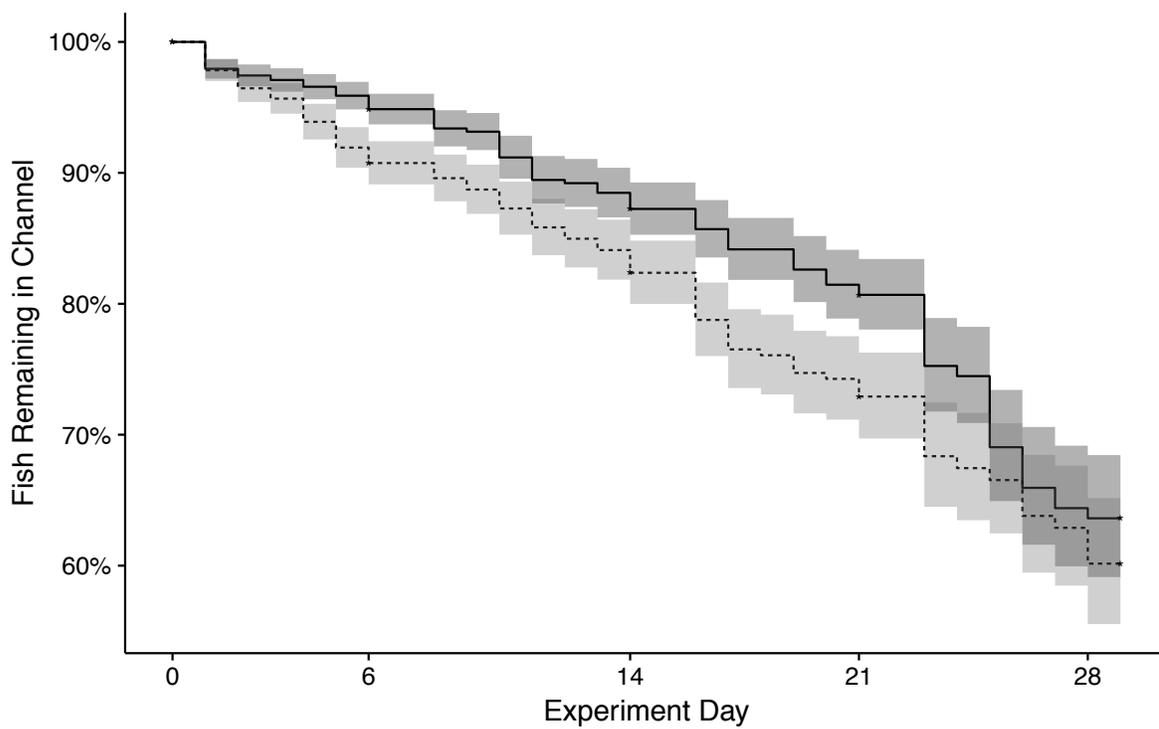
Figure 5.5 – Kaplan-Meier Survival Estimate for percent of fish remaining in carcass channels (dark grey, black line) or control channels (light grey, dashed line). Log-rank test (p = 0.0262).
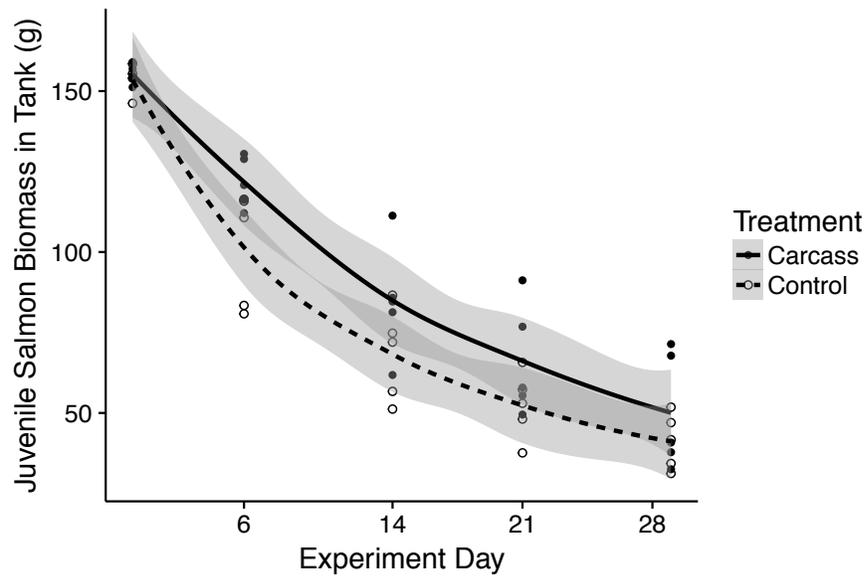
Figure 5.6 – Biomass of juvenile salmon holding in mesocosm over the course of the experiment. Models revealed marginally significant differences between a null and a model containing treatment ($p = 0.095$). Within the treatment, time, and interaction model, there was a strongly significant effect of time ($p = 2.8 * 10^{14}$).
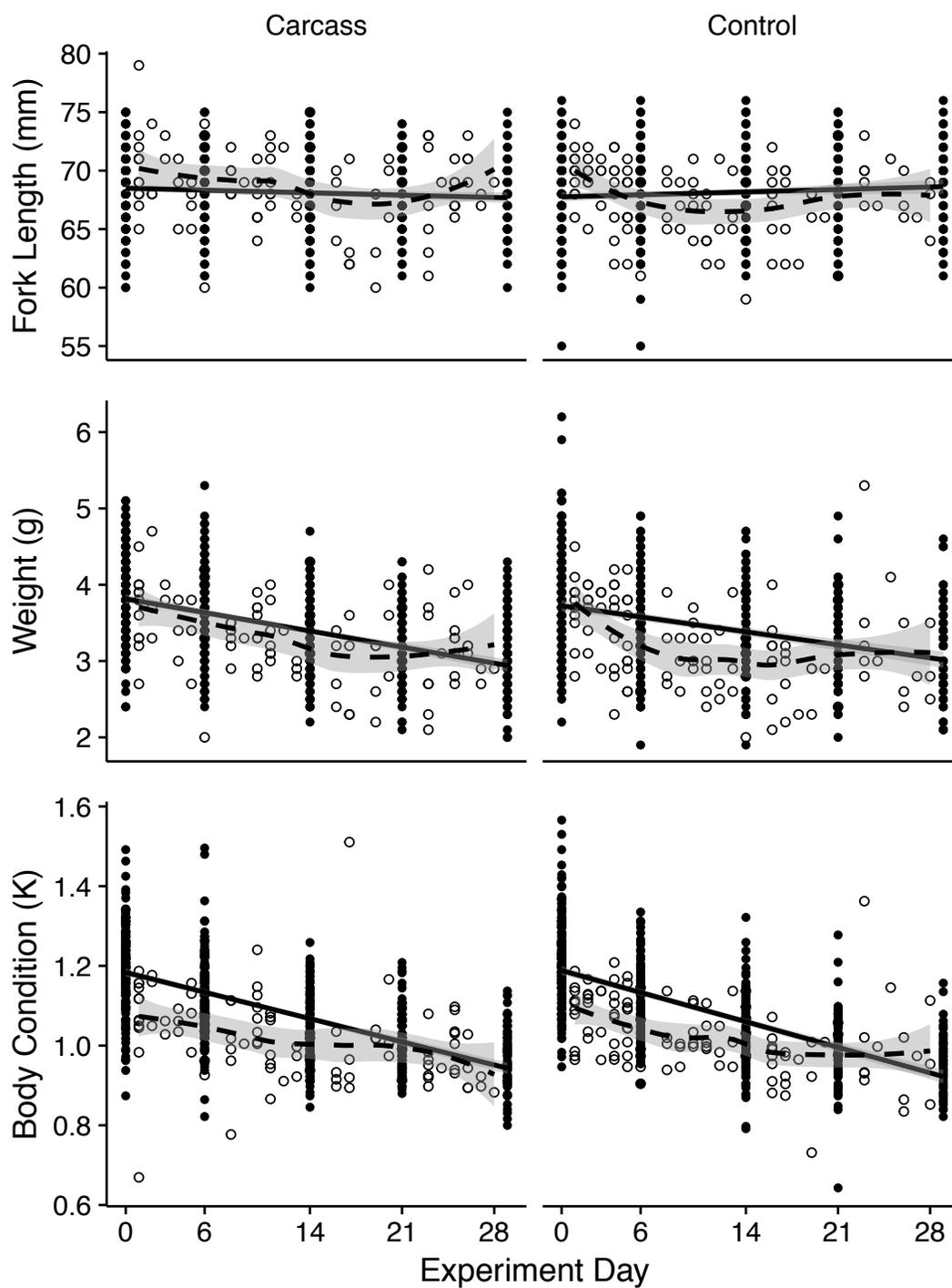
Figure 5.7 – Mean length, weight, and Fulton's body condition (K) of fish holding (linear model, solid line) versus fish emigrating (loess smoothing function, dashed line) in carcass and control channels during experiment.
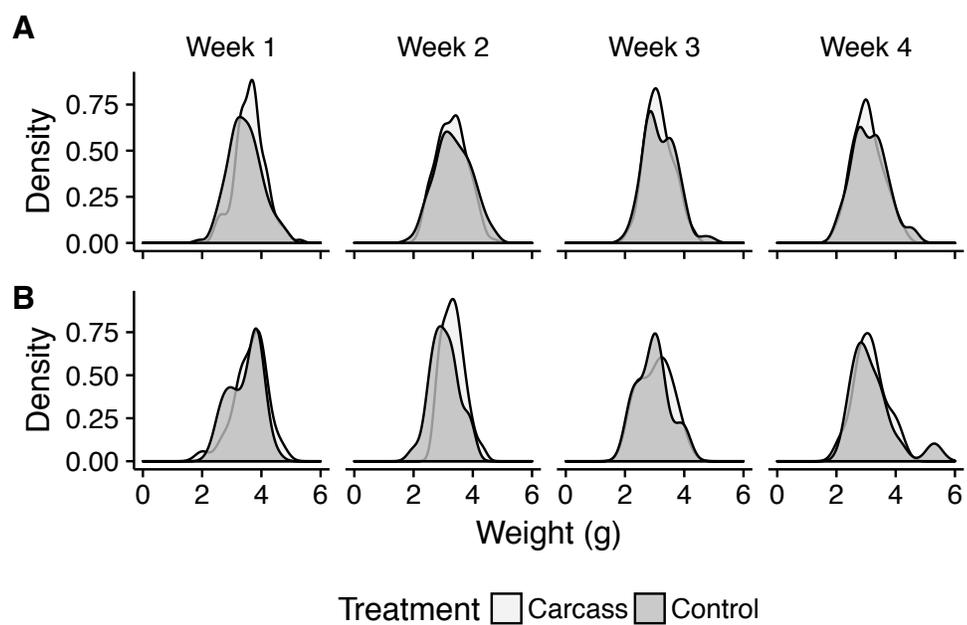
Figure 5.8 – Density plots of weight distribution of fish holding at time of measurement (A) and those which emigrated in the week prior to sampling (B).
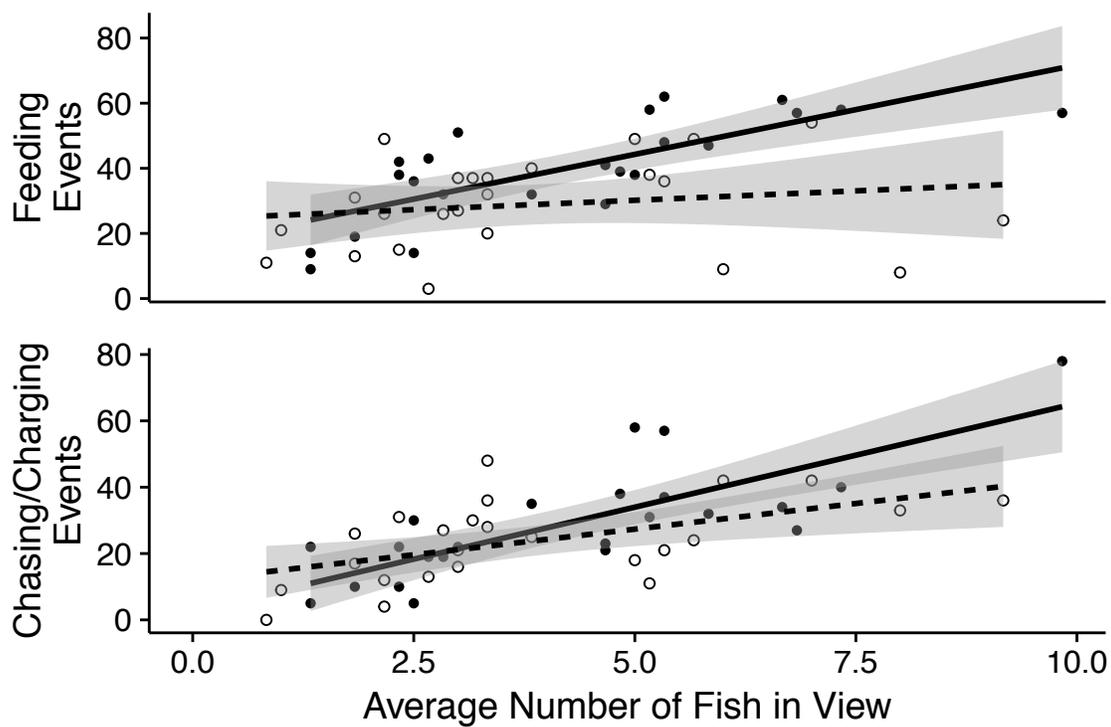
Figure 5.9 – Two most common event types plotted against the average fish observed during 5-minute viewing periods during midday in carcass channels (solid points, solid line) and control channels (open points, dashed line).
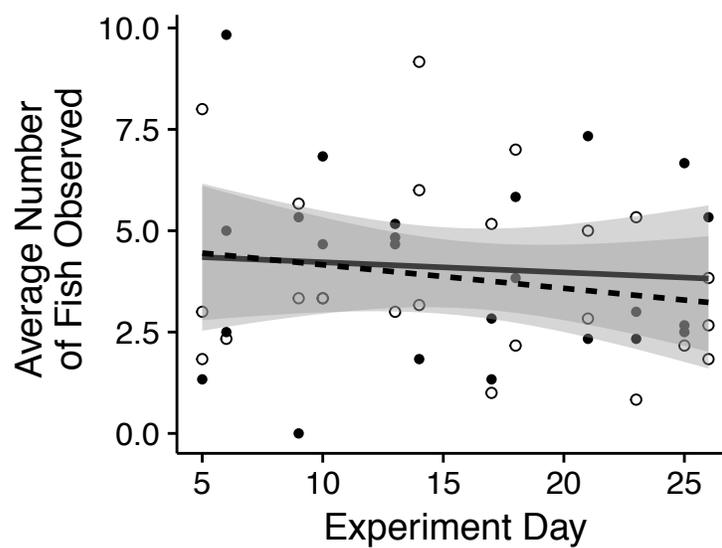
Figure 5.10 – Average number of fish in view over the course of the experiment in carcass channels (solid point, solid line) and control channels (open point, dashed line).
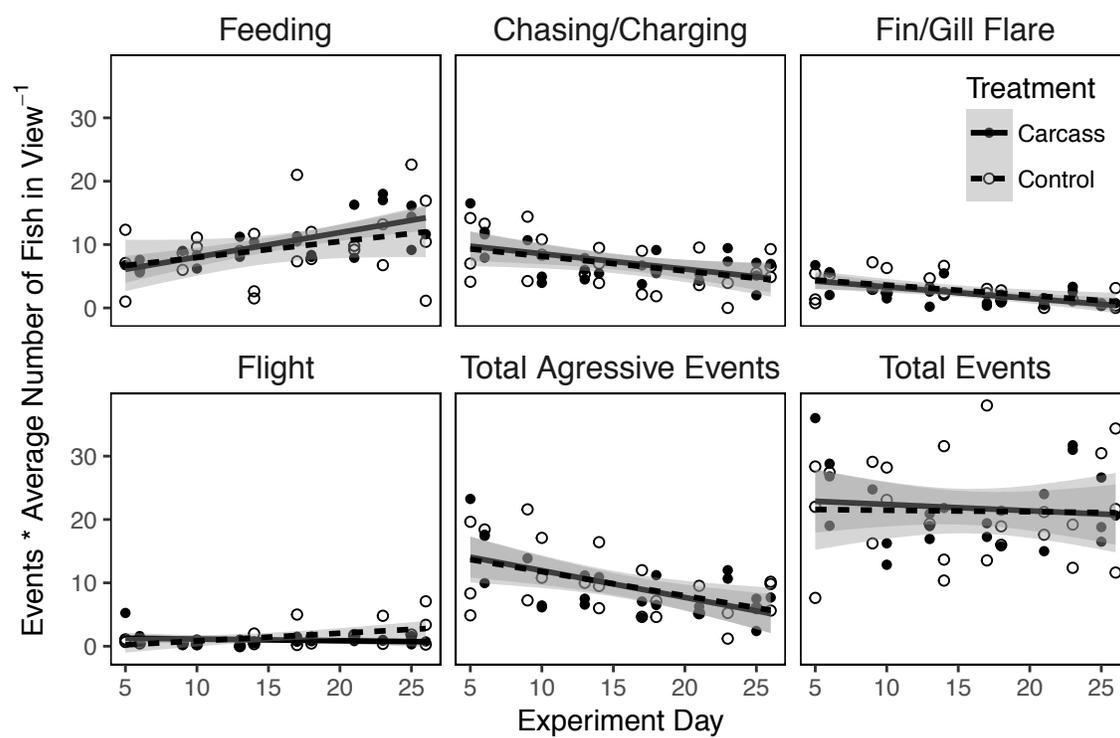
Figure 5.11− Rates of the top four most common event types over the course of experiment in carcass channels (solid points, solid line) and control channels (open points, dashed line).
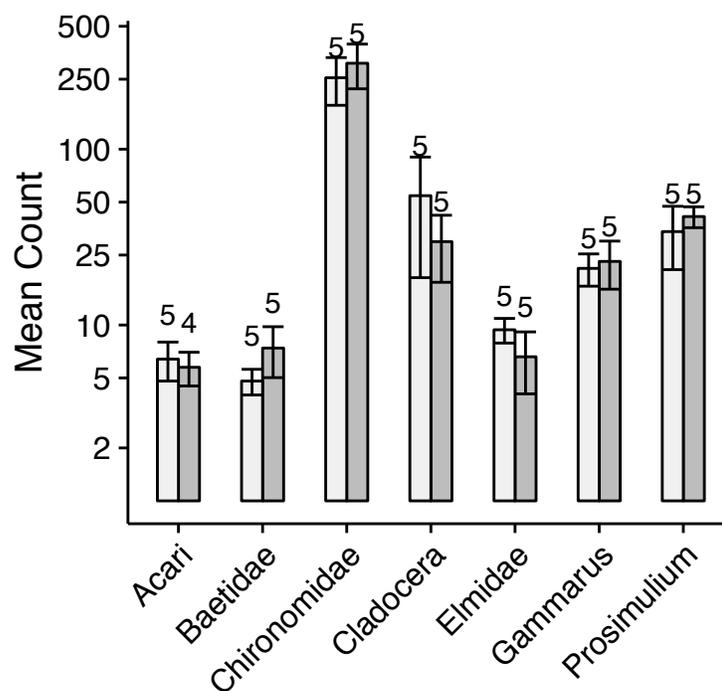
Figure 5.12 – Mean count of invertebrate taxa with ≥ 5 individuals in most samples collected in carcass (light gray) and control (dark gray) mesocosm channels at the end of the experiment. Sample sizes are shown above. No differences in abundance between carcass and control tanks were significant: Acari (p = .768), Baetidae (p = .331), Chironomidae (p = .660), Cladocera (p = .534), Elmidae (p = .371), Gammarus (p = .815), Prosimulium (p = .623). Note the log scale.
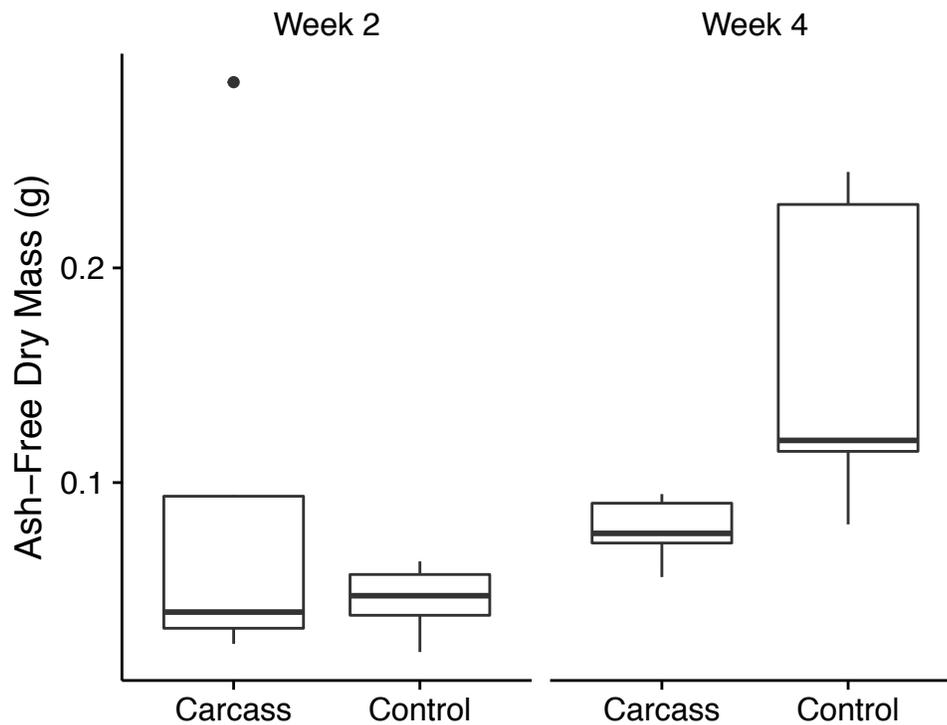
Figure 5.13 -- Ash-free dry mass of periphyton collected on artificial tiles in mesocosm at week 2 and week 4. Two-way ANOVA revealed insignificant main effects of treatment ($p=$ 0.633) and week ($p = 0.136$), but a significant treatment*week interaction ($p = 0.044$).

Chapter 6: General Conclusion

In the studies which comprise this thesis, we present some of the first studies to explicitly examine the role of Pacific lamprey as a vector for marine-derived nutrients into spawning stream food webs. Pacific lamprey are a critical part of the cultures of native peoples throughout their range, but have largely been limited in run size and distribution ro extirpated entirely. Lamprey also represent an species whose carcasses are supplied to spawning streams in a similar way to Pacific salmon, but allow us to examine how differences in form, fate, and phenology of marine-derived nutrients may influence food web responses.

This work presents the outcomes of a quantitative synthesis and modeling exercise, which provided a groundwork for the two main studies that comprise my thesis. In chapter two, we reported that juvenile and resident salmonid responses to carcass material additions are variable, but are potentially shaped by region, phenology, and response species. These analyses revealed that the strongest responses of salmonids to carcass material in the literature were found when assessing either Coho salmon (*Oncorhynchus kisutch*) or Chinook salmon (*Oncorhynchus tshawytsch*), when using artificially added carcass material, and that moderate responses have been observed in the Inland Northwest. Additionally, positive responses were reported for studies in the early summer, coinciding with Pacific lamprey carcass availability in spawning streams.

Our use of a mechanistic stream productivity model revealed that, even under simulations of dense spawning aggregations, Pacific lamprey are unlikely to drive a measurable primary productivity response except under conditions of low water volume and strongly oligotrophic nutrient statuses. These findings result from the fact that lamprey represent a relatively small-scale subsidy when background nutrients are present in spawning streams. Additionally, streams tend to be relatively cold and under high flow conditions early in the lamprey spawning window. Our two seasons of lamprey tracking revealed that spawning in the Inland Northwest portion of the range occurs later than we expected. Our modeling simulations could be updated to reflect the base-flow and relatively warm conditions we observed lamprey spawning in during July of 2015-2016).

Building off these pilot explorations, we chose to evaluate the spatial distribution of Pacific lamprey in spawning streams, because food web responses are likely strongest in fine-scale 'hot spots.' Spatial distribution of resources in a complex habitat mosaic is central in understanding how food webs generally, and mobile consumers in particular, detect and use these resources. We found that lamprey carcasses are detected and removed to the riparian zone at a greater rate than we expected. At least 25-40% of carcasses are moved to the riparian zone by scavengers and represent an actualized trans-boundary nutrient subsidy. Carcasses which decomposed in the wetted stream channel were found in physically complex habitats and associated with woody debris, roots, and boulders, whereas riparian carcasses were adjacent to relatively low complexity riffle and run habitats.

To evaluate how tertiary consumers respond to seemingly high-quality resources from post-spawn anadromous fish, we conducted a controlled artificial stream mesocosm experiment. We evaluated the growth, emigration, and behavior of subyearling Chinook salmon in pool-type habitat patches over the course of four weeks of carcass decomposition. We found little evidence of a growth response that other previous studies have reported, but did find that expressed behaviors and the rate of emigration from carcass channels was different than control channels. Carcass channels not only held more individual fish over the course of the experiment, but also retained more juvenile salmon biomass, despite carcasses breaking down slowly and seemingly little growth benefits for Chinook holding in carcass channels relative to controls.

Together, these studies represent a case study of a historically widespread resource transported to streams by migratory fish. Nuances of stream community phenology are implicit in the results we found. Although much work has explored the role of fall-spawning Pacific salmon, many anadromous-accessible systems along the Pacific rim were subsidized by many species expressing myriad life histories, each with unique phenologies relative to the recipient community's biotic and physical conditions. Understanding the role of these resource pulses and the effects of the dampening these pulses on stream food webs could improve conservation and restoration of endangered fish and the ecosystems that support them.