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The ecological importance of subsidies from salmon to stream-riparian ecosystems: An  
experimental test and implications for approaches to nutrient mitigation

by

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A dissertation

submitted in partial fulfillment

of the requirements for the degree of

DOCTOR OF PHILOSOPHY in the Department of Biological Sciences

IDAHO STATE UNIVERSITY

Summer 2014

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## **Dedication**

This dissertation is dedicated to my parents, Phil and Elora Collins, and to my wife Krista  
for their steadfast love, support, and encouragement.

## Acknowledgments

This dissertation is the culmination of untold hours of work in the field and lab. I am indebted to the many individuals whose hard work over these past six years have made this dissertation possible. Specifically, I would like to thank Dr. Colden Baxter for his insight, mentorship, and friendship during this journey.

I would also like to thank my committee members, Drs. Ernest Keeley, Mark Wipfli, and Amy Marcarelli for their guidance, insight, and diversity of perspective, which has been most beneficial when contemplating the complexities of our natural world.

Funding and support for this research was provided by Bonneville Power Administration, Idaho Department of Fish and Game, and National Science Foundation-EPSCoR. The Office of Research at Idaho State University also provided funding through a GSRSC grant. Financial support was provided by the Department of Biological Sciences in the form of research and teaching assistantships, as well as a teaching fellowship.

Our experiment would not have been possible without the technical and logistical support of Gregg Servheen, Jim Chandler, Lance Hebdon, Katy Kavanagh, Laura Felicetti, Colden Baxter, Amy Marcarelli, and Mark Wipfli. Thank you to the volunteers who assisted in hiking boxes of frozen salmon and analog pellets to our streams to make our experiment possible.

I am grateful to the many members of the Stream Ecology Center for their support and friendship over the years. I would like to thank Wayne Minshall, Amy Marcarelli, Joe Benjamin, Heather Bechtold, Madeleine Mineau, John Davis, Ryan Bellmore, Kevin Donner, Jenny Cornell, Hannah Harris, Ryan Blakadar, Kaleb Heinrich, Kate Behn, and Matt Schenk.

These studies would not have been possible without the small army of technicians who braved the harsh wilderness to collect the necessary samples and spent numerous hours in the laboratory processing the samples. I would like to thank Rebecca Martin, Jesse Haddix, Cameron Morris, Jessica Leuders-Dumont, Maria Pacioretty, Nichelle Heyrend, Hannah Harris, Armin Howell, and Alex Bell for their help. I would like to extend a special thanks to Alex Bell, who somehow managed to either collect, process, pick, or enter data for every facet of my dissertation.

Finally, I would like to thank my friends, family, and my amazing wife Krista for their emotional support.

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## **Abstract**

The annual delivery of nutrients and energy by salmon can greatly influence the productivity of receiving habitats. Unfortunately, human activities have blocked salmon migrations, decoupling the annual subsidy to the generally nutrient-poor natal rearing habitats. It is generally assumed that the loss of these salmon-derived nutrients has had negative effects. Natural resource managers are turning to nutrient additions of different physical and nutrient forms to increase productivity of freshwater streams. The efficacy of such approaches remains in question, based on an evaluation of the underlying assumptions supporting nutrient mitigation (Chapter 1). Over four years I experimentally tested how the physical form of subsidies (carcasses of Pacific salmon, pelletized salmon tissue, referred to as “analog”) influenced direct and indirect responses by organisms across multiple time scales (weeks to years) within two linked, recipient habitats (streams and riparian zones). The experiment was conducted within tributaries of the North Fork Boise River basin, Idaho, USA. I employed a suite of approaches to detect changes in abundance, biomass, and production of individuals, populations, and whole communities of organisms, ranging from algae, insects, fish, spiders and bats, through time. My findings indicated that treatments had short-term effects in both aquatic and terrestrial habitats that directly and indirectly influenced fish production (Chapters 2, 3, 4). Treatments increased both trout production and their consumption of benthic invertebrates, which corresponded with reductions in benthic invertebrate biomass across years (Chapter 2), as well as reduced emergence of their adult life stages. These reductions resulted in fewer Tetragnathidae spiders and reduced activity of select bat species (Chapter 4). Collectively, the removal of carcasses from streams to riparian zones

also had important effects on organisms in both habitats, and these responses reverberated between the adjacent habitats. Numerical responses of terrestrial arthropods were greater in vegetated than un-vegetated riparian patches that received carcasses, indicating recipient patch character can mediate responses of organisms (Chapter 3). Terrestrial Diptera in the riparian zones of treatment reaches increased due to behavioral attraction and emergence of adult Calliphoridae flies from soils, which resulted in increased activity of bat species that preferentially feed on terrestrial arthropods (Chapter 4).

## Preface

Early ecologists viewed ecosystems as closed, with communities of organisms subject to regulation predominantly through local intrinsic dynamics (Forbes 1887). However, it was soon recognized that ecosystems were, in fact, open to the exchange of nutrients, detritus, and organisms (Odum 1955, Likens et al. 1970, Polis and Winemiller 1996, Holt et al. 2004, Baxter et al. 2005). The cross-boundary exchanges of these materials between ecosystems, termed resource subsidies, are ubiquitous and can have an important influence on ecosystem functioning and community structure in many ecosystems (Polis et al. 1997, Loreau and Holt 2004). The donor-recipient paradigm has been a major organizational framework for the study of resource subsidies. In this framework, the magnitude of a resource subsidy is controlled by conditions in the “donor” habitat and the subsidy has a range of potential consequences for population and community dynamics constrained to a recipient habitat (Polis et al. 1997). Though this framework has aided in understanding how materials exchange influences ecosystems, in its present formulation its treatment of spatial and temporal variability is limited.

Resource subsidies come in all shapes and sizes, ranging from dissolved chemical compounds, to detritus, to living organisms (Polis et al. 1997). The donor-recipient framework includes no explicit treatment of such variation subsidy form. The biophysical properties of a subsidy may influence its subsequent distribution in space, interactions with organisms (e.g., translocation, palatability), and how long it persists within the environment. These characteristics may have important consequences for the response of organisms in space and through time (Sears et al. 2004, Yang et al. 2010). Physical characteristics may allow for abiotic (e.g., wind, flooding) or biotic (e.g.,

translocation by organisms) processes to redistribute the resource subsidy to multiple habitats, beyond the initial recipient habitat. Across the potential range of recipient habitats, form may also determine the duration of availability for diverse assemblages of organisms in those habitats. Some subsidies such as animal carcasses (also referred to as carrion) are ephemeral because they are consumed by scavengers and/or decompose, whereas others such detritus can persist for longer periods of time. Additionally, the persistence of a carcass within a habitat can vary depending upon environmental characteristics of the receiving habitat (Cornaby 1974, Bartels et al. 2012). Finally, form may determine the number of pathways into a food web. For example, a structurally simple subsidy like ammonium is only available to microbes or plants. In contrast, a more complex subsidy like that of a deer carcass can release nutrients through an enrichment pathway and be directly consumed by organisms. The range of pathways available to consumers change as the subsidy increases in complexity from dissolved chemical compounds to complex organic structures.

Though ecosystem openness is a central theme of resource subsidy ecology (Holt 2004), the present formulation of the donor-recipient paradigm implies there is only one recipient habitat. Characteristics of subsidy form may determine both the range of potential recipient habitats and the organisms that can utilize the resource in those habitats (Huxel et al. 2002). Conversely, characteristics of the receiving habitat or patch may also mediate the magnitude of response of organisms to a subsidy. For instance, leaf-detritus can be delivered to numerous habitats from a donor. Characteristics of the leaf size may allow for its translocation by wind to open fields, forest floors, streams, and lakes. The response of organisms to the subsidy in each of these recipient habitats may

have additional propagating effects to other habitats. Such effects are often conceptualized as occurring within the confines of the recipient habitat, however if prey are mobile and link habitats, subsidy effects in one may propagate to others. Therefore, factors that mediate the strength of these linkages (e.g., predator efficiency) can potentially affect the sign of the relationship of consumers in adjacent habitats that share a common linkage. Feedbacks are common in ecosystems but are relatively unexplored in the context of propagating effects of resource subsidies (Nakano and Murakami 2001, Baxter et al. 2005).

Diverse assemblages of organisms within the recipient habitat(s) allows for many organisms to directly benefit from a subsidy. The form of the subsidy may determine which organisms can access the resource directly, thus the pathways of entry into the food web. For instance, inputs of dissolved nutrients may only be directly accessible to microbes or plants. Conversely, inputs of insects to streams may be accessible only to fishes but not primary producers. These examples emphasize only a single pathway of entry into a food web. However, subsidies that are biophysically complex can influence food webs via multiple pathways. These resources may influence organisms via nutrient release and through direct consumption by primary and secondary consumers (Wipfli et al. 1998, Huxel et al. 2002, Spiller et al. 2010). The net outcome of these subsidized bottom-up and top-down processes may be non-linear, with unanticipated results (Oksanen et al. 1981, Borer et al. 2006).

The responses of organisms to subsidies vary in time. Effects can manifest relatively quickly, such as behavioral responses, or may take months or year to occur. The timescales of subsidy inputs and the times over which subsidy effects manifest all

influence the response of *in situ* prey and predators (Takimoto et al. 2002, Sears et al. 2004, Takimoto et al. 2009). For instance, short-term availability of a subsidy or its effects on prey may elicit only aggregative responses of consumers because the completion of a consumer life cycle cannot occur within that time frame (Murakami and Nakano 2002, Sabo and Power 2002). In contrast, when a subsidy persists longer, both aggregative and/or demographic responses by consumers are possible. For instance, a prey subsidy to a predator may alleviate (apparent mutualism; Abrams and Matsuda 1996) or amplify apparent competition (Holt 1977) with *in situ* organisms that share a predator. Additionally, when predators are subsidized directly by the subsidy (as opposed to indirectly flow through prey), top-down forces can be strengthened, thereby suppressing *in situ* prey populations with potential cascading effects (Polis et al. 1997).

#### *Decoupled marine-freshwater linkages*

The production of organic matter within marine ecosystems provides an important source of energy and nutrients for many ecosystems across the globe including coastal (e.g., rocky intertidal, beach, island) and in-land freshwater (e.g., rivers, lakes) environments (Polis and Hurd 1996, Marczak et al. 2007). Marine ecosystems can subsidize ecosystems through several potential pathways including the deposition of detritus (e.g., detached seaweed and algae), animal carcasses, and eggs (Anderson and Polis 1999, Sánchez-Piñero and Polis 2000, Bouchard and Bjørndal 2000, Barrett et al. 2005, Spiller et al. 2010, Vander Zanden et al. 2012). Productive marine environments also provide the food resources necessary to fuel large populations of fishes such as anadromous salmon. Salmon obtain most of their biomass during their residence in the

marine environment and subsequently transport marine-derived nutrients and energy to inland freshwaters during spawning migrations. These migrations serve as an important resource linkage between ecosystems (Gende et al. 2002, Naiman et al. 2002, Stockner 2003, Flecker et al. 2010).

Pacific salmon occupy an important role as ecosystem engineers by enriching and disturbing their local freshwater environment (Jones et al. 1994, Moore 2006).

Migrations of Pacific salmon modify local benthic habitats by disturbing the benthic substrate during redd construction (Moore et al. 2007, Rex and Petticrew 2008, Collins et al. 2011) and by providing an important nutrient and food resource for many aquatic and terrestrial organisms (Schindler et al. 2003, Moore and Schindler 2004). Salmon enrich freshwater environments through excretion and metabolic waste, releasing eggs and milt, re-suspending adsorbed nutrients during redd construction, through decomposition of carcasses (Mitchell and Lamberti 2005, Collins et al. 2011, Tiegs et al. 2009, 2011), and the emergence of fry (Gende et al. 2002). Marine-derived nutrients can alleviate nutrient-limitation of microbial biofilms and increase standing crop biomass in streams (Chaloner et al. 2007, Verspoor et al. 2010, R egg et al. 2011), however biofilms can also become saturated and decrease in uptake efficiency (Bernot and Dodds 2005, Earl et al. 2006), or plateau when another limiting or constraining factor is reached (Ambrose et al. 2004). At higher trophic levels, increased rates of growth have been observed for benthic invertebrates (Chaloner and Wipfli 2002, Minakawa et al. 2002), as well as changes in the biomass and/or density in the weeks and months following carcass deposition (Wipfli et al. 1998, Verspoor et al. 2011). Additionally, stream fishes directly consume marine-derived materials (Bilby et al. 1998, Scheuerell et al. 2007, Denton et al. 2009). Salmon

carcasses are also frequently removed from streams to riparian and upland forest habitats where plants (Ben-David et al. 1998, Hocking and Reynolds 2011), arthropods (Hocking and Reimchen 2006), and wildlife (Gende et al. 2004, Quinn et al. 2009) utilize them as a nutrient and food resource.

### *Study background and rationale*

Salmon have declined as a consequence of human development and harvest (Lichatowich 1999, Montgomery 2004), and eliminated from approximately 40% of their historic range in the Pacific Northwest (NRC 1996). Declines in salmon abundance have caused a corresponding decrease in the transport of nutrients and organic matter from marine to freshwater environments, with only an estimated 7% of historic levels entering their limited home range (Gresh et al. 2000). These declines account for a nutrient deficit of 2-3 million kilograms of marine-derived nitrogen per year in areas where anadromous fish were historically abundant (Thomas et al. 2003). Many of the recipient streams and rivers are oligotrophic, with low nutrient inputs from local geology, atmospheric deposition, and human activities (Sanderson et al. 2009). In Idaho, anadromous salmon were once found in more than 60% of the state (Mallet 1974). Prior to development, Idaho produced an estimated 39-45% of Chinook and 55% of the total summer steelhead in the Columbia River basin (Mallet 1974). However, anadromous salmon abundance in Idaho is now roughly 1% of estimated pre-development abundance (NRC 1996). The Boise River, a tributary of the Snake and Columbia Rivers, once supported runs of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*), however it was blocked to anadromous fish after a series of dams and canals were built from 1904-1912.

The loss of marine-derived nutrients and the recognition of their importance to freshwater environments have resulted in policy requiring culpable parties to mitigate negative impacts and recover salmon populations. Mitigating the negative impacts of the dam infrastructure is the responsibility of the Bonneville Power Administration and the Northwest Power and Conservation Council according to the Council's Fish and Wildlife program and the Northwest Power Act of 1980.

Subsequently, institutions across the Pacific Northwest are adding nutrients to streams, rivers, and lakes to offset reductions in nutrient loading with the intent of increasing salmon populations (Kohler et al. 2012). However, the efficacy of such approaches in recovering salmon populations is uncertain. Likewise, such approaches are fish-centric and seldom account for the numerous other ecological impacts salmon have on both aquatic and terrestrial environments. Salmon benefitted many organisms, plant, animal, microbe and mammal. Numerous organisms were negatively impacted by hydroelectric development in some capacity.

Mitigation treatments occur in different physical forms such as dissolved inorganic fertilizer pellets (Wipfli et al. 2010), pelletized salmon tissue (Pearsons et al. 2007, Kohler et al. 2008), and salmon carcasses (Compton et al. 2006). Differences in physical form may have implications for how effective a mitigation tool is at achieving desired management goals. Though considered similar to one another from a policy perspective because the quantities and ratios of nutrients are similar, these forms are unlikely to trigger ecologically equivalent responses due to interactions with organisms in both aquatic and terrestrial environments. Differences in form may have very different effects on organisms across trophic levels, and the extent to which effects propagate

among habitats (e.g., via stream-riparian linkages) might differ as well, though these aspects are seldom considered or addressed.

We conducted a large-scale, multi-year, manipulative field experiment to evaluate two commonly used nutrient mitigation tools: pasteurized salmon carcasses (*O. mykiss*, *O. tshawytscha*) obtained from regional fish hatcheries, and pelletized salmon carcass material, commonly referred to as salmon carcass “analog” (Pearsons et al. 2007).

Transporting salmon carcasses between basins may facilitate the spread of fish disease, therefore all salmon carcasses were frozen for storage then pasteurized (internal temperature of 60° C for 20 minutes). The freezing and pasteurization process was implemented to kill fish pathogens (e.g., whirling disease, *Myxobolus cerebralis*; Noga 2000), as is required by the State of Idaho and US Fish and Wildlife Service. Because of the logistical difficulty of handling, transporting, and potentially pasteurizing fish carcasses, salmon carcass analog is an increasingly popular mitigation tool in streams of the Pacific Northwest (Pearsons et al. 2007, Kohler et al. 2008). Salmon carcass analog material is also pasteurized and pathogen-free, and it is manufactured from fish meal so it contains nutrient content similar to salmon carcasses, but it can also be manipulated so that its nutrient content matches those of naturally spawning fish (Pearsons et al. 2007). We chose these two treatments because they are the most realistic mimics of material delivered by naturally spawning salmon, and include the suite of nutrients including carbon, nitrogen, phosphorus, trace metals and other micronutrients. Moreover, these two treatments are being applied and counted as mitigation activities across the region.

This experiment sought to evaluate the diverse ways that artificial additions of subsidies from salmon influence organisms in both stream and riparian environments.

Such an endeavor required the input of ecologists from differing backgrounds with a common focus, to better understand how stream, riparian, and forest environments benefitted from the annual delivery of salmon. This dissertation presents the responses of organisms in stream and riparian habitats and their interrelationships which cross the boundaries between land and water.

### *Dissertation objectives*

My dissertation attempts to fill gaps in the ecological understanding of resource subsidies by addressing how spatial and temporal variability of organism responses influences the overall effect of salmon subsidies in stream-riparian food webs. In doing so, I hope to contribute to improved understanding of how the physical form of resource subsidies influences consumers in recipient habitats and how these effects propagate throughout food webs. These basic findings will be used to better inform nutrient mitigation efforts by evaluating differing mitigation tools and their effects on organisms in stream-riparian ecosystems. In particular, the objectives of my dissertation were to: (1) evaluate the underlying assumptions that support nutrient mitigation to identify if the current framework is strengthened or weakened by recent ecological findings, (2) determine the pathways by which salmon subsidies influence the productivity of stream fishes and how these structure stream communities, (3) determine the role spatial heterogeneity plays in mediating the effect of subsidies at fine spatial scales and how heterogeneity influences patterns at broader spatial scales, and (4) evaluate the direct and indirect effects of salmon subsidies within and between stream and riparian habitats. To accomplish these objectives, I utilized community and ecosystem approaches to evaluate

the numerous ways salmon subsidies affected organisms in stream and riparian environments.

The results and discussion of my dissertation are presented in four chapters.

In chapter one, I critique and discuss the key assumptions underlying compensatory nutrient mitigation. I relate these assumptions to the most recent ecological literature to identify weaknesses in the conceptual foundation and make several recommendations. In chapter two, I evaluate how salmon subsidies influence the productivity of resident fishes through different direct and indirect pathways and the consequences of this increased productivity for the structure of stream communities. I build on these findings to discuss the importance of subsidy effects through both aquatic and terrestrial pathways. In chapter three, I present the results of an additional experiment (nested within the larger experimental design) in which I evaluated how the character of riparian habitat patches receiving salmon carcasses mediated the response of terrestrial arthropods across trophic levels in the riparian zone. In doing so, I provide one of the first empirical tests to directly evaluate how spatial heterogeneity at fine scales mediates patterns of response to subsidies at broader spatial scales. Based upon these findings I discuss the importance of considering how variability in the environments of recipient habitats can influence both the character of the subsidy as well as the response of organisms across trophic levels. In chapter four, I evaluate the direct and indirect effects of salmon subsidies, how these occur both within and across stream and riparian habitats, and how subsidy form influences these effects. In turn, these findings serve as the basis for discussion of how predator effects can extend across habitat boundaries to influence consumers with a shared resource.

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## **Chapter 1**

A critical assessment of the ecological assumptions underpinning compensatory  
mitigation of marine-derived nutrients

## **Abstract**

Nutrient mitigation programs compensate for reduced nutrient loading once naturally provided by salmon migrations with the intent of recovering salmon populations as well as a range of other organisms thought to be linked to productive salmon runs. Here we critically evaluate some of the key ecological assumptions underpinning the use of nutrient replacement as a means of salmon recovery. These assumptions include: (1) nutrient mitigation mimics the functional roles of salmon (2) mitigation is needed to replace depleted nutrient supplies in order to stimulate aquatic production, and (3) food resources in rearing habitats limit populations of salmon and some resident fishes. First, assumption one is called into question by an array of evidence that points to the multifaceted role played by spawning salmon, including redd-building disturbance, nutrient recycling by live fish, and consumption by terrestrial consumers, none of which are mimicked by standard nutrient mitigation approaches. Second, we show that assumption two may require qualification based upon a more complete understanding of nutrient cycling and limitation in streams. Third, we evaluate the empirical evidence supporting food limitation of fish populations and find it has been only weakly tested. On the basis of our assessment, we urge caution in the application of nutrient mitigation as a management tool and recommendations regarding research priorities aimed at further evaluating its scientific foundation. More studies are needed to quantify both primary and secondary production in mitigation and natural spawning contexts, as well as estimates of food demand by fishes to evaluate whether local aquatic and terrestrial food resources exceed the demands of the fish.

## Introduction

Over the past century, society has witnessed the precipitous decline of Pacific salmon (*Oncorhynchus* spp.) populations across much of their native ranges as a result of overharvest, habitat degradation, hatchery operations, and hydropower dams (Lichatowich 1999, Montgomery 2003), with dramatic ecological, socio-economic, and cultural effects (National Resource Council 1996). Spawning migrations transport large quantities of accrued nutrients and organic material from marine to freshwater environments, which benefit both aquatic and terrestrial biota (Gende et al. 2002). Recent reviews of the ecological services provided by salmon have informed managers and scientists about the importance of salmon in freshwater environments (Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003).

The negative impacts of human development on populations of Pacific salmon within the Columbia River have resulted in legislation requiring responsible parties to compensate for the negative impacts through replacement of functions and values, hence compensatory mitigation (Race and Fonseca 1996). The recovery measures taken by the fisheries community are diverse: hatchery supplementation (Waples 1999), spilling water at dams (Raymond 1979); diversion from turbines (Budy et al. 2002); barging of smolts (Ward et al. 1997); commercial, sport, and subsistence fishing restrictions and closures; and habitat and nutrient enhancement (Stockner 2003). Collectively, these measures are used to justify the relicensing of the very impediments that have contributed to the decline of salmon populations.

Fisheries scientists recognized early on the important role salmon play in transporting nutrients from marine to freshwater ecosystems (Juday 1932, Nelson and

Edmondson 1955). Nutrient mitigation programs seek to compensate for nutrient deficits due to declining or extirpated Pacific salmon populations to increase productivity in recipient habitats (Stockner 2003, Hyatt et al. 2004, Compton et al. 2006). Nutrients are augmented in a number of different forms, ranging from pelletized and liquid inorganic nutrients, salmon analog pellets, and salmon carcasses (Stockner 2003, Wipfli et al. 2010). The conceptual foundation that supports nutrient mitigation is underpinned by the assumptions that current habitats that have lost salmon, principally natal spawning grounds and rearing lakes, are less productive than when salmon runs were at historic levels. Therefore, additions of marine-derived nutrients are necessary to alter the trajectory of these ecosystems back towards a state when salmon actively spawned, thus creating conditions conducive to high recruitment of juvenile salmon. Recurrent themes of replacement and recovery are often used interchangeably regarding nutrient mitigation, however it is important to distinguish the two, as replacement implies solely augmenting nutrient deficits whereas recovery implies that salmon populations increase. Though replacement and recovery are not mutually exclusive, one does not necessitate the other. Here we argue that the conceptual foundation of nutrient mitigation lacks integration of current ecological understanding and subsequently may misconstrue the relative importance of the replacement of nutrients in the recovery of salmon populations.

Often, recovery measures are costly, prone to controversy, and have varying degrees of success (Williams 2008). Compensatory mitigation contexts other than salmon recovery have suffered from premature implementation and subsequent institutionalization as mitigation policy (Race and Fonseca 1996). For instance, initial efforts to replace wetland habitats lost to development seldom functioned in the same

manner as the destroyed habitat (Zedler and Callaway 2003). Here we evaluate whether compensatory mitigation of marine-derived nutrients is on a similar trajectory by reviewing relevant literature to determine the present understanding of ecological dynamics and how they relate to the assumptions that support mitigation. Our central goal is to carefully examine the underlying assumptions behind nutrient mitigation and identify potential knowledge gaps, inconsistencies, and agreements between assumptions and current ecological literature (Fig. 1). We identified three general assumptions that are made when mitigating for the loss of Pacific salmon nutrients: (1) nutrient mitigation mimics the broader ecological roles of salmon, (2) mitigation is needed to replace nutrients to stimulate aquatic production in streams, and (3) food resources in rearing habitats limit populations of salmon and resident fishes. We provide an overview of the most recent literature as it pertains to each assumption. Most of the primary literature cited here focuses on Pacific salmon in streams and rivers, yet our conclusions should be pertinent to Atlantic salmon and other anadromous species (e.g., three-spined stickleback, alewife, shad). Finally, we approach this review and critique with a sense of humility, as some of the assumptions that we outline we have held ourselves in the past, and we use “we” to signify our own participation in the community upon which we are reflecting.

*Assumption 1: Nutrient mitigation mimics the ecological roles of salmon.*

The addition of nutrients to freshwater ecosystems as a mitigation effort presupposes that nutrient enrichment takes primacy over other ecological services provided by salmon, and accurately mimics the functional role of salmon. Yet, scientists have recognized the ecological impacts of spawning disturbance and translocation of

carcasses to riparian and upland forest habitats. It is apparent that simply adding nutrients to streams may not address these two important ecological processes. Below we evaluate this assumption by addressing 2 questions. First, is nutrient enrichment the only ecological service provided by salmon? Second, do mitigation tools mimic the suite of aquatic-terrestrial linkages that are part of the ecology of naturally spawning salmon?

*Is nutrient enrichment the only ecological service provided by salmon?*

Pacific salmon are important ecosystem engineers in freshwater ecosystems, modifying habitat, community structure, and ecosystem processes through both disturbance and enrichment (Moore and Schindler 2004, Tiegs et al. 2009). In the context of nutrient mitigation we frequently focus on salmon as simply agents of enrichment, giving primacy to their contributions of nutrients (and to some extent carbon), and overlook their broader role as ecosystem engineers. For example, disturbance during redd digging can have strong short-term and seasonal effects on stream microbes (Holtgrieve and Schindler 2010, Levi et al. 2013). We conducted an overview of published studies of biological responses to salmon, and found that roughly 18% directly quantified disturbance by salmon in some fashion (Table 1). Although natural spawning runs are characterized by disturbance and enrichment, these phenomena do not always overlap in time or space (i.e., nutrient release continues long after redds are constructed). Moreover, these processes are influenced by species-specific characteristics including spawning densities or habitat preferences. For example dense concentrations of spawning Pink salmon undoubtedly have differing impacts than Coho that are more spatially diffuse in the landscape. The line between what constitutes

enrichment and disturbance is non-linear, such that disturbance releases nutrients and organic matter while also locally reducing biofilm biomass within the redds, yet reductions in stream biofilms in some cases can increase biofilm productivity (Lamberti and Resh 1983).

The ecological impacts of salmon in freshwater ecosystems are more complex than the sole addition of energy and nutrients through decomposition, both in the duration of enrichment through multiple pathways and their ability to modify benthic habitats. Live salmon excrete metabolic waste (e.g., ammonia, urea; Groot et al. 1995) and re-suspend adsorbed nutrients (e.g., nitrate, phosphorus) from benthic substrates into the water column in addition to enrichment through decomposition of carcasses (Tiegs et al. 2011). Thus, enrichment may be a protracted phase involving both living and dead salmon (Tiegs et al. 2009, Janetski et al. 2009). Disturbance by live salmon also modifies benthic stream characteristics including sediment and bed load (Kondolf and Wolman 1993) and flocculent transport (Rex and Petticrew 2008, Albers and Petticrew 2012), standing crop biomass of algae and insects (Peterson and Foote 2000, Moore et al. 2007, Collins et al. 2011), emergence timing of adult aquatic insects (Moore and Schindler 2010), and stream ecosystem metabolism (Holtgrieve and Schindler 2010, Levi et al. 2012). In some instances, nutrient enrichment and heavy disturbance interact, promoting conditions where microbial respiration exceeds primary production, altering the energy balance of the system (Holtgrieve and Schindler 2010). The physical stream environment and spawner density mediates the short-term net effects of disturbance and enrichment through characteristics including benthic substrate size and hydrology (Janetski et al. 2009).

Artificial nutrient additions may not have the desired effect unless accompanied by disturbance. Singular pulses of nutrients may not have the same effect as the more protracted or “slow-release” nutrient enrichment of natural spawning runs in habitats that have been disturbed. Yet, such efforts do not restore the disturbance regime associated with salmon activities. Disturbance by salmon is an important ecological process (Moore et al. 2007), yet the extent to which it influences actual productivity (as opposed to simply standing stocks) across trophic levels and temporal scales remains uncertain.

*Do the aquatic-terrestrial linkages associated with mitigation tools mimic naturally spawning salmon?*

Nutrient mitigation is proposed as a holistic strategy, whereby the replacement of nutrients will influence food web pathways in a manner similar to natural salmon runs. In practice it may fall short, as most efforts focus solely on aquatic habitats and neglect pathways that include terrestrial habitats. For example, wildlife frequently transport salmon carcasses to terrestrial environments where they are consumed, assimilated, excreted and egested, further dispersing nutrients to riparian and forest habitats (Koyama et al. 2005). Mammals such as mink (Ben-David et al. 1997) and bears (Gende et al. 2002) utilize salmon and transfer salmon-derived materials to land. Once in the riparian zone, marine-derived nutrients can facilitate growth and shifts in community composition of riparian plants (Helfield and Naiman 2001, Hocking and Reynolds 2011). Salmon carcasses also provide a subsidy for terrestrial arthropod communities, which can rapidly consume and transform salmon tissue into insect tissue (Meehan et al. 2005, Hocking and Reimchen 2006). These studies point to the direct effects salmon carcasses may have in

terrestrial habitats, yet there has been little exploration of the consequences of these effects on food webs in adjacent habitats.

The effects of salmon carcasses in riparian habitats may have important feedbacks to fish communities. Shifts in vegetation structure, vegetation quality, and community composition may alter the flux of organic material back to the aquatic environment. Helfield and Naiman (2001) reported the potential for positive-feedbacks of increased vegetation growth and arthropod production associated with riparian salmon carcasses. Terrestrial invertebrates comprise an important food resource for juvenile salmon (Wipfli 1997, Allan et al. 2003, Wipfli and Baxter 2010), and the rate of terrestrial invertebrate input and subsequent effects on fish vary with riparian vegetation composition and structure (Baxter et al. 2005, Saunders and Fausch 2012). What remains unclear is the degree to which nutrient replacement indirectly influences terrestrial to aquatic linkages.

Unless explicitly expressed within program proposals, it is unlikely that nutrient mitigation efforts will address the alternate aquatic-terrestrial pathways discussed above (Fig. 2). Moreover, the degree to which in-stream additions of nutrients have effects via these linkages is probably context dependent. It is likely that some riparian vegetation will benefit from subsurface flows of nutrients derived from stream environments, yet many other riparian and upland forest plants lack the root structure to utilize this pathway. Likewise, many riparian organisms (e.g., terrestrial insects) can utilize salmon carcasses only if they are exposed or removed from the stream. If salmon carcasses are added to streams as part of a mitigation program, it is likely that translocation of carcasses to the adjacent terrestrial environment will occur naturally by wildlife. Conversely, if the treatment were pelletized salmon carcass material, commonly referred

to as salmon carcass “analog” (Pearsons et al. 2007), or an inorganic fertilizer (Stockner 2003, Wipfli et al. 2010), natural transfer to the riparian zone may not occur. The physical form of analog and fertilizer pellets is likely not consumed directly by terrestrial arthropods. Some consumers may indirectly benefit through increased aquatic insect emergence, however to our knowledge this has not been evaluated. Indeed, the physical form of a mitigation tool may determine its range of food web effects across both aquatic and terrestrial habitats.

*Assumption 2: Mitigation is needed to replace nutrients from diminished salmon returns to stimulate primary and invertebrate production in streams.*

The central crux of nutrient mitigation is the presumption that replacement of nutrients is needed, and that additional nutrients are necessary for increased primary and secondary productivity. We limit our critique of assumption 2 to addressing three questions. First, do we expect ubiquitous responses from additions of marine-derived nutrients? Second, how important are salmon to overall ecosystem nutrient budgets? Third, do additions of nutrients and carbon increase primary and secondary productivity?

*Are the ecological effects of salmon ubiquitous and homogeneous?*

There are a multitude of chemical, physical, and biological conditions that can affect the ecological outcome and magnitude of MDN effects in freshwater ecosystems (Wipfli et al. 1999). Characteristics of species-specific spawning migrations influence the magnitude (e.g., dense sockeye vs. diffuse Chinook), timing, and location (e.g., inland or coastal streams) of subsidy delivery within the landscape (Janetski et al. 2009). These

local patterns are nested within larger regional patterns across the native ranges of salmon species, which encompass both geologic and climatic variability. Responses of dissolved nutrients, algal biomass, and fish physiological characteristics to natural salmon runs vary spatially due to differences in the size of salmon runs, stream discharge, and sediment size (Janetski et al. 2009), and, similarly, biofilm responses are highly variable among ecoregions within the Northern Pacific Rim (Rüegg et al. 2012). Taken together, such findings suggest that effects of natural salmon runs are not ubiquitous, but subject to local, landscape, and regional influences. Similarly, the efficacy of nutrient mitigation approaches is likely to vary across the salmon's home range. Regional, landscape and local variability of ecological responses to the addition of nutrients indicates that select watersheds may benefit more so than others.

*How important are salmon to ecosystem nutrient budgets?*

Historically, an estimated 160-240 million kg of salmon biomass annually entered freshwater systems across the Pacific Northwest, variably apportioned in space and time across the region by species-specific traits and heterogeneity of the environment (Gresh et al. 2000). Differences in land use practices, geology, physical characteristics, and atmospheric N deposition (Compton et al. 2006) influence the rate of nutrient inputs from the surrounding landscape, such that marine-derived nutrients may be more important in some contexts and less in others. For example, Gross et al. (1998) estimated that historic contributions of phosphorus from sockeye salmon migrations only comprised 3% of the total annual P budget for Redfish Lake (Idaho, USA), and this is an oligotrophic lake that receives very low inputs of P from its watershed.

Often overlooked, freshwater microbes within salmon rearing streams and lakes may compensate for nutrient reductions by shifting communities of planktonic and benthic organisms. For instance, nitrogen fixation ( $N_2$  gas) by cyanobacteria, which transforms atmospheric  $N_2$  to a biologically usable form, may provide a very important and overlooked source of N in both streams and lakes (Marcarelli and Wurtsbaugh 2009). When N concentrations are high,  $N_2$  fixation generally declines (Marcarelli and Wurtsbaugh 2006), likely due to a competitive disadvantage with other microbes. Alternatively, when N levels are low,  $N_2$ -fixers may compensate and make important contributions to nutrient cycling. There is an unexplored possibility that, when salmon-derived subsidies of N are reduced,  $N_2$ -fixers within microbial communities compensate. It is uncertain whether one large and acute pulse of  $N_2$  from salmon equals the chronic yet subtle supply of N from  $N_2$ -fixers. Still, these microbes are present in streams and lakes across the salmon's home range.

The perception of salmon rearing streams and lakes as static entities whose ecosystem state changes only as a function of marine-derived nutrients is inaccurate. Ecosystems are dynamic, and as fisheries ecologists, we should be mindful that freshwater environments might have already compensated for the loss of marine-derived nutrients to some degree. As described in the previous section, some watersheds may be better candidates for nutrient mitigation than others, due to spatial variability in microbial communities that are themselves structured by the surrounding landscape (Fierer et al. 2007).

*Do additions of nutrients increase primary and secondary productivity?*

There is a common perception that reduced salmon migrations have led to a decrease in the *in situ* productivity of organisms in freshwater ecosystems, particularly those organisms that feed rearing salmon. Curiously, diversity is often overlooked, though a diverse food base may also be needed to provide a reliable year-round food supply. Production, by definition, is the accumulation of tissue through time:  $\text{g m}^{-2} \text{y}^{-1}$  (Huryn and Wallace 2000). Often, the term production or productivity is used interchangeably with standing crop biomass, however these metrics represent different phenomena. Only 2 out of 33 studies in our review measured primary productivity and only 2 out of 33 studies measured the annual secondary production of aquatic insects (Table 1). In contrast, approximately 42% and 33% evaluated standing crop biomass and/or density of stream biofilms and invertebrates, respectively. Additionally, 51% of the studies evaluated the effects of salmon subsidies on stream fishes, primarily at the individual level (i.e., growth rate, condition). Curiously, only 6% measured the effects of salmon subsidies on the density of salmon. Instead, studies quantified responses at short-term intervals, evaluating changes in standing crop biomass of algae, insects, and fish, though they did not ascertain whether these effects persisted for longer periods within or across years. The inferences that can be drawn from these measurements are limited because they often reflect short-term accrual rather than long-term responses to enrichment and may result in a misinterpretation of ecological phenomena. Long-term enrichment studies have demonstrated that complex changes to the structure of communities of organisms required many years to occur (Slavik et al. 2004, Cross et al. 2006), well beyond the temporal scope of many MDN studies.

Direct measures of production responses to marine-derived nutrients are becoming more frequent. For instance, bioturbation of the benthos decreased net primary production during the weeks when salmon were spawning in streams (Holtgrieve and Schindler 2010, Levi et al. 2012). Consequently, during these periods, respiration from both salmon and benthic heterotrophs exceeded primary productivity (Holtgrieve and Schindler 2010), however these effects appeared to scale with spawner density (Levi et al. 2012). The next step will require measurement of ecosystem productivity for the duration of the year at the broader watershed scale to better understand longer-term dynamics of spawning disturbance and enrichment.

It is surprising, considering the decades of ecological investigations conducted in salmon-bearing streams, but to our knowledge secondary production of the invertebrate assemblage has been estimated in only two studies in salmon rearing streams (Lessard et al. 2009, Bellmore et al. 2012). In streams of Southeast Alaska, invertebrate production was measured for a subset of dominant aquatic insects, and mayfly production was generally lower in reaches that received salmon, whereas production of Chironomidae midges was higher (Lessard et al. 2009). This finding suggests that annual production of aquatic invertebrates does not necessarily and uniformly increase with spawning salmon. Declines may be due to negative effects of disturbance or increased predation pressure from stream fishes. The evaluation of invertebrate production and food demand by fish populations, including juvenile salmon, in a restored Idaho river-floodplain complex was highly variable, but estimates of invertebrate production exceeded fish demand (Bellmore et al. 2012).

The limited number of secondary production estimates across the range of salmon, particularly in regions wherein nutrient mitigation is ongoing or proposed, signifies a real weakness in the rationale for these programs. Most studies evaluate changes in invertebrate biomass standing crop over relatively short time scales, demonstrating that nutrients do have an effect, however these changes do not reflect the overall accumulation of insect tissue over the duration of a year and cannot separate the potential effect of colonization by drifting insects or top-down control of biomass. Without estimates of production of invertebrates, there is no sound rationale for these nutrient mitigation programs because we fail to demonstrate whether recipient ecosystems are nutrient and/or food limited.

*Assumption 3: Food resources in rearing habitats limit populations of salmon.*

The premise that populations of rearing salmon are limited by food is central to the application of nutrient mitigation as a management tool. Yet, this is a longstanding question in fisheries science and a topic of much debate (Lindroth 1965, Chapman 1966, Mason 1976, Wipfli and Baxter 2010). Evidence suggests this may be a false dichotomy and a more contextual perspective may be needed (Waters 1988, Huryn 1996, Bellmore et al. 2012). In the previous section, we identified empirical gaps in the literature regarding primary and secondary productivity estimates. The next assumption is that any increase in invertebrate production will be consumed, that this will translate into higher growth and survival of salmonids, and, in turn, that this will lead to population increases. Again, we assess this assumption with three questions. First, what are the sources of food that sustain salmon? Second, do responses by individuals (e.g. growth rate, condition)

translate to responses at population levels? Third, does productivity of rearing habitats relate to the population dynamics of naturally spawning salmon over long time scales?

*What are the sources of food that sustain salmon?*

Fishes obtain food and energy from multiple pathways including *in situ* benthic production, as well subsidies from terrestrial and marine environments (Wipfli and Baxter 2010). Evaluation of the production of benthic invertebrates versus demand of fish has shown that local invertebrate production is often less than annual fish production, highlighting the importance of these alternative sources of food (Allen 1951, Huryn 1996). Inputs of terrestrial invertebrates are key energy resources for salmon (Wipfli 1997, Allan et al. 2003). Headwater tributaries also subsidize salmon with drifting benthic insects and organic matter (Wipfli and Gregovich 2002, Piccolo and Wipfli 2002). Salmon directly consume high quality marine subsidies delivered by the previous generation of spawning salmon, including eggs, muscle tissue, and emerging fry (Scheuerell et al. 2007, Denton et al. 2009, Wipfli and Baxter 2010) and indirectly through benthic insect and terrestrial pathways.

The extent that mitigation tools may influence the flow of energy through aquatic and terrestrial environments varies by its physical form. For instance, liquid or inorganic fertilizers may only have bottom-up pathways, whereas analog pellets and carcass have both bottom-up and direct consumption pathways (Fig. 2). Direct consumption is an important and efficient pathway for fishes due to close stoichiometric similarities between salmon carcass tissue and living fish tissue, as opposed to the consumption of invertebrate tissue. Additionally, energy is lost due to inefficient transfers from one

trophic level to the next. Salmon subsidies influence food webs through complex pathways, though these effects must be substantive to have impacts beyond individual fishes to whole populations.

*Do responses by individual fishes translate to population levels?*

It is important to differentiate the responses of individuals from those of a population. Appraisal of the studies that quantified fish responses to artificially placed salmon carcasses, salmon analog pellets, inorganic fertilizers, and naturally deposited salmon revealed that approximately 51% evaluated individual growth rates, condition, or other physiological metrics (Table 1). Salmon smolts and resident fishes tend to exhibit increased growth rates and condition when subsidies of marine-derived nutrients are available (Wipfli et al. 2003, Scheuerell et al. 2007), though not in all cases (Shaff and Compton 2009, Harvey and Wilzbach 2010). Direct consumption of salmon carcass and salmon carcass analog material greatly increases energy intake, resulting in increased growth and/or condition (Scheuerell et al. 2007, Martin et al. 2010).

Do physiological responses of individuals translate to the population level increases? Though positive effects are often detected at the individual level, the magnitude of these responses may not be strong enough to influence population levels. In a coastal river, additions of inorganic nitrogen and phosphorus fertilizers resulted in bottom-up effects across trophic levels that ultimately increased outmigration of salmon smolts and returns of adults (Slaney et al. 2003, Ward et al. 2003). Still, factors such as oceanic conditions or the numbers of dams along the migration corridor may also influence populations of salmon. The mechanisms that link these two levels are

dependent on increased survival throughout the salmon's life history and increased fecundity (Chapman 1966, Mason 1976). Determining whether fish populations respond to salmon nutrients added either via naturally spawning or via nutrient mitigation requires long-term, multi-generation studies, while most of the studies we reviewed study responses over <1-3 years. However, long term studies relating populations of naturally spawning salmon to productivity of natal and spawning habitats may shed light onto the potential effects of nutrient mitigation on fish populations over longer timescales.

*Does productivity of rearing habitats relate to the population dynamics of naturally spawning salmon over long time scales?*

Factors that limit populations can be complex and seemingly elusive, and what may limit a population in one habitat may differ in another. The complex life histories of salmon often make it difficult to understand the factors that limit populations because they occupy multiple habitat types throughout their life history (Rabeni and Sowa 1996, Budy and Schaller 2007). Studies that have evaluated population level responses to additions of nutrients at time scales that encompass the whole life history of salmon are limited, yet there is evidence in coastal streams and lakes that additions of nutrients and subsequent increases in invertebrate prey base can positively influence returns of adult salmon (Stockner 2003). Strong paleolimnological relationships were observed between primary production and sockeye escapement in Karluk Lake, Alaska (Finney et al. 2000). However, similar analyses of other Alaskan lakes found considerable inter-annual variability between historic MDN inputs and primary production (inferred via fossil pigments in lake sediments), and salmon production, suggesting other environmental

factors may influence primary production more so than marine-derived nutrients (Schindler et al. 2005, Brock et al. 2007). Likewise, stocking-recruitment models have indicated that marine-derived nutrients can be a poor predictor of sockeye stock productivity (Uchiyama et al. 2008). The inconsistent relationships reported between productivity of spawning and rearing habitats and salmon population dynamics suggest that there is great systematic variability between aquatic environments. As addressed above, we anticipate productivity to vary spatially as a function of local, landscape, and regional factors (Poff and Huryn 1998). Likewise, increased invertebrate productivity may not positively affect fish if it is by non-drifting or predator resistant taxa or if it is generated in habitats where fishes do not forage. Until food demand by fishes is evaluated relative to food produced, such assumptions underpinning the use of nutrient mitigation approaches remain untested (Huryn 1996, Bellmore et al. 2013).

### **Synthesis**

The ecological effects of salmon spawning migrations are complex and difficult to fully understand, appreciate, and duplicate. The addition of nutrients on the basis of replacement is probably one of the more achievable ecological processes. Treating salmon as units of carbon and chemicals can readily be done with a few calculations, however this abstracts the ecological role of salmon in freshwater environments to a detriment. The artificial addition of nutrients will not be similar to natural spawning events unless systems are also disturbed in a manner similar to spawning salmon. Furthermore, the extent of food web pathways (i.e., direct consumption, aquatic-terrestrial linkages) influenced by nutrient mitigation across aquatic and terrestrial

habitats will be dependent on the form (e.g., carcass, analog or inorganic pellet). Salmon numbers have declined, so it is only logical that mitigation efforts require salmon numbers to increase, yet these responses are rarely measured on timescales that allow quantification of fish population responses. The strong bottom-up effects of enrichment, from algae and invertebrates to fish, presuppose a serial set of phenomena that is the basis of nutrient mitigation. Benthic invertebrate production (and accompanying community dynamics and nutritional status) has not been thoroughly evaluated in streams.

Additionally, we often give primacy to benthic invertebrates as a food source, but inputs of terrestrially derived invertebrates are an important component of salmon diets and the effect of salmon on this linkage needs further exploration (Wipfli and Baxter 2010).

Pelletized subsidies will not likely be removed by wildlife, and therefore will not replicate the suite of aquatic-terrestrial feedbacks that may be vital for supporting fish and ecosystem production. Finally, missing from this framework is any consideration of how local, landscape, and regional factors may mediate responses at any trophic level or consideration of the timing of resource availability and quality (e.g., egg, smolts) of food resources (Wipfli and Baxter 2010).

The relationship between marine-derived nutrient loading and the productivity of salmon is variable across aquatic environments and influenced by environmental and other ecological processes (Wipfli et al. 1999). We must consider that inter- and intraspecific competition is occurring in fish communities, and any increased food may potentially go consumers other than salmon. Likewise, we must also consider that density-dependent effects may reduce growth. Finally, salmon occupy multiple habitats

throughout their life history where other factors such as oceanic conditions and harvest can influence their abundance.

On the basis of our assessment, we recommend caution in the application of nutrient mitigation as a management tool, and we provide recommendations. First and foremost, studies are needed to quantify both primary and secondary production in mitigation and natural spawning contexts, as well as demand by salmonids, as a step to set the stage and evaluate the potential for effective mitigation. The data gap that exists is troubling, given that much of the conceptual basis for nutrient mitigation depends on productivity metrics. Second, estimates of food demand by fishes should be quantified to evaluate whether local aquatic and terrestrial food resources exceed the demands of the fish. Third, programs need to account for aquatic-terrestrial linkages, which may require the addition of MDN to riparian as well as aquatic habitats (Fig. 2). Taken together, we judge that the underlying assumptions are unsupported due to a lack of empirical evidence, and therefore that feedback is not occurring that might inform improved management practices (Walters and Holling 1990; Fig. 1).

Blindly mitigating without a clear understanding of the limitations can be a waste of money, time, and resources. We are concerned that, like wetland mitigation, premature institutionalization of nutrient mitigation may undermine salmon recovery efforts. Recognition of the limitations of nutrient mitigation, via data and feedback, allows for more realistic goals and expectations. As scientists and resource managers, we often distill and simplify phenomena as a means of describing complex patterns in nature. We inherently know that these constructs cannot explain all phenomena, yet it is paramount that there is a logical internal consistency. Based on our review, the

assumptions underlying the practice of nutrient replacement to recover imperiled salmon populations are only weakly supported. The overemphasis of the ecological effects of salmon nutrients and the predominance of the salmon-nutrient enrichment paradigm may actually undermine population recovery efforts by diverting resources and allowing other factors that may, in truth, be limiting salmon populations (e.g., dams, degraded habitat conditions or food web interactions in mainstem rivers, etc.).

We conclude with treatment of a final, likely contentious, issue. Is it ethical to receive credit for mitigating if there is reasonable doubt regarding the efficacy of the mitigation practice in question? Simply put, as a scientific community, do we recognize the addition of nutrients as an acceptable means of mitigation for loss or reduction of salmon runs if we have reason to suspect that the broader ecological roles of salmon are not mimicked or salmon populations may not recover by these actions?

It is the responsibility of state, federal, and tribal parties to accurately define mitigation based on current science. Loosely defined or interpreted terms, like mitigation, undermine the accountability of parties who have had detrimental effects on fish and wildlife, which is contrary to the intent of mitigation policies. As stewards of natural resources, scientists and managers must continually ensure that mitigation, and more broadly, salmon recovery adheres to current scientific understanding (Lichatowich and Williams 2009). Like hatcheries, fish ladders and barging of smolts, nutrient mitigation as a recovery strategy appears to provide an incomplete solution to a complex issue and diverts focus from the larger impediments limiting salmon recovery. In this review we focused on whether we ‘can’ mitigate. The real issue facing ecologists and managers is whether we ‘should’.

## **Acknowledgements**

We thank the many people whose hard work influenced the content of this paper. This review was funded by the Bonneville Power Administration (2007-332-00), Idaho Department of Fish and Game, and Idaho Power. The use of trade names or products does not constitute endorsement by the U.S. Government.

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## Tables

Table 1. Summary of abiotic and biotic responses to the natural deposition of salmon carcasses and nutrient augmentation experiments. Studies are organized by focal response of each respective study. Conclusion statements are those held by the current authors. Due to space constraints, conclusions do not reflect the full suite for each respective paper.

| Study                         | System                         | Subsidy                 | Focal Response(s)                                 | Response Variable       | Conclusion                                                                                                                                                                         |
|-------------------------------|--------------------------------|-------------------------|---------------------------------------------------|-------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Holtgrieve and Schindler 2011 | Stream                         | Salmon carcass          | Gross primary productivity, ecosystem respiration | Open-channel metabolism | Strong heterotrophic responses to increased salmon nutrients and disturbance of stream benthos.                                                                                    |
| Levi et al. 2012              | Stream                         | Salmon carcass          | Gross primary productivity, ecosystem respiration | Open-channel metabolism | Stream GPP varies in response to salmon derived nutrient concentrations, land-use history, spawner density, and reach level characteristics.                                       |
| Mitchell and Lamberti 2005    | Stream, artificial stream      | Salmon carcass          | Dissolved nutrients, periphyton                   | Concentration, biomass  | Increase in phosphorus and increases in periphyton during spawning run. Variable responses in periphyton attributed to environmental factors.                                      |
| Ambrose et al. 2004           | Stream                         | Salmon carcass          | Periphyton                                        | Biomass                 | Salmon carcasses had little effect on stream periphyton. Instead, periphyton positively responded to increased light availability.                                                 |
| Rüegg et al. 2011             | Stream                         | Salmon carcass          | Periphyton                                        | Concentration, biomass  | Salmon runs alleviated nutrient limitation of biofilms in streams of southeastern Alaska.                                                                                          |
| Rüegg et al. 2012             | Stream                         | Salmon carcass          | Periphyton                                        | Concentration, biomass  | Biofilm responses to marine-derived nutrients vary greatly from stream to stream.                                                                                                  |
| Verspoor et al. 2010          | Stream                         | Salmon carcass          | Periphyton                                        | Concentration, biomass  | A negative relationship was observed between spawner-density and periphyton. A positive relationship was observed between periphyton and dissolved phosphorus.                     |
| Wipfli et al. 1998            | Artificial and natural streams | Salmon carcass addition | Periphyton, benthic invertebrates                 | Density, density        | Addition of salmon carcasses increased stream biofilms by 15 times in natural streams and insect density by 8 to 25 times greater in artificial and natural streams, respectively. |

|                          |                                |                         |                                                                                 |                                  |                                                                                                                                                                                                                  |
|--------------------------|--------------------------------|-------------------------|---------------------------------------------------------------------------------|----------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Chaloner et al. 2004     | Stream                         | Salmon carcass          | Periphyton, benthic invertebrates                                               | Biomass                          | Reaches with salmon carcasses experienced increased periphyton and chironomidae midge biomass, and decreased biomass of certain mayfly genera.                                                                   |
| Kohler et al. 2008       | Stream                         | Analog pellet           | Periphyton, benthic invertebrates                                               | Abundance, biomass               | Additions of analog pellets increased biomass of both periphyton and benthic invertebrate biomass.                                                                                                               |
| Kohler and Taki 2010     | Stream                         | Analog pellet           | Periphyton, benthic invertebrates                                               | Ordination of response variables | Ordination analysis indicated visual separation of data points which resulted from additions of analog pellets. Separation was driven by both periphyton and benthic invertebrate responses to analog additions. |
| Claeson et al. 2006      | Stream                         | Salmon carcass          | Dissolved nutrients, biofilm, benthic invertebrates                             | Density, stable isotope          | Ammonium concentrations increased near salmon carcasses, however biofilms were highly variable. Invertebrate densities of select taxa were greatest near salmon carcasses.                                       |
| Rinella et al. 2013      | Stream                         | Salmon carcass          | Dissolved nutrients, periphyton, benthic invertebrates, <i>Salvelinus malma</i> | Concentration, stable isotope    | Marine-derived nutrient signature persisted within the stream for months in the tissue of benthic invertebrates and Dolly Varden.                                                                                |
| Riesinger et al. 2013    | Streams                        | Salmon carcass          | Biofilm, <i>O. kisutch</i>                                                      | Stable isotope                   | Streams vary in the degree to which they utilize marine-derived carbon and nitrogen.                                                                                                                             |
| Chaloner and Wipfli 2002 | Artificial and natural streams | Salmon carcass addition | Benthic invertebrates                                                           | Abundance, biomass               | Salmon carcasses were colonized by several taxa in both artificial and stream environments. Numeric and temporal responses were taxa dependent.                                                                  |
| Verspoor et al. 2011     | Stream                         | Salmon carcass          | Benthic invertebrates                                                           | Abundance                        | A positive relationship was observed between aquatic insect abundance and spawner-density 10 months after spawning took place. These relationships are carry-over effects from the previous year.                |

|                          |                                |                                      |                                                                     |                                                                        |                                                                                                                                                                                       |
|--------------------------|--------------------------------|--------------------------------------|---------------------------------------------------------------------|------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Lessard and Merritt 2006 | Stream                         | Salmon carcass                       | Benthic invertebrates                                               | Biomass, density, richness, diversity                                  | Salmon runs decreased richness and diversity of aquatic insect communities. Reaches that experienced salmon spawning had greater density and biomass of aquatic Diptera.              |
| Wipfli et al. 1999       | Artificial stream, Stream      | Salmon carcass                       | Periphyton, benthic invertebrates                                   | Biomass, density                                                       | The addition of carcasses to natural and artificial streams increased both periphyton and benthic invertebrates. Effects increased with spawner densities.                            |
| Lessard et al. 2009      | Stream                         | Salmon carcass                       | Benthic invertebrates                                               | Production                                                             | Secondary production increased for chironomidae midges and decreased for mayfly genera.                                                                                               |
| Kiernan et al. 2010      | Artificial stream              | Salmon carcass                       | Periphyton, benthic invertebrates, <i>O. mykiss</i>                 | Biomass                                                                | Variable and modest effect of carcass on periphyton and invertebrate abundance. Steelhead trout benefitted more from direct consumption than indirect pathways.                       |
| Cram et al. 2011         | Artificial stream              | Salmon carcass                       | Periphyton, <i>O. clarki</i> , <i>kisutch</i> , <i>Cottus spp.</i>  | Biomass, growth                                                        | Limited evidence of increased periphyton or resident fish growth resulting from salmon carcass additions.                                                                             |
| Wipfli et al. 2010       | Artificial stream              | Salmon carcass, inorganic fertilizer | Nutrient concentration, periphyton, invertebrate, <i>O. kisutch</i> | Concentration, biomass, density, growth, body condition, lipid content | Water chemistry and biotic responses were greatest in salmon carcass treatments. Salmon carcasses have substantially greater effects than inorganic fertilizers.                      |
| Chaloner and Wipfli 2002 | Artificial and natural streams | Salmon carcass addition              | <i>O. kisutch</i>                                                   | Stable isotope                                                         | Biofilm, invertebrate, and coho salmon all exhibited patterns of the utilization of MDN.                                                                                              |
| Harvey and Wilzbach 2010 | Stream                         | Salmon carcass                       | <i>O. mykiss</i>                                                    | Biomass, growth rate, retention                                        | No effect of carcass addition on biomass, growth or retention during the winter.                                                                                                      |
| Bilby et al. 1998        | Stream                         | Salmon carcass addition              | <i>O. kisutch</i> , <i>mykiss</i>                                   | Density, condition, stable isotope                                     | Densities of both species increased after additions of salmon carcasses. Both species had increased body condition. Diet and isotope indicate strong utilization of carcass material. |

|                        |                           |                                         |                                      |                                             |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|------------------------|---------------------------|-----------------------------------------|--------------------------------------|---------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Wilzbach et al. 2005   | Stream                    | Salmon carcass addition                 | <i>O. clarki, mykiss</i>             | Biomass, density, growth rate               | Total biomass and density of both species responded to canopy removal, not carcass additions. Greater differences in growth rate were observed in removed canopies. Both species exhibited increased rates of growth following additions of salmon carcasses. Coho production and lipid content strongly responded to additions of both carcasses and analog pellets. Cutthroat production, lipid content, and condition were significantly higher in streams treated with analog pellets. Direct consumption of salmon tissue and eggs as well as Diptera maggots resulted in increased rates of growth. |
| Wipfli et al. 2003     | Artificial stream         | Salmon carcass addition                 | <i>O. clarki, Salvelinus malma</i>   | Growth rate                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Wipfli et al. 2004     | Artificial stream, Stream | Salmon carcass, analog pellet           | <i>O. kisutch, O. clarki</i>         | Condition, production, lipid content        |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Denton et al. 2009     | Pond                      | Natural spawning run                    | <i>Salvelinus malma</i>              | Growth rate                                 | Juvenile coho demonstrated clear patterns of the utilization of MDN in beaver pond habitats. Variable growth rate and body condition responses to natural and artificial deposition of carcass material. Little evidence of short term growth influencing over-winter survival and outmigration. Both species substantially increased energy intake while subsidies of salmon were available. Differential selection of food resources were observed.                                                                                                                                                     |
| Hicks et al. 2005      | Pond                      | Salmon carcass addition                 | <i>O. kisutch</i>                    | Stable isotope                              |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Lang et al. 2006       | Pond                      | Natural spawning run, carcass additions | <i>O. kisutch</i>                    | Growth, body condition, outmigration        |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Scheuerell et al. 2007 | Stream                    | Natural spawning run                    | <i>O. mykiss, Thymallus arcticus</i> | Ration size and energy intake               | Direct consumption of analog material plus increased invertebrate abundance in treatment diets resulted in increased condition of coho. Spawner density influenced the magnitude of effect for all response variables. Coho salmon benefitted more than Dolly Varden.                                                                                                                                                                                                                                                                                                                                     |
| Martin et al. 2010     | Stream                    | Analog pellet                           | <i>O. kisutch</i>                    | Diet, condition                             |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Rinella et al. 2012    | Stream                    | Natural spawning run                    | <i>O. kisutch, Salvelinus malma</i>  | Growth rate, energy density, stable isotope |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |

Table 2. Summary of the relationship between marine-derived nutrients and recipient system productivity.

| Study                        | System | Species               | Response Variable                                          | Analytical approach        | Conclusion                                                                                                                   |
|------------------------------|--------|-----------------------|------------------------------------------------------------|----------------------------|------------------------------------------------------------------------------------------------------------------------------|
| Finney et al. 2000           | Lake   | <i>O. nerka</i>       | <i>sediment <math>\delta^{15}N</math>, microfossils</i>    | Sediment chronology        | Reduction in salmon population returns from harvest and climate reduced nutrient loading and subsequent lake productivity.   |
| Moore and Schindler 2004     | River  | <i>O. nerka</i>       | kg N, P                                                    | Mass-balance               | Systematic variability in nutrients exported by smolts. Theoretically possible for smolts to export more than adults import. |
| Schindler et al. 2005        | Lake   | <i>O. nerka</i>       | <i>sediment <math>\delta^{15}N</math>, fossil pigments</i> | Sediment chronology        | No support for relationship between salmon population dynamics and primary productivity.                                     |
| Scheuerell and Williams 2005 | River  | <i>O. tshawytscha</i> | kg P                                                       | Mass-balance               | Decreased escapement resulted in increased export of P to marine environment.                                                |
| Brock et al. 2007            | Lake   | <i>O. nerka</i>       | <i>algal <math>\delta^{15}N</math>, fossil pigments</i>    | Sediment chronology        | Considerable historic inter-annual variability between MDN and primary production, suggesting other potential drivers.       |
| Uchiyama et al. 2008         | Lake   | <i>O. nerka</i>       | <i>smolt <math>\delta^{15}N</math></i>                     | Ricker stock-recruit model | MDN poor predictor of sockeye stock productivity.                                                                            |

## Figures

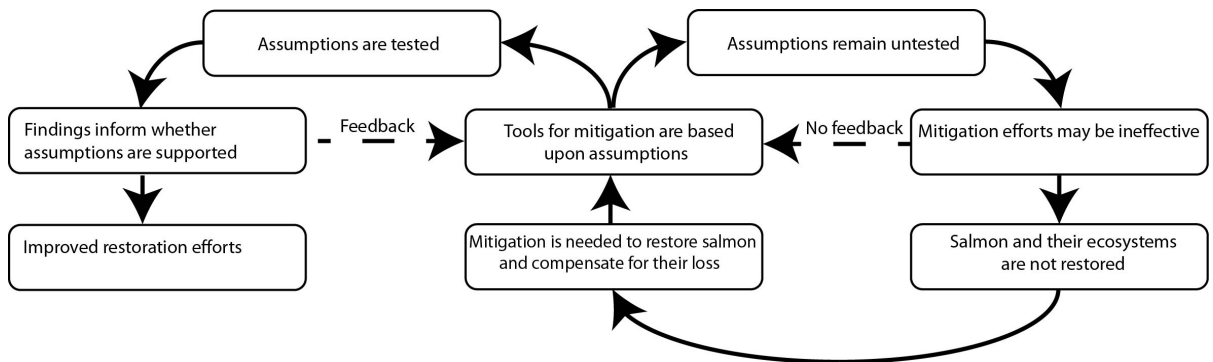


Figure 1. Tools for mitigation are developed based on underlying assumptions. If these assumptions are untested then the mitigation efforts may be ineffective. More importantly, necessary feedbacks (dashed line) do not take place to better inform the assumptions of mitigation. Instead, ineffective mitigation efforts do little for salmon and further exacerbate the need for more restoration efforts, resulting in more mitigation.

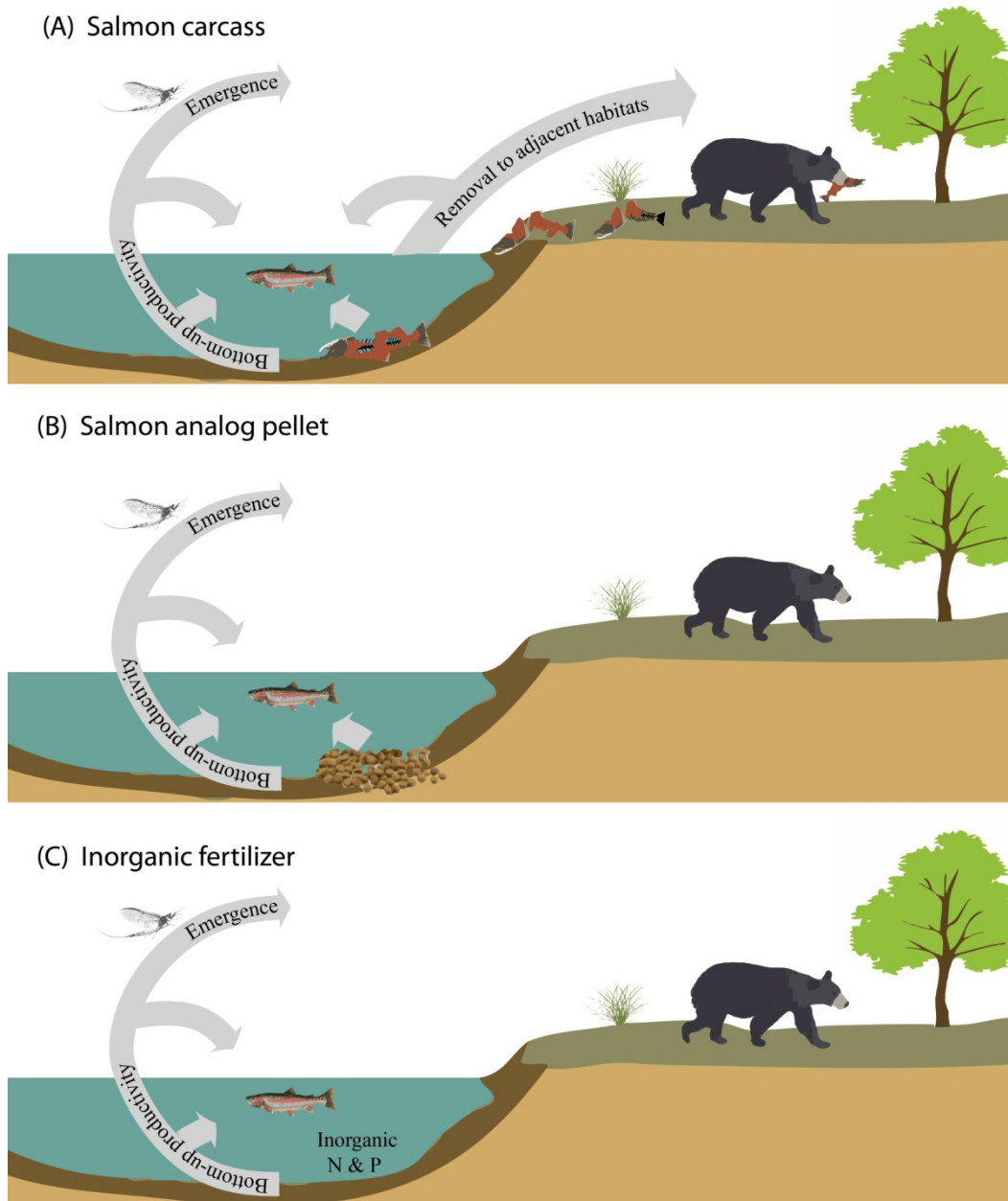


Figure 2. (A) The flow of energy and nutrients from salmon carcasses is complex. Salmon subsidies directly influence stream consumers like fishes through the direct consumption of flesh, eggs, milt, and young salmon fry. These subsidies can also indirectly benefit in-stream consumers through aquatic (e.g., algae, larval and adult insects) and terrestrial pathways (e.g., terrestrial arthropods). Salmon carcasses removed to adjacent terrestrial habitats also benefit a suite of terrestrial plants, insects, and

animals. (B) Fish also directly consume salmon carcass analog (i.e., pelletized salmon tissue), however it is not removed to adjacent riparian and upland forest habitats. (C) Inorganic fertilizers (e.g., liquid drip, pellet) are neither directly consumed by in-stream consumers nor removed to adjacent terrestrial habitats.

## Appendix

Appendix 1a. List of references from Tables 1 and 2.

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## **Chapter 2**

Production of resident fish benefits from experimental salmon subsidies via direct and indirect pathways that cross stream-riparian boundaries

## Abstract

Nutrient additions to streams are commonly employed to mitigate for the loss or decline in marine-derived subsidies delivered by salmon. These additions, which can take various forms from inorganic fertilizer to salmon carcasses, generally assume that the central pathway by which stream fish production may be enhanced is via bottom-up effects of the subsidies on primary and secondary production. However, stream salmonids derive food through multiple sources (e.g., terrestrial, marine) that are typically overlooked in the context of nutrient mitigation, and they may consume salmon-derived subsidies directly. The net outcome of nutrient mitigation efforts may be dependent on whether subsidies indirectly intensify predation on *in situ* prey via increases in a shared predator or alleviate such predation pressure. We conducted a 3-year experiment across nine tributaries of the N. Fork Boise River, Idaho, USA, consisting of 500-m stream reaches treated with salmon carcasses (n=3), salmon carcass analog (n=3), and un-treated control reaches (n=3). We observed 2-8 fold increases in streambed biofilms in the 2-6 weeks following additions of both salmon subsidy treatments across years and a 1.5 fold increase in standing crop biomass of aquatic invertebrates to carcass additions in the second year of our experiment. In the following two years, responses by benthic invertebrates were not detected because the consumption of benthic invertebrates by stream fishes increased 110-140% and 44-66% in carcass and analog streams, which appeared to mask invertebrate responses. Resident trout directly consumed 10-24 g m<sup>-2</sup> yr<sup>-1</sup> of salmon carcass and <1-11 g m<sup>-2</sup> yr<sup>-1</sup> of analog material, which resulted in 1.2-2.9 g m<sup>-2</sup> yr<sup>-1</sup> and 0.03-1.4 g m<sup>-2</sup> yr<sup>-1</sup> of trout production. Additionally, feedbacks of terrestrial maggots that colonized salmon carcasses exposed to the air or that had been removed

(principally by black bears) to riparian areas contributed  $0\text{--}2\text{ g m}^{-2}\text{ yr}^{-1}$  to trout production. Overall, treatments increased annual trout production by 2-3 fold. Nutrient mitigation programs should consider the multiple pathways of energy and nutrient flow to account for the complex effects of salmon subsidies in stream-riparian ecosystems. Our results indicate the strength of bottom-up and top-down responses to subsidy additions is asymmetrical, with top-down forces masking bottom-up effects. This pattern was not instantaneous, but required multiple years to manifest.

## **Introduction**

Globally, salmon have declined as a consequence of habitat degradation and harvest (Lichatowich 1999, Montgomery 2004), and in the Pacific Northwest they have been eliminated from approximately 40% of their historic range (NRC 1996). Declines in salmon abundance have caused a corresponding decrease in the transport of nutrients and organic matter from marine to freshwater environments, with only an estimated 7% of historic levels of nutrients being returned to natal streams by spawning runs (Gresh et al. 2000). Early recognition of the ecological importance of nutrient deposition to lakes by returning salmon led to a series of fertilization experiments aimed at enhancing populations and augmenting harvest (Juday et al. 1932, Stockner 2003, Hyatt et al. 2004). Though initially developed in lakes, these programs were later adapted to streams (Naiman et al. 2002). Conceptually, these fertilization programs are based upon the assumption that the delivery of nutrients by adult salmon is necessary to sustain greater productivity of juvenile salmon because the additions of dissolved nutrients increase primary productivity, which in turn is transferred to primary and secondary consumers

(Nelson and Edmondson 1955, Stockner 2003). Such fertilization practices were initially developed as a means of stock enhancement, but more recently applied as a management approach for the recovery of salmon populations (Hyatt et al. 2004, Compton et al. 2006). Managers are turning to compensatory nutrient mitigation to potentially offset the negative effects of dams and other disturbances on salmon populations. However, the efficacy of these approaches is uncertain because key assumptions remain largely unevaluated (Stockner 2003, Guyette et al. 2013, Chapter 2).

Nutrient mitigation as a management tool is rooted in assumptions that amendments are needed to compensate for reduced returns of adult salmon, and that such compensation will increase productivity across multiple trophic levels, ultimately stimulating not only juvenile salmon but resident fishes as well. Moreover, it is generally assumed that this occurs via stimulation of aquatic primary production by salmon-derived nutrients and subsequent transfer to fishes via invertebrates. Yet, there are alternate pathways, typically overlooked in the context of nutrient mitigation, by which salmon-derived subsidies may subsidize natal stream food webs and influence fishes. These include the direct consumption of salmon material (i.e., carcass tissue, eggs, milt, emerging fry). Direct consumption of subsidy material is an energetically efficient pathway. In addition, salmon subsidies are not limited to aquatic environments. Carcasses are frequently removed to adjacent riparian habitats where invertebrates and vertebrates readily consume, convert, and transport the marine-derived energy and nutrients throughout the landscape (Hocking and Reimchen 2006, Quinn et al. 2009). This leads to potential for reciprocal feedback to stream ecosystems through increased inputs of terrestrial arthropods, which, in turn, may contribute to sustaining stream fish

populations (Wipfli and Baxter 2010). However, the occurrence of this feedback and its importance to production of stream fishes has not been experimentally evaluated.

Effective nutrient mitigation requires an understanding of how nutrients and energy flow within food webs and how these changes influence the response of prey and predators. Based upon ecological theory, the effects of nutrient fertilization on stream organisms across trophic levels should be the result of a complex dynamic between bottom-up effects that originate from stimulation of primary producers and top-down influences of predation (Borer et al. 2006). Subsidies of salmon carcasses can have bottom-up effects on stream food webs, first by alleviating nutrient-limitation of microbial biofilms and increasing standing crop biomass (Chaloner et al. 2007, Verspoor et al. 2010, Rüegg et al. 2011) that may subsequently translate into increased insect growth rates (Chaloner and Wipfli 2002, Minakawa et al. 2002) and elevated levels of invertebrate biomass and/or density that may persist through the weeks and months following carcass deposition (Wipfli et al. 1998, Verspoor et al. 2011). Stream fishes also directly consume marine-derived materials (Bilby et al. 1998, Scheuerell et al. 2007, Denton et al. 2009), which can improve their growth and condition (Wipfli et al. 2004), but it is uncertain if these changes influence their top-down effects. The outcome of salmon subsidy additions may be dependent on the relative strength of responses of consumers across trophic levels, the net effect between co-occurring top-down and bottom-up forces (Borer et al. 2006), and the efficiency of predators and their regulating influence on prey (Power et al. 1992, Marks et al. 2000).

Ecological theory also predicts that the net outcome of bottom-up and top-down processes in response to subsidies like salmon-derived materials is further dependent on

the timescales of subsidy inputs, the duration of subsidy availability within streams, and the times over which subsidy effects manifest (Sears et al. 2004, Takimoto et al. 2009, Spiller et al. 2010). Though salmon subsidies themselves are relatively ephemeral, strong short-term effects such as increased biomass or density across trophic levels may carry on throughout the remaining year (Verspoor et al. 2011), and potentially influence the distribution of biomass across trophic levels (Moore and de Ruiter 2012). The net outcome is complicated because subsidies of salmon can affect responses of both prey and predators. The outcome may be dependent on whether salmon-derived subsidies indirectly intensify predation on *in situ* prey via increases in a shared predator (apparent competition, Holt 1977), or alleviate such predation pressure (e.g., by providing an alternate prey source; Abrams and Matsuda 1996). Moreover, the strength of indirect influences of subsidy additions in food webs may depend on the timing (i.e., short-term, lagged) and duration of both subsidy availability and numerical responses of prey (Takimoto et al. 2009). Predicting changes in biomass and production of organisms is difficult, however understanding these changes through time is necessary to evaluate the efficacy of nutrient mitigation as a management strategy.

Mitigation treatments occur in different physical forms such as dissolved or pelletized inorganic fertilizers (Wipfli et al. 2010), pelletized salmon tissue (Pearsons et al. 2007, Kohler et al. 2008, 2012), and salmon carcasses. Variation in subsidy form may have implications for the pathways of energy and nutrient flow through a community of organisms and influence how effective a mitigation tool is at achieving desired management goals. Though considered similar to one another from a policy perspective based upon similar quantities and ratios of nitrogen, phosphorus and other micronutrients,

these forms are unlikely to trigger ecologically equivalent responses. The treatment forms may have very different effects on organisms across trophic levels, and the extent to which effects propagate among habitats and influence stream-riparian linkages might differ as well, though these possibilities are seldom considered or addressed. For instance, responses may differ between carcass and analog pellets due to duration of persistence, palatability to consumers, and potential for translocation to terrestrial habitats. There is need for an analog-carcass comparison that accounts for the extended suite of potential interactions and feedbacks in stream-riparian food webs.

We hypothesized that salmon subsidies influence the productivity of aquatic communities through multiple pathways including (1) the bottom-up pathway through the stream biofilm and aquatic invertebrates (i.e., enrichment of biofilms), (2) direct consumption of marine-derived subsidies by fishes (i.e., tissue, eggs), and (3) and feedbacks from terrestrial habitats. We predicted that the cumulative effects of subsidies on aquatic and terrestrial prey populations, as well as the direct consumption of the subsidy material, would result in increased productivity of resident fishes. Because salmon subsidies can affect multiple trophic levels simultaneously, we hypothesized that the net effect of salmon subsidies on bottom-up and top-down processes across trophic levels would be asymmetrical. We predicted that strong subsidy effects on fishes would increase top-down predation on benthic insects over the duration of our experiment. Finally, we hypothesized that the efficacy of mitigation tools (carcass vs. analog pellet) would differ due to varied pathways by which these subsidies influence the recipient food web. We predicted that carcasses would have the greatest effects because their physical

form allows for the removal to riparian habitats and where they can influence multiple pathways that may feed back to influence fish productivity.

Here we present the results of a four-year manipulative experiment to evaluate the hypotheses described above, conducted in streams of central Idaho that historically received returns of Pacific salmon. Annually, we added salmon carcasses or salmon carcass analog to streams and quantified both short-term and annual responses of periphyton, benthic invertebrates, and resident trout. Using the trophic basis of production approach (Benke and Wallace 1980), we quantified the varied indirect and direct pathways from these subsidies to resident fishes and the relative contribution of each pathway to fueling trout production.

### *Study area*

This study was conducted in nine 1-3<sup>rd</sup> order streams located in the North Fork Boise River drainage in central Idaho, USA (Fig. 1, Table 1). This 980 km<sup>2</sup> drainage ranges in elevation from 1060 – 2990 m.a.s.l., is entirely contained within the Boise National Forest, and is located on the Idaho Batholith, a large geologic formation in central Idaho comprised primarily of granites, resulting in very low geologic inputs of nutrients. This region also experiences some of the lowest atmospheric nutrient deposition rates in the country (NADP 2012), resulting in nutrient poor, low conductivity, poorly buffered surface water. Studies in other streams draining the Idaho Batholith including the North Fork Boise River have demonstrated that stream biofilms are co-limited by N and P (Marcarelli and Wurtsbaugh 2007, Sanderson et al. 2009, Marcarelli et al. 2014). The annual hydrograph of the North Fork Boise River is dominated by a

spring snowmelt pulse peaking in late May, followed by a prolonged base flow period beginning in mid-late July. Although anadromous fish including Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) were historically abundant in this tributary of the Snake River (NWPCC 2004), the Boise River was blocked by the construction of 3 dams between 1906 and 1915, such that salmon migrations have been eliminated for over a century. Populations of resident fishes were also affected by the loss of annual subsidies of salmon. Mitigation for the loss of salmon should consider the full range of organisms adversely affected. Fish communities within our study site were dominated by three species: rainbow trout (*O. mykiss*), non-native brook trout (*Salvelinus fontinalis*), and mottled sculpin (*Cottus bairdii*).

## Methods

### *Experimental treatments and design*

We evaluated two commonly used nutrient mitigation tools in our experiment: pasteurized salmon carcasses (*O. mykiss*, *O. tshawytscha*) obtained from regional fish hatcheries, and pelletized salmon carcass material, commonly referred to as salmon carcass “analog” (Pearsons et al. 2007). To address concerns highlighted by Compton et al. (2006) that transporting salmon carcasses between basins may facilitate the spread of fish disease, all salmon carcasses were frozen for storage then pasteurized (internal temperature of 60° C for 20 minutes). The freezing and pasteurization process was implemented to kill fish pathogens (e.g., whirling disease, *Myxobolus cerebralis*; Noga 2000), as is required by the State of Idaho and US Fish and Wildlife Service. Because of

the logistical difficulty of handling, transporting, and potentially pasteurizing fish carcasses, salmon carcass analog is an increasingly popular mitigation tool in streams of the Pacific Northwest (Pearsons et al. 2007, Kohler et al. 2012), including central Idaho (Kohler et al. 2008). Salmon carcass analog material is also pasteurized and pathogen-free, and it is manufactured from fish meal so it contains nutrient content similar to salmon carcasses, but it can also be manipulated so that its nutrient content matches those of naturally spawning fish (Pearsons et al. 2007). Several studies have shown that stream producers and consumers utilize nutrients from analog pellets (Wipfli et al. 2004, Kohler et al. 2012). We chose these two treatments because they are the most realistic mimics of material delivered by naturally spawning salmon, and include a full suite of nutrients including carbon, nitrogen, phosphorus, trace metals and other micronutrients. Moreover, these two treatments are being applied and counted as mitigation activities across the region.

We used a randomized complete-block design in which nine streams with similar physical (e.g., discharge, substrate) and biotic (e.g., species assemblages) characteristics were selected. Carcass loading rates were based on a target of 0.5 salmon carcasses / m<sup>2</sup> of wetted stream channel, chosen to reflect a high spawner density based upon historical data for streams of this region (IDFG 1985). We matched analog loading rates to match P loads from salmon carcasses, which were 5.5 g P / m<sup>2</sup>. Carcass or analog treatments were applied annually to the same 500 m reaches of their respective streams during the first week of August for three consecutive years (2008-2010; Table 1). At control sites, stream and riparian habitats were disturbed with similar intensity as treatment applications.

### *Measurement of periphyton and benthic invertebrate biomass*

We quantified responses of periphyton and benthic invertebrate biomass within riffles of all study streams to test the hypothesis that carcass and analog additions have bottom-up effects. We sampled periphyton standing crop biomass prior to and two and six weeks following treatment application in 2008, and prior to and one month following treatment application in 2009 and 2010, and one year following the final application in 2011 at seven random locations within the bottom half of the treatment reach (0 – 250 m). Standing crop biomass was estimated as chlorophyll *a* and AFDM using standard methods (APHA 2005). Planar rock area was determined by tracing the rocks onto paper and weighing the cutout (Bergey and Getty 2006). Benthic macroinvertebrates were sampled at the same seven random locations as periphyton, once per year prior to treatment applications. We sampled riffle habitats with a Surber sampler (0.09 m<sup>2</sup>, 250 µm mesh size) to a depth of approximately 10 centimeters (Surber 1937). In the laboratory, macroinvertebrates were separated from detritus, identified to genus, and then measured to the nearest 0.5 millimeter. The biomass of each taxon was then calculated using length-weight relationships obtained from the literature (Benke et al. 1999).

### *Resident fish gut contents, abundance, biomass, and annual production*

Fish assemblages were dominated by rainbow trout (*O. mykiss*), brook trout (*Salvelinus fontinalis*), and mottled sculpin (*Cottus bairdii*). There was no systematic distribution of these species by treatment, therefore treatment effects were not confounded by differences in fish species. We refer to responses by resident trout instead

of specific trout species because rainbow and brook trout were sympatric in a subset of streams. Likewise, sculpin were present in a subset of streams. From 2008-2011, 1438 trout and sculpin were tagged, with 863 recaptures. Changes in weight of tagged (PIT tag) and recaptured fishes between sampling periods were used to determine the rate of growth. The gut contents from a sample ( $n=10-15$ ) of fishes from each stream were non-lethally collected during each sample period using gastric lavage. Samples were stored in 90% ethanol until processing. In the laboratory, organisms in gut samples were identified to Family, dried, and weighed. Density and biomass of stream fishes were estimated annually prior to experimental treatment additions. At each stream, fishes were sampled within 100 m reach using a backpack electrofisher ( $\sim 500$  V, 45 Hz). The 100 m reaches were blocked at the upstream and downstream ends with 6 mm diameter mesh netting. After each pass, all fish were measured (Salmonidae, fork length; Cottidae, total length), weighed, and tagged. We estimated fish age using length-frequency graphs (Isely and Grabowski 2007). We used the removal module of program CAPTURE to estimate population size for each age class (White 1982). We then calculated density and biomass for each age class by dividing abundance by reach area. To account for fishes not collected during the multi-pass removal sampling, biomass was calculated by multiplying the average weight of fish within each age class by the density of the same age class. Annual production was estimated at each stream using the increment summation method for each age class based upon population estimates and growth rates (Newman and Martin 1983, Hayes et al. 2007). Sculpin were present in only 6 of the 9 study streams, one of which was a control stream, which precluded statistical analysis. Though sculpin were not present in all streams, we report their annual production because they are an

often-underrepresented yet important component of the stream food web (Swain et al. 2013).

*Trophic basis of trout production and annual consumption of benthic invertebrates*

To quantify the different pathways of energy and nutrient flow to trout affected by subsidy additions we used the trophic basis of production approach (Benke and Wallace 1980). This approach accounts for both the quality and quantity of a diet item in its contribution to production. Production ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) and gut content (proportion of mass) data were used to quantify the production attributable to diet items (i.e., treatment material, benthic invertebrates, terrestrial maggots) consumed by trout and the annual quantity of each item consumed (Benke and Wallace 1980, Cross et al. 2013).

Proportions of diet items consumed during our experiment were averaged for each sample period for each stream. The portion of short-term production attributed to a given diet item ( $F_i$ ) was calculated as:

$$F_i = (G_i \times AE_i \times NPE)$$

where  $G_i$  is the proportion of food type  $i$  in the consumers diet,  $AE_i$  is the assimilation efficiency of food type  $i$ , and NPE is the net production efficiency (Bellmore et al. 2013, Cross et al. 2013). Assimilation efficiencies for resident trout and sculpin were: 0.75 for benthic aquatic invertebrates, 0.70 for terrestrial invertebrates, and 0.95 for fish tissue and brook trout eggs (Warren and Davis 1967, Elliott 1976). Net production efficiency was 0.21 and 0.12 for age 0 and age 1+ to account for allometric relationships between fish consumption and growth with fish size (Donner 2011, Bellmore et al. 2013). To

determine the relative contribution of each diet item to fish production for each sampling interval, we used:

$$PF_{ij} = (F_i / \sum_{i=1}^n F_i) \times P_j$$

where  $P_j$  is the total sum of production estimates for each fish species. Finally, to determine the total annual consumption of benthic invertebrates by trout and sculpin, annual flows from each food type  $i$  to consumer  $j$  were calculated by dividing  $PF_{ij}$  by the product of  $AE_i$  and NPE for short-term and overwinter time periods.

### *Statistical analyses*

To evaluate the hypotheses that salmon subsidies take multiple pathways (i.e., bottom-up, direct consumption, terrestrial feedbacks) of energy flow through the food web to resident fishes, we quantified responses across trophic levels and through time. Data were analyzed using repeated-measures analysis of variance (rmANOVA) with treatment (carcass, analog, control) as the fixed factor and stream biofilm, benthic invertebrate biomass (total biomass and by Order), fish biomass and density, annual consumption of invertebrates, and annual production of resident trout as response variables. We further hypothesized that subsidies would asymmetrically affect both bottom-up (biofilm, invertebrates) and top-down processes. The life histories of organisms in our study ranged from hours (i.e., microbes) to years (i.e., stream fishes). Likewise, the timing (short, lagged) and duration of ecological processes influenced by subsidies will influence how communities of organisms are structured; therefore we used the treatment  $\times$  time interaction to assess the responses of these organisms and corresponding bottom-up and top-down effects. Finally, because we hypothesized that

the efficacy of mitigation tools (carcass vs. analog pellet) would differ due to varied pathways by which these subsidies influence the recipient food web, *a priori* contrasts between treatments and control were conducted for all main treatment effects, with significance considered at  $\alpha = 0.05$ . In all analyses, block effects were evaluated as a fixed effect to address concerns of spatial autocorrelation, but were dropped from models because they were not significant (Winer et al. 1991). All response variables were log transformed to correct for non-normality of residuals and heteroscedasticity. Analyses were conducted using SAS v.9.2 (SAS Institute, Cary, North Carolina, USA).

## Results

### *Periphyton and insect biomass*

We observed bottom-up responses of chlorophyll *a* (Treatment,  $F_{2,6} = 4.45$ ,  $p = 0.065$ ) and AFDM (Treatment,  $F_{2,6} = 4.47$ ,  $p = 0.064$ ) to subsidies in the weeks following annual treatment additions. However, these short term increases in standing crop did not carry over to the following year, such that streams that were treated with salmon subsidies the previous year did not have significantly elevated periphyton biomass the following summer (Fig. 2A, B). Chlorophyll *a* biomass (Treatment  $\times$  Time,  $F_{2,6} = 3.67$ ,  $p = 0.091$ ) and AFDM (Treatment  $\times$  Time,  $F_{2,6} = 5.90$ ,  $p = 0.038$ ) increased 2 – 6 times in the short term (2–6 weeks) following treatment additions. Short-term increases occurred in 2008-2010 for analog and 2008 and 2009 for carcass treatments (Fig. 2A, B). Overall, treatment additions increased total benthic invertebrate biomass (Treatment,  $F_{2,6} = 9.79$ ,  $p = 0.012$ ), with carcasses having the strongest effect (Carcass

vs. control,  $F_{1,6} = 18.46$ ,  $p = 0.005$ ; Carcass vs. analog,  $F_{1,6} = 9.41$ ,  $p = 0.022$ ). Benthic invertebrate biomass increased following the first year of salmon carcass additions (Year  $\times$  Treatment,  $F_{6,18} = 2.68$ ,  $p = 0.048$ ); however, this pattern was not observed in analog treatments, nor were the effects of either treatment detected in 2010 or 2011 (Fig. 3; Appendix 2a). During 2009, standing crop biomass of invertebrates in salmon carcass streams was 2 times that of control streams and 1.5 times that of analog (Fig. 3). Within the aquatic insect assemblage, biomass of Diptera larvae increased in carcass streams (Treatment,  $F_{2,6} = 8.37$ ,  $p = 0.018$ ), doubling in biomass from 2008 to 2009, one year after the initial treatment additions (Treatment  $\times$  Year,  $F_{6,18} = 2.37$ ,  $p = 0.073$ ), however this pattern was not observed in 2010 or 2011. There were no significant overall effects of treatment, or treatment by year interactions, for the Orders Plecoptera, Trichoptera, or Ephemeroptera (rmANOVA,  $p$  for all  $> 0.05$ ).

#### *Biomass, density, growth rates, and annual production of resident fishes*

We detected no overall effects of treatment additions on the standing crop biomass (Treatment,  $F_{2,6} = 2.34$ ,  $p = 0.177$ ) or density (Treatment,  $F_{2,6} = 0.39$ ,  $p = 0.694$ ) of resident trout, nor were any treatment effects detected across years (Year  $\times$  Treatment,  $p > 0.05$ ; Fig. 4A, B; Appendix 2b). The average weight of trout collected during annual samplings (July) did not differ by treatments for age-1 (Treatment,  $F_{2,6} = 1.02$ ,  $p = 0.416$ ), age-2 (Treatment,  $F_{2,6} = 1.78$ ,  $p = 0.247$ ), or age-3+ (Treatment,  $F_{2,6} = 0.26$ ,  $p = 0.782$ ; Fig. 5A, B, C). However, the rate of growth of individual fishes was influenced by treatments (Fig. 6). In the weeks following treatment additions, growth rates of age 1+ trout were five times greater than controls (Treatment,  $F_{2,6} = 7.44$ ,  $p = 0.023$ ) and

three to six times greater for age 3+ trout (Treatment,  $F_{2,6} = 14.84$ ,  $p = 0.004$ ; Fig. 6).

Increased growth rates did not differ between carcass and analog treatments for age 1+ trout (Carcass vs. analog,  $F_{1,6} = 0.18$ ,  $p = 0.685$ ), however differences were observed for age-3+ trout (Carcass vs. analog,  $F_{1,6} = 20.49$ ,  $p = 0.004$ ), with carcass having the stronger effect. Overwinter rates of growth were greater for age 1+ trout (Treatment,  $F_{2,6} = 8.41$ ,  $p = 0.018$ ) in carcass treatments (Carcass vs. control,  $F_{1,6} = 6.33$ ,  $p = 0.045$ ). In contrast, overwinter growth rates of age-3+ trout did not differ from controls (Treatment,  $F_{2,6} = 3.18$ ,  $p = 0.114$ ; Fig. 6).

Treatment additions caused an increase in estimated annual trout production of approximately 2 to 3 times (Fig. 7A; Appendix 2c; Treatment,  $F_{2,6} = 12.23$ ,  $p = 0.007$ ). Within control streams, we estimated the annual production of trout ranged from 3.1 to 4.2 g m<sup>-2</sup> y<sup>-1</sup> over the duration of our experiment (Fig. 7A), whereas within analog and carcass treated streams it ranged from 6 to 8 g m<sup>-2</sup> y<sup>-1</sup> and 8 to 12.5 g m<sup>-2</sup> y<sup>-1</sup>, respectively. Contrasts indicated that carcass (Carcass vs. control,  $F_{1,6} = 20.60$ ,  $p = 0.002$ ) and analog (Analog vs. control,  $F_{1,6} = 10.47$ ,  $p = 0.017$ ) both differed from control, but not from each other (Carcass vs. analog,  $F_{1,6} = 2.63$ ,  $p = 0.155$ ).

Sculpin production at both Banner (Control: 2.15–5.11 g m<sup>-2</sup> yr<sup>-1</sup>, SD: 1.48) and Little Beaver Cr. (Carcass: 1.40–4.01 g m<sup>-2</sup> yr<sup>-1</sup>, SD: 1.49) fluctuated over the years of the experiment, initially increasing, then decreasing, whereas their production at Pikes Fork Cr. (Analog: 1.01–4.08 g m<sup>-2</sup> yr<sup>-1</sup>, SD: 1.64) declined over the duration of the experiment. In contrast, sculpin production at German (Analog: 0.01–0.33 g m<sup>-2</sup> yr<sup>-1</sup>, SD: 0.16), Trail (Carcass: 0.63–4.91 g m<sup>-2</sup> yr<sup>-1</sup>, SD: 2.21), and Big Owl creeks (Carcass: 1.08–4.94 g m<sup>-2</sup> yr<sup>-1</sup>, SD: 1.96) all increased through time.

*Diet, trophic basis of trout production, and annual consumption of benthic invertebrates*

The trophic basis of resident trout production was influenced by salmon subsidies via both aquatic and terrestrial pathways. Proportionally, carcass and analog material comprised from 10-50% and 10-20% of gut contents in the weeks following treatment additions, respectively (Fig. 8A). Trout populations directly consumed 10–24 g m<sup>-2</sup> yr<sup>-1</sup> of salmon carcass tissue and <1–11 g m<sup>-2</sup> yr<sup>-1</sup> of analog material during the weeks it was available. This accounted for an estimated 3–5% of the carcass material added and 4–11% of analog material added. This direct consumption of carcass and analog material accounted for 17% and 6% of trout annual production, respectively (Fig. 8B). Small sculpin and rainbow trout fry varied through time and by treatment, ranging from 5-40% of gut proportions (Fig 8A). Trout predation on sculpin, rainbow trout fry, and brook trout eggs resulted in roughly 2.1 g m<sup>-2</sup> yr<sup>-1</sup> of trout production attributable to piscivory in carcass treatments, relative to control and analog streams. The occurrence of maggots of terrestrial Diptera was highly variable among streams that were treated with carcasses, and did not occur in control or analog-treated streams. In turn, trout production attributable to consumption of maggots ranged from 0 to 2.09 g m<sup>-2</sup> yr<sup>-1</sup> (SD: 1.08), or 7% of annual trout production in salmon carcass treatments.

The annual estimated consumption of benthic invertebrates by trout and sculpin increased across years in treatment streams based on the annual flow of benthic invertebrate tissue required to produce the fish production we observed (Treatment,  $F_{2,6} = 6.28$ ,  $p = 0.033$ ; Fig. 7B). Overall, consumption of benthic invertebrates in both carcass (carcass vs. control,  $F_{1,6} = 14.96$ ,  $p = 0.008$ ) and analog (analog vs. control,  $F_{1,6}$

= 5.17,  $p = 0.063$ ) was greater than control streams, but not between treatments (carcass vs. analog,  $F_{1,6} = 2.54$ ,  $p = 0.161$ ). Consumption of aquatic invertebrates by resident fishes did not differ between treatments and controls during the first year of the experiment. However, in the following two years consumption of benthic invertebrates increased 110-140% and 44-66% in carcass and analog-treated streams, respectively.

## Discussion

Findings from our multi-year manipulative experiment demonstrated that the annual delivery of salmon-derived subsidies influenced multiple food web pathways across aquatic and terrestrial environments. The diverse contributions of aquatic and terrestrial prey to resident fish production indicates that the strict bottom-up pathway (i.e., biofilm, benthic insects) that informs nutrient mitigation efforts oversimplifies the ecological role of salmon in aquatic and terrestrial ecosystems. These pathways altered the structure of stream communities by affecting co-occurring bottom-up and top-down processes. Contributions from our experiment expand the basic understanding of resource subsidies and their effects on ecological processes occurring in space and through time. Our experiment used subsidies that had potential to enter food webs at multiple trophic levels. Fishes were not dependent solely on energy and nutrient transfer through benthic insects, as would be expected through strict bottom-up responses. Instead, they could directly utilize the available resources around them derived from aquatic, terrestrial, and (owing to our additions) marine habitats. Our results highlight that when a subsidy directly affects multiple trophic levels, the net effect of co-occurring bottom-up and top-down processes may be asymmetrical, such that top-down effects of

subsidies can be greater than bottom-up effects. Moreover, the effects we observed were not instantaneous, and in the context of our experiment required multiple years to manifest.

Our findings indicate that salmon subsidies affected the productivity of stream fishes via multiple pathways, as opposed to the singular bottom-up pathway (i.e., stream biofilm and benthic invertebrates) that is the focus of most mitigation efforts. The pathways affected by salmon subsidies in our experiment more closely resembled those described by Wipfli and Baxter (2010), spanning aquatic (i.e., benthic invertebrates, subsidy material) and terrestrial (i.e., terrestrial invertebrates) habitats. Benthic biofilms increased in the short-term following treatment additions during the first two years of our experiment, however in the final year, we observed no increase. Likewise, benthic insect biomass doubled after the first treatment year in carcass treated streams, and then no effect was detected in the final two years. The consumption of subsidy material provided a direct and efficient linkage from subsidy to fish. Both carcass and analog material were readily consumed in the weeks when it was available to fishes. Trout consumed more carcass than analog material, which resulted in more production attributable to the treatment. Others have documented the direct consumption of marine subsidies by fishes, suggesting this utilization may be commonplace (Scheuerell et al. 2007, Denton et al. 2009). We further detected increased piscivory in both treatments, with the strongest effects in carcass treatments. The increase in piscivory may have been a consequence of increased growth rates and subsequent increases in the gape size of predators as well as increases in sculpin populations, though the lack of replication for the latter limited the scope of inference. The application of treatments affected both species of trout, which

were pooled, however it is important to recognize that trout species may not be functionally redundant (Griffith 1974, Benjamin et al. 2012). It is apparent that in some contexts, co-occurring salmonid species can respond similarly (Scheuerell et al. 2007), however in others, responses to subsidies can be positive but vary by species (Rinella et al. 2012). We also observed that sculpin production increased in two of three streams treated with carcasses, and the combination of these findings suggest that intra-guild predation may be another means by which marine-derived nutrients and energy structures communities.

The response of terrestrial invertebrates to salmon subsidies exposed near the wetted stream margins or removed entirely from the stream resulted in increased feedbacks to the stream environment that increased the productivity of stream fishes. Feedbacks from terrestrial invertebrates to streams fishes have been confirmed by the presence of maggots in fish diets (Scheuerell et al. 2007, Denton et al. 2009), but their contribution to annual production has not been determined previously. Our results indicated that when averaged across streams, the input of maggots (Family: Calliphoridae) to streams accounted for 7% of annual trout production in streams with salmon carcasses. This feedback was not present in analog streams because analog was not removed from the stream. However, both carcass and analog had similar feedback effects through adult flies. We observed that 6 to 9% of annual trout production was from the consumption of terrestrial arthropods (excluding maggots) in carcass and analog treatments, respectively, which was a slight increase from the 4% observed in controls. This pattern indicated that the presence of salmon and analog material acts as an attractant, drawing aerial insects towards the stream (Chapter 4). The dual role of salmon

carcasses as both substrate and attractant indicates that subsidy form can impact both the magnitude and mechanism of consumer responses (i.e., behavioral, demographic) in adjacent habitats.

The net outcome of co-occurring bottom-up fertilization and increased top-down predation resulted in a complex dynamic by which effects of predation by fishes masked responses of benthic invertebrates to subsidies. The asymmetrical outcome we observed between bottom-up and top-down responses is consistent with results of other enrichment experiments summarized by Borer et al. (2006). In addition, our experiment demonstrated that the observed asymmetries were not instantaneous, but required multiple years to manifest. It required multiple years to detect these changes, which were apparently the result of increased production by fishes and their corresponding efficiency in consuming available resources. These lagged responses echo those of other multi-year enrichment experiments (Slavik et al. 2004, Cross et al. 2006). Bottom-up treatment effects of benthic invertebrates manifested in the second year, but were not detected in the following two years. Based on these findings, we might have concluded that treatments have no effect during these years. However, estimates of secondary production (i.e., accrual of biomass per year) of resident trout increased 125–282% and 78–161% in carcass and analog treatments, respectively, over the duration of the experiment. Furthermore, by quantifying the annual consumption of benthic invertebrates by fishes, we reconciled the lack of detectable response of invertebrate biomass in the latter years of our experiment, such that increased production and consumption by fishes culled invertebrate biomass down to levels near controls, masking any treatment effect, with apparent competition occurring between the resource subsidies

and *in situ* prey. The specific mechanisms influencing this pattern are uncertain because we did not evaluate foraging behaviors of trout, though feeding on drifting insects and picking insects from the benthos may have contributed. The presence of gravel in the diets of trout suggests the latter likely occurred in concert with the interception of drifting insects (S.F. Collins, *personal observation*).

Differences in the top-down and bottom up responses to subsidies appeared to be influenced by strength of bottom-up effects and the efficiency with which trout consumed benthic invertebrates, which varied through time. We observed a 125% increase in trout production during the first year in carcass treatments and a 151–282% increase in the following two years, though no changes in biomass. The annual consumption of benthic invertebrates did not differ between treatments and control in the first year, however it did in the latter two years. We reason that this is why we observed increased standing-crop biomass of aquatic invertebrates during the pre-treatment sample in the second year of our experiment. In this first year, inefficient predation of benthic invertebrates by resident fishes allowed bottom-up effects to manifest. In the following years, we measured increased consumption of benthic invertebrates by fishes in treated streams, which, we reason, was why we did not detect treatment effects on biomass of benthic insects in these years. The transition in predator efficiency from the first to second and third experimental years, and resultant trophic interactions, are consistent with theoretical predictions of predators regulating influence on prey (Oksanen et al. 1981, Power et al. 1992, Marks et al. 2000). The net outcome between these opposing forces varied through time, suggesting a potential ‘priming’ effect of subsidy additions across years, as trophic levels compensated to a new and annual source of energy and nutrients.

The strength of organism responses to experimental subsidies varied between forms, with stronger responses generally observed in carcass treatments. Responses in our experiment were similar to other studies evaluating the effects of carcasses or analog conducted elsewhere in Idaho (Kohler et al. 2008) as well as Alaska (Wipfli et al. 1998, 2004). Indeed, our findings indicate pelletized salmon tissue is not, in fact analogous to salmon carcasses. We found that the interaction of salmon carcasses with aquatic and terrestrial consumers provided both more and enhanced pathways of material flow that we assume ultimately benefitted fish production. The most effective mitigation tool was the application of salmon carcasses, which had the most complex pathways expected in natural settings. Though similar with respect to the ratio of nutrients that comprises the subsidy material and equal loading vales, the use of nutrients as the common denominator could not account for the suite of responses across aquatic and terrestrial habitats. Our study focused primarily on responses of aquatic organisms, however, other aquatic and terrestrial organisms that are usually not considered under such mitigation projects may also be influenced by these subsidies (Chapter 1).

A primary goal of nutrient mitigation is to increase productivity of salmonids (e.g., resident, anadromous) by producing more and larger fish (Stockner 2003, Chapter 1). Our findings suggest a disparity may occur between the measured response of individuals versus those of populations, and different metrics used to evaluate population level changes may yield different perspectives. We observed individual fishes readily consumed subsidy material and maggots when they were available in the short-term, which contributed to strong increases in their annual production, yet we did not detect responses in fish population biomass or density, metrics that are much more commonly

assessed than production. Standing crop biomass and density of fishes represent a snapshot in time. We hypothesize that higher short-term growth increased the metabolic requirements of fishes, resulting in a cropping of invertebrates through winter and spring, which reduced food resources and allowed density-dependent factors to regulate biomass and abundance of resident fishes. This may well have contributed to emigration by subsidized fishes to potentially more profitable or less competitive habitats outside of the reaches we monitored. These larger fish may have moved throughout the river network, thus dispersing demographic responses from our study reaches and making them less detectable. Studies at sub-watershed scales may be needed to better address demographic responses to salmon subsidies. Moreover, multiple generations of resident fishes may need to experience these resource pulses to induce a local population effect, however, the timescales necessary for multiple generations of stream salmonids exceeded the duration of our four-year experiment.

Our four-year experiment represents one of the longer-term evaluations of multi-trophic level responses to additions of resource subsidies. Yet, for perspective, the addition of phosphorus to the Kuparuk River, Alaska lasted sixteen years, with substantive changes to the ecosystem occurring around the eighth year, nearly twice the duration of our experiment (Slavik et al. 2004). A five-year addition of dissolved nitrogen and phosphorus to forested streams in North Carolina resulted in increased primary consumer production of benthic invertebrates over the first few years, however these effects did not transfer to predators because of shifts in the prey community towards predator resistant taxa (Cross et al. 2006, Davis et al. 2010). In a coastal British Columbia river, inorganic nitrogen and phosphorus fertilizers were continuously (May-

September) added to a 29 km stretch over multiple years, resulting in bottom-up stimulatory effects across trophic levels that ultimately increased outmigration of salmon smolts, ocean survival, and returns of adults (Slaney et al. 2003, Ward et al. 2003). In contrast to these studies, our experimental treatments released dissolved nutrients and could also be directly consumed by consumers. All told, these multi-year experiments, including our own, indicate that changes to the structure of aquatic communities were not instantaneous, but required multiple years to occur.

Determining the efficacy of mitigation tools is complicated by the fact that short-term studies are often extrapolated to draw inferences regarding organism and ecosystem responses at longer timescales. Yet, evidence from this experiment indicated that changes in organism biomass in response to annual subsidy additions varied from year to year and reconciling these patterns required the use of ecosystem metrics (i.e., rates of production). Patterns of increased standing crop biomass of benthic invertebrates after the first year were not observed in the latter two years. In effect, the use of the first year of experimental data was a poor predictor of later changes to the standing crop biomass of benthic invertebrates. To truly determine the efficacy of subsidy additions as a means of recovering populations of resident and anadromous fish requires the monitoring of organism responses across multiple years, perhaps even decades. To insure that assumptions are justified, mitigation programs should be nested within an adaptive management framework (Walters and Holling 1990) so that results from well designed and monitored experiments can better inform whether such projects are effective management or, if new strategies should be considered.

## **Acknowledgments**

This experiment was conducted in collaboration with K. Kavanagh, C. Robbins, J. Chandler, L. Hebdon, L. Felicetti, G. Servheen, T. Wheeler, and A. Noble-Stuen. We are grateful to past and present members of the Stream Ecology Center at Idaho State Universities for their field, lab, and intellectual support, particularly R. Martin, A. Bell, H. Bechtold, J. Benjamin, J.R. Bellmore, C. Morris, J. Leuders- Dumont, J. Haddix, N. Tillotson, M. Pacioretty, and H. Harris. We additionally thank the volunteers who assisted in deploying carcass and analog treatments each year. This project was funded by Bonneville Power Administration (2007-332-00), Idaho Power, and the Idaho Department of Fish and Game. The use of trade names or products does not constitute endorsement by the U.S. Government.

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## Tables

Table 1. Stream reach characteristics and annual loading rates of experimental subsidies at each of nine streams in the North Fork Boise River, Idaho, USA. Salmon carcasses and salmon analog pellets were added to the same 500-meter reaches each year.

| Treatment | Stream            | Drainage Area (km <sup>2</sup> ) | Median particle Size (mm) | Average discharge (L/sec) | Treatment loading values (kg) |      |      | Electrofishing reach characteristics |        |            |                              |                  |
|-----------|-------------------|----------------------------------|---------------------------|---------------------------|-------------------------------|------|------|--------------------------------------|--------|------------|------------------------------|------------------|
|           |                   |                                  |                           |                           | 2008                          | 2009 | 2010 | Volume (m <sup>3</sup> )<br>Pool     | Riffle | Length (m) | Reach area (m <sup>2</sup> ) | Woody debris (#) |
| Control   | Banner Cr.        | 23                               | 30                        | 66.4                      | -                             | -    | -    | 56.6                                 | 64.0   | 93.5       | 321.8                        | -                |
|           | Beaver Cr.        | 15                               | 45                        | 32.7                      | -                             | -    | -    | -                                    | 29.1   | 80.7       | 217.9                        | 7                |
|           | Hungarian Cr.     | 11                               | 15                        | 52.4                      | -                             | -    | -    | 1.0                                  | 18.7   | 88.6       | 151.9                        | 49               |
| Carcass   | Trail Cr.         | 20                               | 75                        | 66.5                      | 1466                          | 1478 | 1486 | 2.7                                  | 32.0   | 92.8       | 194.5                        | 16               |
|           | Little Beaver Cr. | 6                                | 10                        | 26.9                      | 977                           | 979  | 976  | 18.9                                 | 35.6   | 87.0       | 203.9                        | 7                |
|           | Big Owl Cr.       | 18                               | 20                        | 39.5                      | 1312                          | 1311 | 1326 | 9.0                                  | 31.9   | 102.3      | 174.6                        | 3                |
| Analog    | German Cr.        | 23                               | 55                        | 109.8                     | 494                           | 499  | 494  | 15.0                                 | 59.1   | 103.1      | 310.0                        | 7                |
|           | Hunter Cr.        | 16                               | 60                        | 60.4                      | 461                           | 290  | 290  | 5.7                                  | 42.7   | 95.3       | 262.8                        | -                |
|           | Pikes Fork Cr.    | 28                               | 30                        | 61.2                      | 461                           | 417  | 461  | 28.1                                 | 99.9   | 107.8      | 352.8                        | 21               |

Table 2. Results of repeated measures analysis of variance on resident trout biomass and density responses to experimental treatment additions over the duration of our experiment. Trt = Treatment

| Cohort | Effect   | Resident trout |          |                |          |
|--------|----------|----------------|----------|----------------|----------|
|        |          | <u>Biomass</u> |          | <u>Density</u> |          |
|        |          | <i>F</i>       | <i>p</i> | <i>F</i>       | <i>p</i> |
| Age 0+ | Trt      | 0.24           | 0.79     | 0.2            | 0.82     |
|        | Year     | 0.17           | 0.91     | 0.81           | 0.50     |
|        | Trt*Year | 0.21           | 0.96     | 0.35           | 0.90     |
| Age 1  | Trt      | 1.19           | 0.36     | 0.46           | 0.65     |
|        | Year     | 1.00           | 0.41     | 1.05           | 0.39     |
|        | Trt*Year | 0.29           | 0.93     | 0.27           | 0.94     |
| Age 2+ | Trt      | 3.62           | 0.09     | 2.21           | 0.19     |
|        | Year     | 0.97           | 0.42     | 1.47           | 0.25     |
|        | Trt*Year | 0.63           | 0.7      | 1.39           | 0.27     |

## Figures

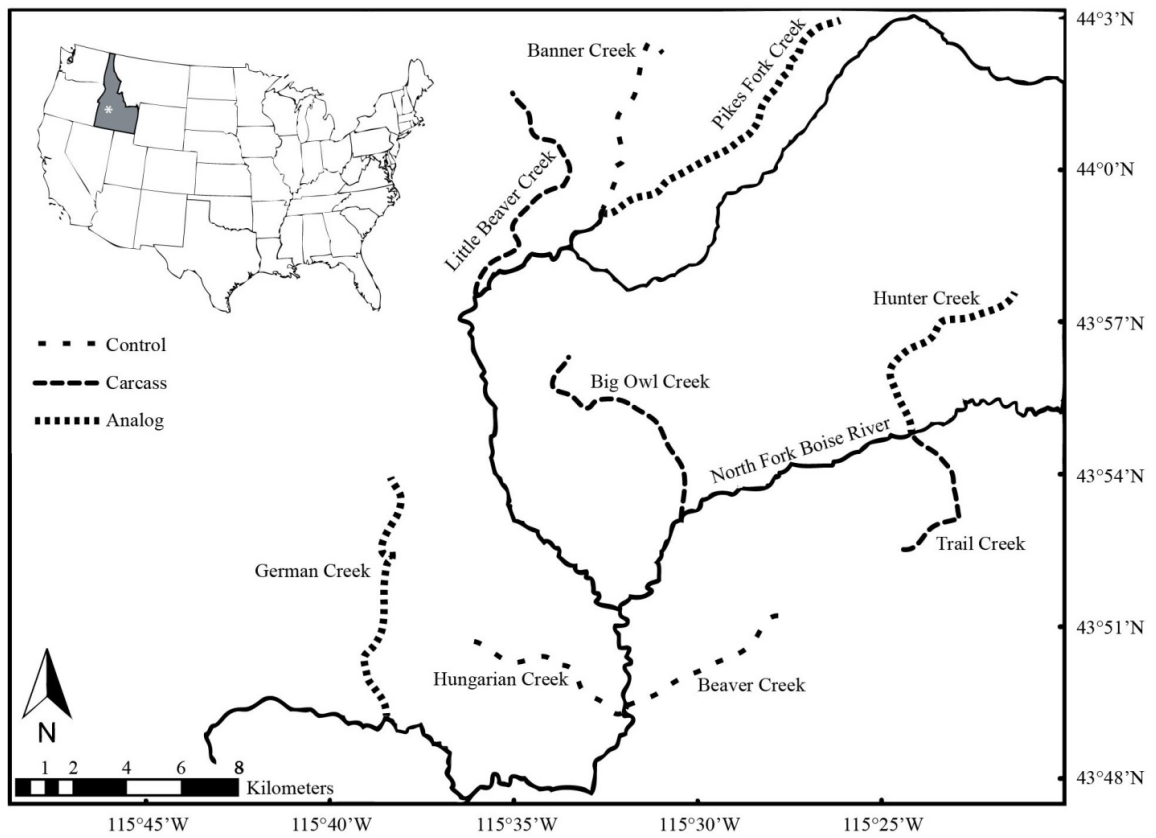


Figure 1. Map of experimental streams and study area in the North Fork Boise River, Idaho, USA. Dashed lines indicate study streams.

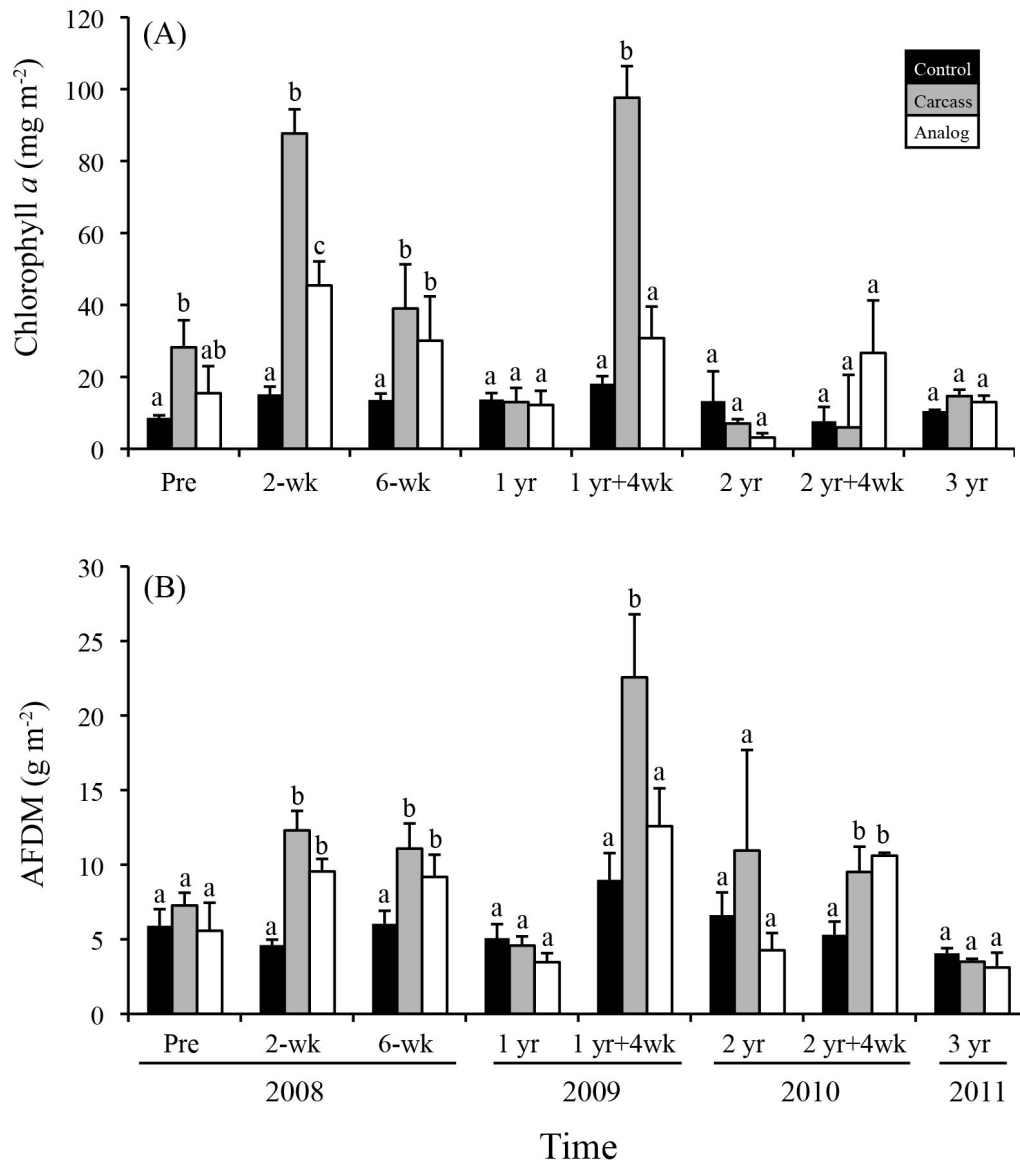


Figure 2. Chlorophyll *a* (A) and ash-free dry mass (AFDM) (B) of stream biofilms sampled prior to (Pre, 2008), and the weeks and years following annual treatment additions from 2008-2011. Groups of columns represent treatments and control for specific sampling periods. Samples 1, 2 and 3 yr represent inter-annual sampling that occurred prior to annual treatment additions. Treatment additions occurred during August of 2008-2010. Error bars are ±1 SE (n=3).

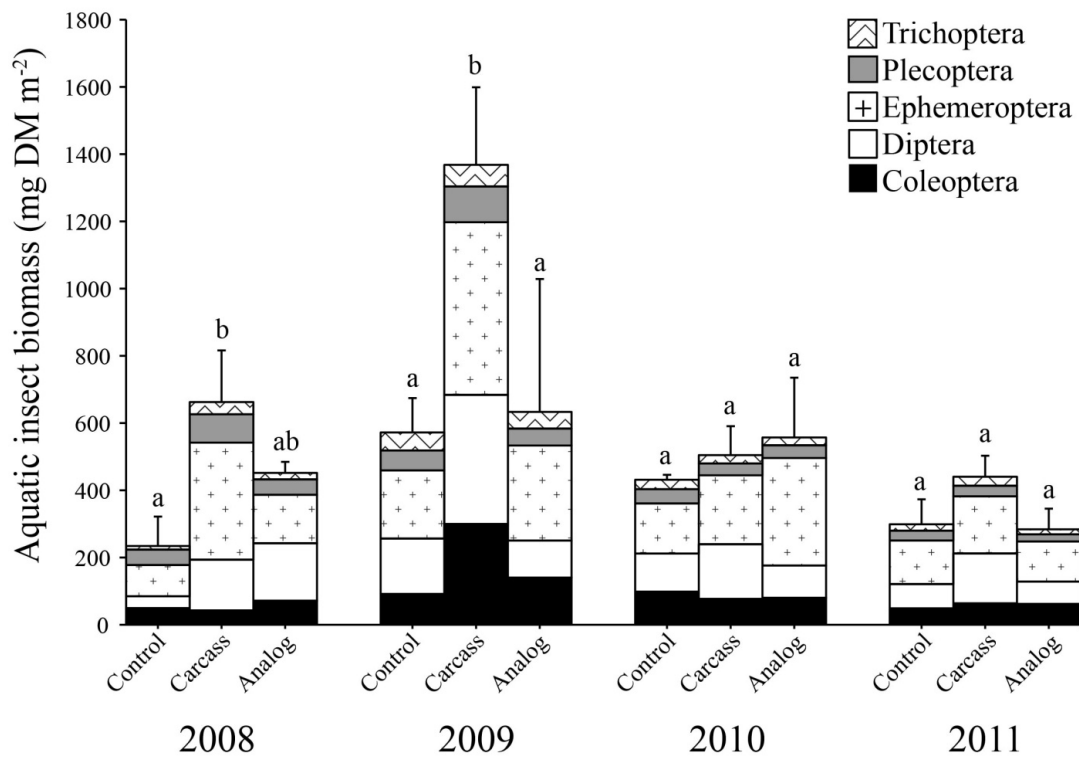


Figure 3. Annual biomass (mg dry mass m<sup>2</sup>) of larval aquatic insects sampled from 2008 to 2011. Insect biomass increased significantly during summer 2009 in carcass treatments, but not in 2010 or 2011. Error bars are  $\pm 1$  SE (n=3). DM = dry mass

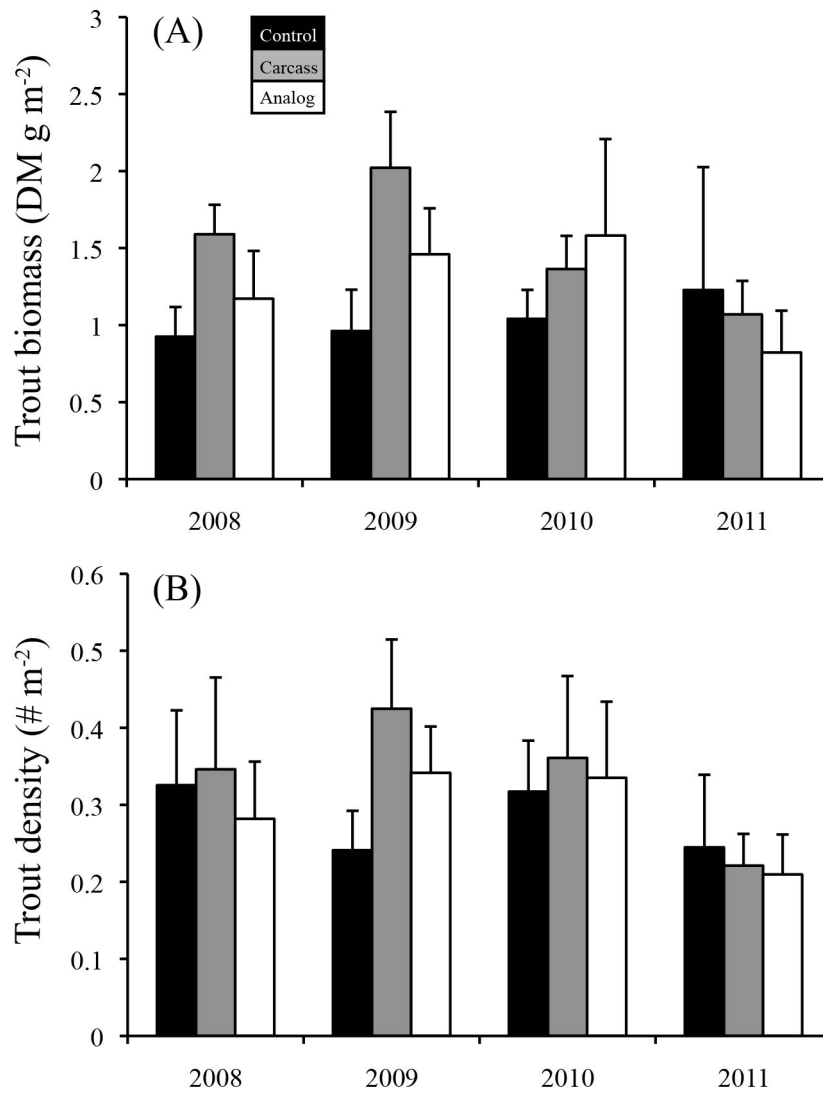


Figure 4. Biomass (A) and density (B) of trout in streams of the North Fork Boise basin during annual sampling events for years 2008-2011. Error bars are  $\pm 1$  SE (n=3).

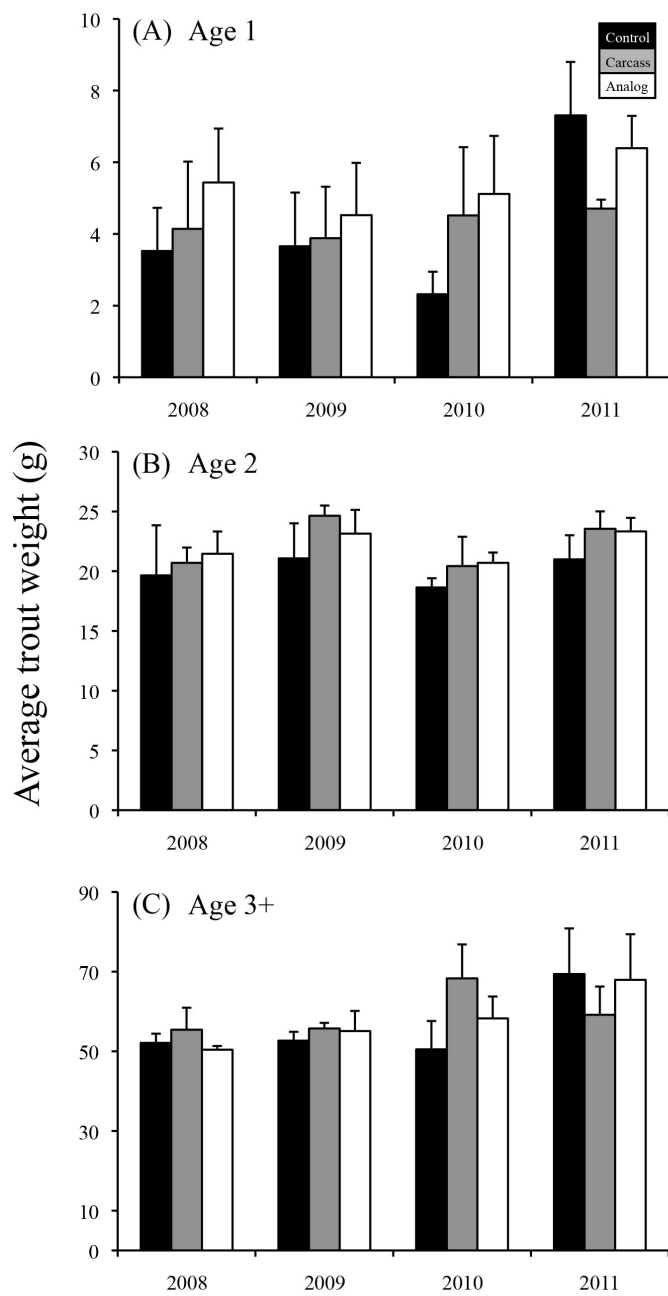


Figure 5. Average weight of (A) age 1, (B) age 2, and (C) age 3+ trout sampled during annual (July) population surveys for years 2008-2011. Error bars are  $\pm 1$  SE (n=3).

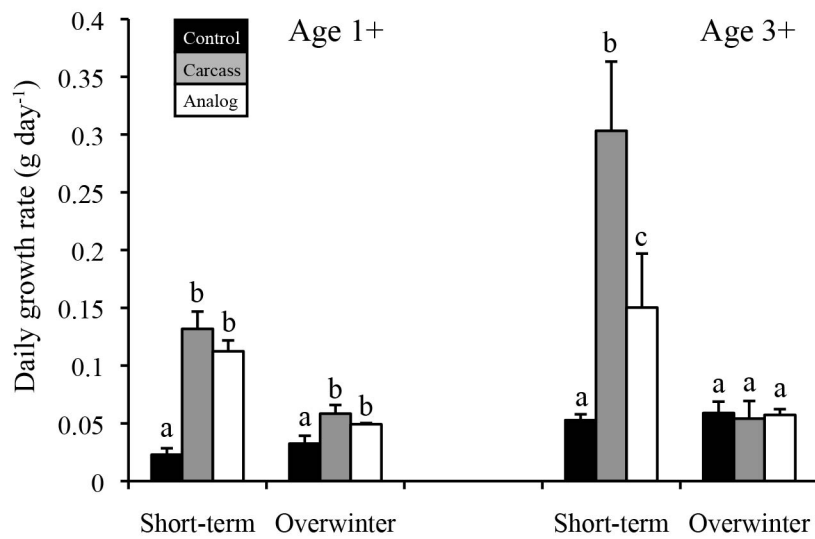


Figure 6. Growth rates of resident trout for age 1+ and age 3+ trout. Short-term responses occurred in the 0-6 weeks post treatment applications of each year. Overwinter growth rates account for periods of time from early October, through winter, to sampling periods occurring in July. Error bars are  $\pm 1$  SE (n=3).

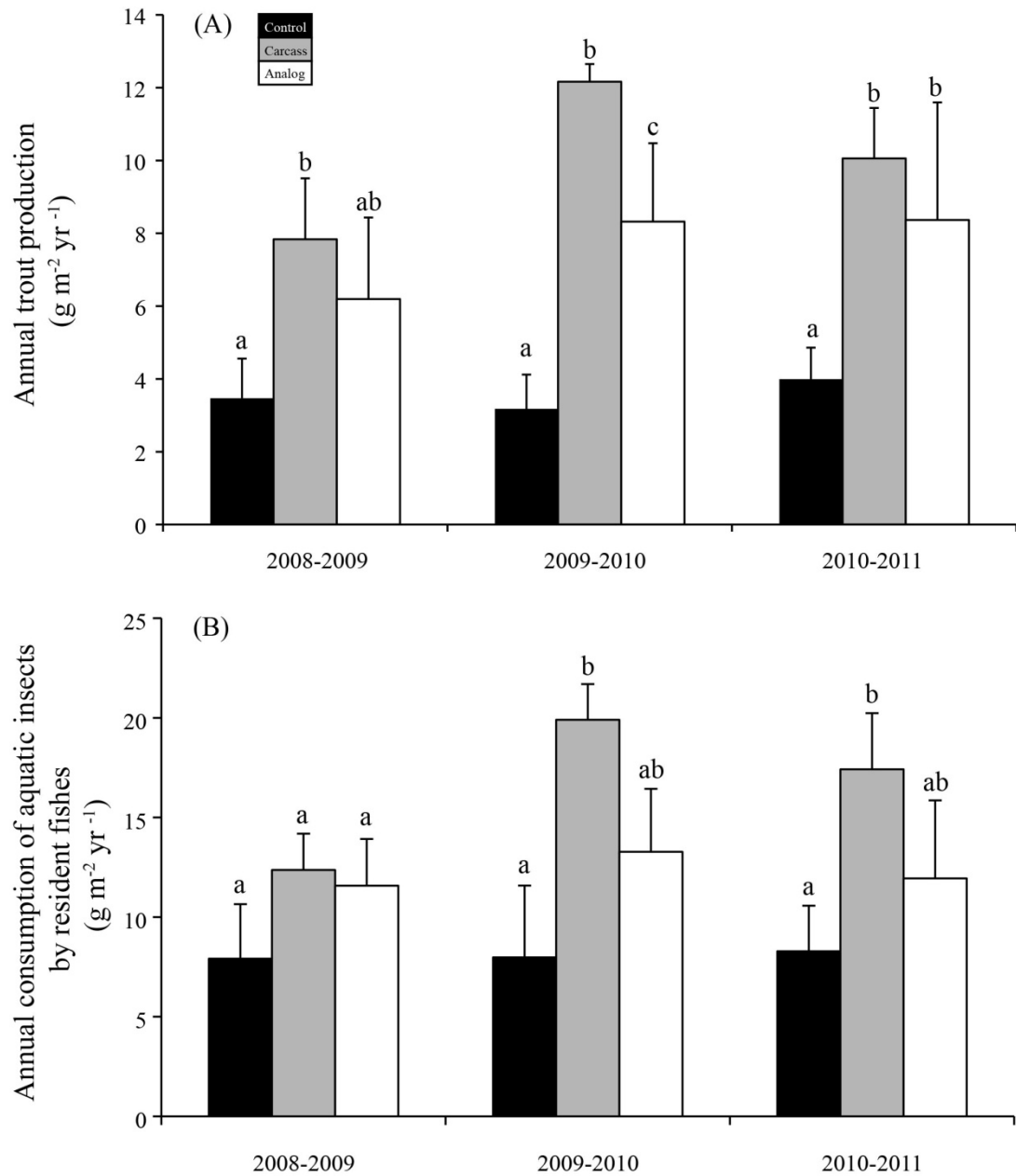


Figure 7. (A) Annual production of resident trout and (B) the estimated consumption of benthic invertebrates by resident fishes over the duration of the experiment. Error bars are  $\pm 1$  SE ( $n=3$ ).

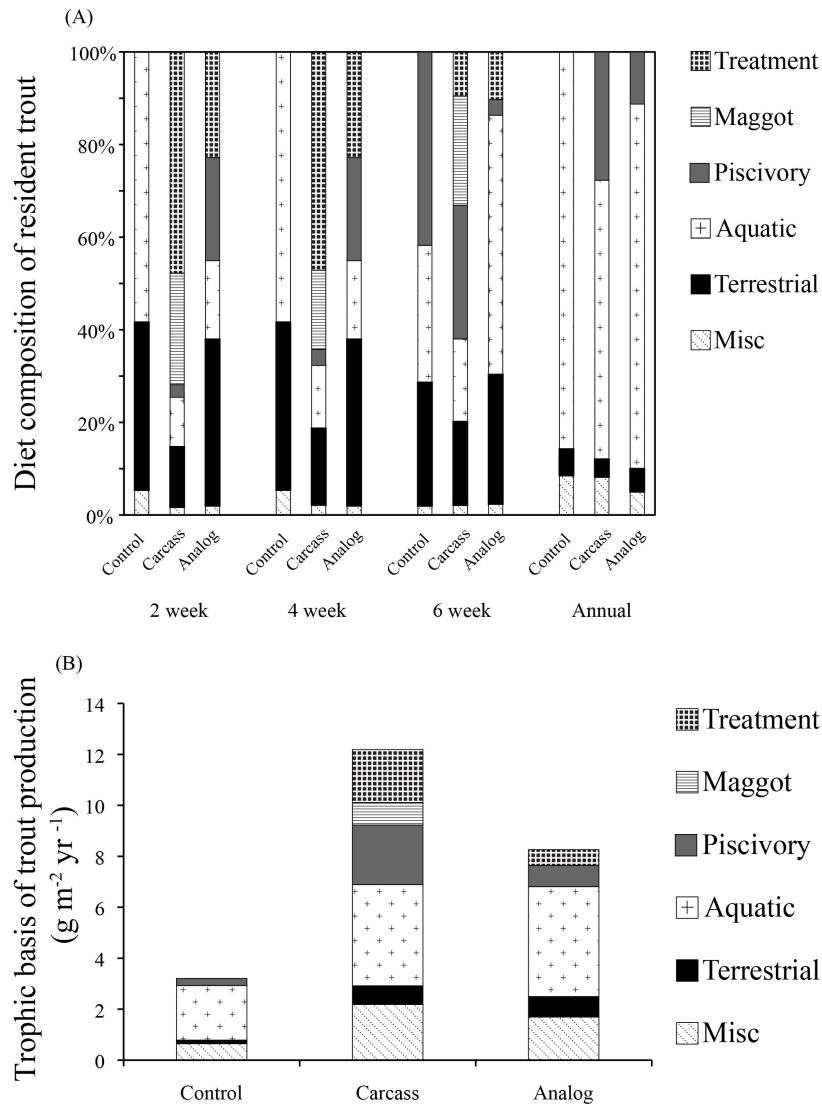


Figure 8. (A) Average diet composition of resident trout populations 2, 4, and 6 weeks after treatment additions and annual sampling events. (B) Trophic basis of trout production for aquatic, terrestrial, and marine diet items. Treatment additions increased the trophic basis of trout production through the consumption of benthic invertebrates, piscivory, and direct consumption of both salmon carcass and salmon carcass analog material. Additionally, indirect feedbacks via the input of terrestrial maggots were observed in carcass treatments, but not analog.

## Appendix

Appendix 2a. Summary of benthic invertebrate density (#/m<sup>2</sup>) and biomass (mg/m<sup>2</sup> DM) and associated standard errors (n=3) for years 2008-2011. Genera represent larval stages unless otherwise noted.

| Year | Treatment | Order         | Family          | Genus                    | Density (SE)<br>#/m <sup>2</sup> | Biomass (SE)<br>mg/m <sup>2</sup> |
|------|-----------|---------------|-----------------|--------------------------|----------------------------------|-----------------------------------|
| 2008 | Control   | Coleoptera    | Elmidae         | <i>Cleptelmis</i> Adult  | 0.75 (0.25)                      | 6.51 (2.3)                        |
|      |           |               |                 | <i>Cleptelmis</i> Larvae | 6.6 (2.21)                       | 49.41 (12.74)                     |
|      |           |               |                 | <i>Lara</i>              | 2.35 (2.35)                      | 13.8 (13.8)                       |
|      |           | Diptera       | Athericidae     | <i>Atherix</i>           | 0.07 (0.07)                      | 0.68 (0.68)                       |
|      |           |               |                 | <i>Bezzia</i>            | 0.29 (0.14)                      | 4.14 (1.97)                       |
|      |           |               | Ceratopogonidae | Larvae                   | 6.99 (4.38)                      | 22.48 (12.02)                     |
|      |           |               |                 | Pupae                    | 5.94 (5.83)                      | 15.84 (15.3)                      |
|      |           |               | Chironomidae    | Pupae                    | 0.03 (0.03)                      | 0.46 (0.46)                       |
|      |           |               |                 | <i>Pericoma</i>          | 0.79 (0.01)                      | 5.71 (0.35)                       |
|      |           |               | Simuliidae      | <i>Simulium</i> Larvae   | 2.54 (1.21)                      | 10.1 (3.42)                       |
|      |           |               | Tipulidae       | <i>Tipula</i>            | 0.14 (0.14)                      | 1.31 (1.31)                       |
|      |           | Ephemeroptera | Ameletidae      | <i>Ameletus</i>          | 1.68 (1.11)                      | 7.7 (2.79)                        |
|      |           |               |                 | <i>Baetis</i>            | 14.57 (7.68)                     | 55.22 (26.47)                     |
|      |           |               | Baetidae        | <i>Drunella</i>          | 0.38 (0.33)                      | 3.29 (3.01)                       |
|      |           |               |                 | <i>Ephemerella</i>       | 2.99 (2.08)                      | 11.89 (4.62)                      |
|      |           |               | Heptageniidae   | <i>Cinygmula</i>         | 7.53 (0.7)                       | 27.45 (1.36)                      |
|      |           |               |                 | <i>Epeorus</i>           | 6.08 (3.05)                      | 34.8 (22.67)                      |
|      |           |               | Rithrogena      | <i>Rithrogena</i>        | 3.47 (0.96)                      | 19.77 (7.79)                      |
|      |           |               |                 | <i>Paraleptophlebia</i>  | 3.7 (3.18)                       | 14.68 (9.13)                      |
|      |           | Plecoptera    | Leptophlebiidae | <i>Chloroperla</i>       | 2.05 (2.05)                      | 16.47 (16.47)                     |
|      |           |               |                 | <i>Kathoperla</i>        | 1.06 (0.35)                      | 7.47 (1.07)                       |
|      |           |               | Yoraperla       | <i>Yoraperla</i>         | 0.97 (0.97)                      | 3 (3)                             |
|      |           |               |                 | <i>Zapada</i>            | 0.95 (0.95)                      | 10.65 (10.65)                     |
|      |           |               | Paraleuctridae  | <i>Paraleuctra</i>       | 2.14 (1.75)                      | 10.41 (5.47)                      |
|      |           |               |                 | <i>Yoraperla</i>         | 2.78 (2.37)                      | 18.91 (15.35)                     |
|      |           |               | Peltoperlidae   | <i>Doroneuria</i>        | 1.09 (0.46)                      | 12.8 (4.13)                       |
|      |           |               |                 | <i>Megarcys</i>          | 2.8 (1.63)                       | 19.88 (9.58)                      |
|      |           |               | Perlidae        | <i>Skwala</i>            | 1.63 (1.63)                      | 8.8 (8.8)                         |
|      |           |               |                 | <i>Brachycentrus</i>     | 0.38 (0.33)                      | 1.28 (0.88)                       |
|      |           | Trichoptera   | Glossosomatidae | <i>Glossosoma</i>        | 0.14 (0.09)                      | 1.71 (1.14)                       |
|      |           |               |                 | <i>Arctopsyche</i>       | 0.25 (0.13)                      | 5.51 (3.31)                       |
|      |           |               | Hydropsychidae  | <i>Hydropsyche</i>       | 0.1 (0.06)                       | 2.76 (2.17)                       |
|      |           |               |                 | <i>Doliphoides</i>       | 0.29 (0.15)                      | 5.46 (3.21)                       |
|      |           |               | Philopotamidae  | <i>Rhyacophila</i>       | 0.38 (0.2)                       | 6.9 (3.47)                        |
|      |           |               |                 | <i>Cleptelmis</i> Adult  | 0.62 (0.11)                      | 4.79 (1.19)                       |
|      |           | Carcass       | Coleoptera      | <i>Cleptelmis</i> Larvae | 5.9 (2.35)                       | 43.57 (17.81)                     |
|      |           |               |                 | <i>Atherix</i>           | 0.09 (0.09)                      | 0.63 (0.63)                       |
|      |           |               | Diptera         | <i>Bezzia</i>            | 0.51 (0.07)                      | 7.49 (1.19)                       |
|      |           |               |                 | Larvae                   | 23.4 (2.47)                      | 115.01 (12.06)                    |
|      |           |               | Pupae           | <i>Pupae</i>             | 0.8 (0.21)                       | 7.05 (2.99)                       |
|      |           |               |                 | <i>Deutrophlibidae</i>   | 0.03 (0.03)                      | 0.27 (0.27)                       |

|        |               |                 |                          |               |                |
|--------|---------------|-----------------|--------------------------|---------------|----------------|
| Analog | Ephemeroptera | Dixidae         | <i>Dixa</i>              | 0.03 (0.03)   | 0.46 (0.46)    |
|        |               | Psychodidae     | <i>Pericoma</i>          | 9.59 (6.14)   | 80.41 (50.24)  |
|        |               | Simuliidae      | <i>Simulium</i> Larvae   | 1.34 (0.8)    | 10.84 (6.08)   |
|        |               |                 | <i>Simulium</i> Pupae    | 0.1 (0.1)     | 0.94 (0.94)    |
|        |               | Tipulidae       | <i>Hexatoma</i>          | 0.03 (0.03)   | 1.87 (1.87)    |
|        |               |                 | <i>Tipula</i>            | 0.7 (0.22)    | 8.54 (2.23)    |
|        |               | Ameletidae      | <i>Ameletus</i>          | 4.32 (2.31)   | 44.22 (13.35)  |
|        |               | Baetidae        | <i>Baetis</i>            | 31.13 (14.35) | 157.48 (67.81) |
|        |               | Ephemerellidae  | <i>Drunella</i>          | 0.07 (0.03)   | 1.03 (0.52)    |
|        |               |                 | <i>Ephemerella</i>       | 7.47 (0.54)   | 46.24 (1.3)    |
|        |               |                 | <i>Serratella</i>        | 3.61 (3.4)    | 15.54 (13.3)   |
|        | Plecoptera    | Heptageniidae   | <i>Cinygmula</i>         | 24.56 (6.92)  | 101.19 (29.25) |
|        |               |                 | <i>Epeorus</i>           | 4.25 (3.22)   | 15.13 (8.71)   |
|        |               |                 | <i>Rithrogena</i>        | 12.94 (6.28)  | 83.55 (24.7)   |
|        |               | Leptophlebiidae | <i>Paraleptophlebia</i>  | 4.03 (1.23)   | 34.95 (9.79)   |
|        |               | Chloroperlidae  | <i>Kathoperla</i>        | 0.57 (0.57)   | 6.22 (6.22)    |
|        |               |                 | <i>Sweltsa</i>           | 0.94 (0.47)   | 12.28 (6.53)   |
|        |               |                 | <i>Yoraperla</i>         | 2.88 (2.88)   | 16.04 (16.04)  |
|        |               | Nemouridae      | <i>Zapada</i>            | 3.95 (0.73)   | 31.35 (10.51)  |
|        |               | Paraleuctridae  | <i>Paraleuctra</i>       | 1.02 (0.55)   | 6.74 (0.7)     |
|        |               | Peltoperlidae   | <i>Yoraperla</i>         | 0.19 (0.19)   | 2.08 (2.08)    |
| Analog | Trichoptera   | Perlidae        | <i>Doroneuria</i>        | 2.75 (2.45)   | 26.01 (14.27)  |
|        |               | Perlodidae      | <i>Megarcys</i>          | 5.86 (0.76)   | 43.51 (5.33)   |
|        |               | Brachycentridae | <i>Skwala</i>            | 3.51 (2.39)   | 30.1 (17.84)   |
|        |               |                 | <i>Brachycentrus</i>     | 0.19 (0.05)   | 1.78 (0.62)    |
|        |               |                 | <i>Glossosoma</i>        | 0.81 (0.38)   | 17.62 (13.1)   |
|        |               | Glossosomatidae | <i>Micrasema</i>         | 0.73 (0.73)   | 8.03 (8.03)    |
|        |               |                 | <i>Arctopsyche</i>       | 1.91 (0.58)   | 46.87 (19.8)   |
|        |               | Hydropsychidae  | <i>Hydropsyche</i>       | 0.17 (0.17)   | 1.63 (1.63)    |
|        |               |                 | <i>Doliphoides</i>       | 1.23 (0.64)   | 35.52 (20.75)  |
|        |               | Philopotamidae  | <i>Rhyacophila</i>       | 0.39 (0.11)   | 7.79 (3.12)    |
|        | Coleoptera    | Elmidae         | <i>Cleptelmis</i> Adult  | 3.05 (1.97)   | 25.47 (17.23)  |
|        |               |                 | <i>Cleptelmis</i> Larvae | 8.43 (2.7)    | 65.64 (15.92)  |
|        |               | Athericidae     | <i>Atherix</i>           | 0.17 (0.09)   | 1.62 (1.13)    |
|        |               |                 | <i>Bezzia</i>            | 0.78 (0.22)   | 12.66 (3.85)   |
|        |               | Chironomidae    | Larvae                   | 19.01 (8.11)  | 105.18 (40.23) |
|        |               |                 | Pupae                    | 3.85 (1.23)   | 28.64 (8.37)   |
|        |               | Dixidae         | <i>Dixa</i>              | 0.19 (0.14)   | 1.78 (1.27)    |
|        |               | Psychodidae     | <i>Pericoma</i>          | 7.62 (2.23)   | 55.1 (4.23)    |
|        |               | Simuliidae      | <i>Simulium</i> Larvae   | 0.78 (0.53)   | 4.41 (2.44)    |
|        |               |                 | <i>Simulium</i> Pupae    | 0.1 (0.1)     | 1.26 (1.26)    |
| Analog | Diptera       | Tipulidae       | <i>Hexatoma</i>          | 0.14 (0.07)   | 4.92 (2.56)    |
|        |               |                 | <i>Tipula</i>            | 0.34 (0.15)   | 4.47 (1.26)    |
|        |               | Ameletidae      | <i>Ameletus</i>          | 1.3 (0.6)     | 15.54 (10.08)  |
|        |               |                 | <i>Baetis</i>            | 13.55 (2.96)  | 65.44 (9.25)   |
|        |               | Ephemerellidae  | <i>Drunella</i>          | 0.18 (0.08)   | 2.77 (0.66)    |
|        |               |                 | <i>Ephemerella</i>       | 2.56 (0.89)   | 14.68 (5.37)   |
|        |               |                 | <i>Serratella</i>        | 0.1 (0.1)     | 0.84 (0.84)    |
|        |               | Heptageniidae   | <i>Cinygmula</i>         | 12.93 (2.22)  | 50.03 (12.02)  |

|      |         |                |                       |                          |                         |                |                |
|------|---------|----------------|-----------------------|--------------------------|-------------------------|----------------|----------------|
| 2009 | Control |                |                       | <i>Epeorus</i>           | 4.7 (1.13)              | 19.77 (4.96)   |                |
|      |         |                |                       | <i>Rithrogena</i>        | 5.39 (0.15)             | 23.55 (4.39)   |                |
|      |         |                | Plecoptera            | Leptophlebiidae          | <i>Paraleptophlebia</i> | 1.85 (0.92)    | 15.16 (6.91)   |
|      |         |                |                       | Chloroperlidae           | <i>Chloroperla</i>      | 0.21 (0.21)    | 3.33 (3.33)    |
|      |         |                |                       |                          | <i>Kathoperla</i>       | 1.51 (0.99)    | 16.71 (10.63)  |
|      |         |                |                       |                          | <i>Sweltsa</i>          | 1.49 (1.15)    | 8.76 (4.88)    |
|      |         |                |                       |                          | <i>Yoraperla</i>        | 0.35 (0.35)    | 2.48 (2.48)    |
|      |         |                |                       |                          | Nemouridae              | <i>Zapada</i>  | 2.68 (2.51)    |
|      |         |                | Paraleuctridae        | <i>Paraleuctra</i>       | 0.81 (0.66)             | 5.45 (3.4)     |                |
|      |         |                | Perlidae              | <i>Doroneuria</i>        | 0.32 (0.05)             | 7.39 (1.16)    |                |
|      |         |                | Perlodidae            | <i>Megarcys</i>          | 7.06 (2.31)             | 31.58 (6.55)   |                |
|      |         |                |                       | <i>Skwala</i>            | 8.02 (7.81)             | 32.62 (31.03)  |                |
|      |         | Trichoptera    | Brachycentridae       | <i>Brachycentrus</i>     | 0.33 (0.17)             | 2.79 (1.44)    |                |
|      |         |                | Glossosomatidae       | <i>Glossosoma</i>        | 1.08 (0.61)             | 9.26 (4.08)    |                |
|      |         |                |                       | <i>Micrasema</i>         | 0.23 (0.23)             | 2.45 (2.45)    |                |
|      |         |                |                       | Hydropsychidae           | <i>Arctopsyche</i>      | 0.49 (0.2)     | 9.16 (2.91)    |
|      |         |                | Limniphilidae         | <i>Eocosmoecus</i>       | 0.1 (0.06)              | 7.26 (4.08)    |                |
|      |         |                | Philopotamidae        | <i>Doliphoides</i>       | 0.53 (0.31)             | 9.03 (4.16)    |                |
|      |         | Coleoptera     | Rhyacophilidae        | <i>Rhyacophila</i>       | 0.41 (0.1)              | 7.3 (1.41)     |                |
|      |         |                | Elmidae               | <i>Cleptelmis</i> Adult  | 1.83 (0.69)             | 20.02 (10.05)  |                |
|      |         |                |                       | <i>Cleptelmis</i> Larvae | 19.91 (6.52)            | 89.94 (18.09)  |                |
|      |         |                |                       | <i>Lara</i>              | 0.84 (0.48)             | 14.34 (9.29)   |                |
|      |         |                | Diptera               | Athericidae              | <i>Atherix</i>          | 0.03 (0.03)    | 0.54 (0.54)    |
|      |         |                |                       | Ceratopogonidae          | <i>Bezzia</i>           | 0.42 (0.02)    | 7.18 (0.66)    |
|      |         |                |                       | Chironomidae             | Larvae                  | 28.22 (11.94)  | 112.84 (45.58) |
|      |         |                |                       |                          | Pupae                   | 0.2 (0.1)      | 1.76 (0.88)    |
|      |         |                |                       | Dixidae                  | <i>Dixa</i>             | 0.49 (0.27)    | 5.19 (2.92)    |
|      |         |                |                       | Simuliidae               | <i>Simulium</i> Larvae  | 13.04 (1.78)   | 61.16 (6.27)   |
|      |         |                | <i>Simulium</i> Pupae |                          | 0.1 (0.1)               | 0.94 (0.94)    |                |
|      |         |                | Tabanidae             | <i>Tabanus</i>           | 0.38 (0.08)             | 7.32 (1.15)    |                |
|      |         | Tipulidae      | <i>Antocha</i>        | 0.1 (0.1)                | 1.77 (1.77)             |                |                |
|      |         |                | <i>Hexatoma</i>       | 0.03 (0.03)              | 1.27 (1.27)             |                |                |
|      |         |                | <i>Tipula</i>         | 0.28 (0.02)              | 5.79 (1.53)             |                |                |
|      |         |                |                       |                          |                         |                |                |
|      |         | Ephemeroptera  | Ameletidae            | <i>Ameletus</i>          | 0.1 (0.1)               | 1.63 (1.63)    |                |
|      |         |                | Baetidae              | <i>Baetis</i>            | 18.43 (4.79)            | 83.73 (17.05)  |                |
|      |         |                | Ephemerellidae        | <i>Drunella</i>          | 2.17 (1.05)             | 21.01 (5.37)   |                |
|      |         |                |                       | <i>Ephemerella</i>       | 6.52 (2.22)             | 35.19 (8.81)   |                |
|      |         |                |                       | <i>Serratella</i>        | 7.08 (6.88)             | 34.08 (31.71)  |                |
|      |         |                |                       |                          |                         |                |                |
|      |         |                | Heptageniidae         | <i>Cinygmula</i>         | 38 (27.13)              | 129.31 (87.13) |                |
|      |         |                |                       | <i>Epeorus</i>           | 4.4 (1.21)              | 34.19 (9.65)   |                |
|      |         |                |                       | <i>Rithrogena</i>        | 0.28 (0.28)             | 2.9 (2.9)      |                |
|      |         |                |                       |                          |                         |                |                |
|      |         |                | Plecoptera            | Leptophlebiidae          | <i>Paraleptophlebia</i> | 19.48 (19.48)  | 63.41 (63.41)  |
|      |         |                |                       | Chloroperlidae           | <i>Kathoperla</i>       | 5.14 (1.18)    | 33.73 (14.53)  |
|      |         | Paraleuctridae |                       | <i>Paraleuctra</i>       | 0.09 (0.09)             | 1.33 (1.33)    |                |
|      |         | Peltoperlidae  |                       | <i>Yoraperla</i>         | 1.65 (1.23)             | 15.34 (11.9)   |                |
|      |         | Perlidae       |                       | <i>Doroneuria</i>        | 0.26 (0.13)             | 6.34 (3.17)    |                |
|      |         | Perlodidae     |                       | <i>Megarcys</i>          | 6.81 (4.43)             | 27.54 (15.36)  |                |
|      |         | Trichoptera    |                       | <i>Skwala</i>            | 0.24 (0.24)             | 3.01 (3.01)    |                |
|      |         |                | Brachycentridae       | <i>Brachycentrus</i>     | 0.57 (0.31)             | 7.01 (3.16)    |                |
|      |         |                |                       |                          |                         |                |                |

|         |               |                  |                           |               |                |
|---------|---------------|------------------|---------------------------|---------------|----------------|
| Carcass | Coleoptera    | Glossosomatidae  | <i>Glossosoma</i>         | 0.56 (0.33)   | 3.99 (2.43)    |
|         |               |                  | <i>Micrasema</i>          | 1.76 (0.86)   | 20.19 (9.73)   |
|         |               | Hydropsychidae   | <i>Arctopsyche</i>        | 0.22 (0.16)   | 8.76 (5.17)    |
|         |               |                  | <i>Hydropsyche</i> Larvae | 0.03 (0.03)   | 0.82 (0.82)    |
|         |               |                  | <i>Hydropsyche</i> Pupae  | 0.14 (0.14)   | 3.32 (3.32)    |
|         |               | Lepidostomatidae | <i>Lepidostoma</i>        | 0.03 (0.03)   | 0.92 (0.92)    |
|         |               | Limniphilidae    | <i>Eocosmoecus</i>        | 0.26 (0.08)   | 8.64 (0.14)    |
|         |               | Philopotamidae   | <i>Doliphoides</i>        | 2.53 (1.14)   | 30.39 (12.65)  |
|         |               | Rhyacophilidae   | <i>Rhyacophila</i> Larvae | 1.01 (0.32)   | 19.7 (6.36)    |
|         |               |                  | <i>Rhyacophila</i> Pupae  | 0.19 (0.03)   | 3.87 (0.68)    |
|         |               | Elmidae          | <i>Cleptelmis</i> Adult   | 2.78 (0.26)   | 23.85 (2.08)   |
|         |               |                  | <i>Cleptelmis</i> Larvae  | 21.8 (6.25)   | 140.57 (28.18) |
|         |               |                  | <i>Lara</i>               | 0.36 (0.04)   | 5.59 (0.37)    |
|         | Diptera       | Athericidae      | <i>Atherix</i>            | 0.1 (0.06)    | 1.62 (1.02)    |
|         |               | Ceratopogonidae  | <i>Bezzia</i>             | 3.93 (1.78)   | 16.97 (4.24)   |
|         |               | Chironomidae     | Larvae                    | 34.41 (12.77) | 150.42 (30.06) |
|         |               |                  | Pupae                     | 0.14 (0.09)   | 1.14 (0.67)    |
|         |               | Dixidae          | <i>Dixa</i>               | 0.03 (0.03)   | 0.5 (0.5)      |
|         |               | Simuliidae       | <i>Simulium</i> Larvae    | 19.36 (2.57)  | 92.99 (12.43)  |
|         |               |                  | <i>Simulium</i> Pupae     | 0.31 (0.17)   | 3.69 (2.12)    |
|         |               | Tabanidae        | <i>Tabanus</i>            | 0.24 (0.03)   | 4.59 (0.39)    |
|         |               | Tipulidae        | <i>Antocha</i>            | 0.17 (0.17)   | 2.71 (2.71)    |
|         |               |                  | <i>Hexatoma</i>           | 0.17 (0.03)   | 8.57 (3.2)     |
|         |               |                  | <i>Tipula</i>             | 0.23 (0.09)   | 4.2 (1.68)     |
|         | Ephemeroptera | Ameletidae       | <i>Ameletus</i>           | 1.55 (0.96)   | 8.01 (1.63)    |
|         |               | Baetidae         | <i>Baetis</i>             | 33.32 (3.51)  | 150.38 (4.56)  |
|         |               | Ephemerellidae   | <i>Drunella</i>           | 1.07 (0.45)   | 14.72 (2.34)   |
|         |               |                  | <i>Ephemerella</i>        | 7.92 (1.51)   | 55.01 (4.13)   |
|         |               |                  | <i>Serratella</i>         | 1.88 (0.47)   | 23.42 (6.46)   |
|         |               | Heptageniidae    | <i>Cinygmula</i>          | 21.42 (3.24)  | 92.71 (16.86)  |
|         |               |                  | <i>Epeorus</i>            | 4.94 (2.53)   | 39.86 (22.89)  |
|         |               |                  | <i>Rithrogena</i>         | 3.23 (3.23)   | 29.1 (29.1)    |
|         |               | Leptophlebiidae  | <i>Paraleptophlebia</i>   | 2.45 (1.34)   | 18.72 (10.24)  |
|         | Oligochaeta   |                  |                           | 0.69 (0.69)   | 20.65 (20.65)  |
|         | Plecoptera    | Chloroperlidae   | <i>Kathoperla</i>         | 5.18 (2.63)   | 35.54 (10.2)   |
|         |               |                  | <i>Sweltsa</i>            | 0.76 (0.4)    | 9.52 (4.99)    |
|         |               | Nemouridae       | <i>Zapada</i>             | 0.14 (0.14)   | 1.64 (1.64)    |
|         |               | Paraleuctridae   | <i>Paraleuctra</i>        | 1.43 (1.17)   | 7.31 (5.97)    |
|         |               | Peltoperlidae    | <i>Yoraperla</i>          | 0.03 (0.03)   | 0.29 (0.29)    |
|         |               | Perlidae         | <i>Doroneuria</i>         | 1.52 (1.08)   | 14.56 (8.08)   |
|         |               | Perlodidae       | <i>Megarcys</i>           | 4.34 (1.92)   | 18.56 (7.41)   |
|         |               |                  | <i>Skwala</i>             | 0.95 (0.73)   | 10.78 (7.92)   |
|         | Trichoptera   | Brachycentridae  | <i>Brachycentrus</i>      | 2.61 (2.61)   | 10.21 (10.21)  |
|         |               | Glossosomatidae  | <i>Glossosoma</i> Larvae  | 0.03 (0.03)   | 0.67 (0.67)    |
|         |               |                  | <i>Glossosoma</i> Pupae   | 0.12 (0.12)   | 1.69 (1.69)    |
|         |               |                  | <i>Micrasema</i>          | 0.07 (0.07)   | 0.62 (0.62)    |
|         |               | Hydropsychidae   | <i>Arctopsyche</i>        | 0.03 (0.03)   | 0.31 (0.31)    |
|         |               | Limniphilidae    | <i>Eocosmoecus</i>        | 0.25 (0.08)   | 9.54 (2.98)    |
|         |               |                  | <i>Eocosmoecus</i> Pupae  | 0.07 (0.07)   | 2.35 (2.35)    |

|        |               |                 |                           |              |               |
|--------|---------------|-----------------|---------------------------|--------------|---------------|
| Analog | Coleoptera    | Philopotamidae  | <i>Doliphoides</i>        | 0.87 (0.3)   | 14.17 (6.79)  |
|        |               | Rhyacophilidae  | <i>Rhyacophila</i>        | 0.73 (0.1)   | 14.27 (1.93)  |
|        |               |                 | <i>Rhyacophila</i> Pupae  | 0.31 (0.04)  | 6.87 (1.15)   |
|        |               | Elmidae         | <i>Cleptelmis</i> Adult   | 2.74 (1.82)  | 17.53 (9.63)  |
|        |               |                 | <i>Cleptelmis</i> Larvae  | 13.93 (4.61) | 78.86 (27.22) |
|        |               |                 | <i>Lara</i>               | 0.08 (0.06)  | 1.96 (1.6)    |
|        | Diptera       | Athericidae     | <i>Atherix</i>            | 0.14 (0.03)  | 1.76 (0.21)   |
|        |               | Ceratopogonidae | <i>Bezzia</i>             | 1.3 (1.09)   | 6.96 (3.41)   |
|        |               | Chironomidae    | Larvae                    | 13.76 (5.43) | 46.71 (15.3)  |
|        |               | Simuliidae      | <i>Simulium</i> Larvae    | 3.41 (1.46)  | 19.01 (7.43)  |
|        |               |                 | <i>Simulium</i> Pupae     | 1.32 (1.32)  | 15.19 (15.19) |
|        |               | Tabanidae       | <i>Tabanus</i>            | 0.14 (0.07)  | 2.89 (1.48)   |
|        |               | Tipulidae       | <i>Antocha</i>            | 0.09 (0.09)  | 1.82 (1.82)   |
|        |               |                 | <i>Hexatoma</i>           | 0.08 (0.04)  | 1.9 (1.17)    |
|        |               |                 | <i>Tipula</i>             | 0.1 (0)      | 2.33 (0.38)   |
|        | Ephemeroptera | Ameletidae      | <i>Ameletus</i>           | 0.14 (0.14)  | 1.51 (1.51)   |
|        |               | Baetidae        | <i>Baetis</i>             | 15.18 (8.68) | 69.93 (37.02) |
|        |               | Ephemerellidae  | <i>Drunella</i>           | 0.7 (0.23)   | 12.09 (4.18)  |
|        |               |                 | <i>Ephemerella</i>        | 4.8 (2.28)   | 34.31 (14.32) |
|        |               |                 | <i>Serratella</i>         | 1.15 (0.69)  | 14.28 (8.62)  |
|        |               | Heptageniidae   | <i>Cinygmula</i>          | 7.44 (3.18)  | 45.35 (18.46) |
|        |               |                 | <i>Epeorus</i>            | 4.22 (1.73)  | 31.88 (13.8)  |
|        |               |                 | <i>Rithrogena</i>         | 5.07 (3.93)  | 35.57 (26.71) |
|        |               | Leptophlebiidae | <i>Paraleptophlebia</i>   | 0.76 (0.76)  | 9.03 (9.03)   |
|        | Plecoptera    | Chloroperlidae  | <i>Kathoperla</i>         | 1.8 (0.68)   | 20.04 (11.97) |
|        |               |                 | <i>Sweltsa</i>            | 0.21 (0.17)  | 3.14 (2.57)   |
|        |               | Nemouridae      | <i>Zapada</i>             | 0 (0)        | 0 (0)         |
|        |               | Paraleuctridae  | <i>Paraleuctra</i>        | 0.03 (0.03)  | 0.57 (0.57)   |
|        |               | Peltoperlidae   | <i>Yoraperla</i>          | 0.07 (0.07)  | 0.48 (0.48)   |
|        |               | Perlidae        | <i>Doroneuria</i>         | 0.1 (0)      | 2.42 (0.17)   |
|        |               | Perlodidae      | <i>Megarcys</i>           | 1.92 (1.3)   | 11.33 (5.43)  |
|        | Trichoptera   | Brachycentridae | <i>Brachycentrus</i>      | 0.47 (0.34)  | 5.06 (3.39)   |
|        |               | Glossosomatidae | <i>Glossosoma</i> Pupae   | 0.47 (0.24)  | 6.75 (3.38)   |
|        |               |                 | <i>Micrasema</i>          | 0.52 (0.52)  | 5.28 (5.28)   |
|        |               | Hydropsychidae  | <i>Arctopsyche</i>        | 0.45 (0.23)  | 10.41 (5.22)  |
|        |               | Limniphilidae   | <i>Eocosmoecus</i>        | 0.11 (0.07)  | 3.99 (2.67)   |
|        |               | Philopotamidae  | <i>Doliphoides</i>        | 0.33 (0.2)   | 4.14 (2.43)   |
|        |               | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.68 (0.29)  | 13.96 (6.67)  |
|        |               |                 | <i>Rhyacophila</i> Pupae  | 2.13 (1.27)  | 15.31 (8.67)  |
|        | 2010 Control  | Elmidae         | <i>Cleptelmis</i> Adult   | 0.65 (0.28)  | 5.23 (2.3)    |
|        |               |                 | <i>Cleptelmis</i> Larvae  | 21.44 (5.83) | 95.55 (28.25) |
|        |               |                 | <i>Lara</i>               | 0.1 (0.06)   | 1.66 (1.01)   |
|        | Diptera       | Athericidae     | <i>Atherix</i>            | 0.21 (0.06)  | 2.79 (0.7)    |
|        |               | Ceratopogonidae | <i>Bezzia</i>             | 1.17 (0.39)  | 11.85 (4.41)  |
|        |               | Chironomidae    | Larvae                    | 18.21 (0.87) | 81.09 (9.69)  |
|        |               |                 | Pupae                     | 0.68 (0.44)  | 8.33 (5.71)   |
|        |               | Dixidae         | <i>Dixa</i>               | 0.5 (0.5)    | 5.74 (5.74)   |
|        |               | Simuliidae      | <i>Simulium</i> Larvae    | 5.97 (0.73)  | 27.77 (8.53)  |
|        |               |                 | <i>Simulium</i> Pupae     | 0.33 (0.33)  | 2.1 (2.1)     |

|  |               |                 |                           |              |                |
|--|---------------|-----------------|---------------------------|--------------|----------------|
|  |               | Tabanidae       | <i>Tabanus</i>            | 0.1 (0)      | 1.99 (0.09)    |
|  |               | Tipulidae       | <i>Hexatoma</i>           | 0.26 (0.16)  | 4.19 (1.53)    |
|  |               |                 | <i>Tipula</i>             | 0.18 (0.03)  | 2.78 (0.54)    |
|  | Ephemeroptera | Ameletidae      | <i>Ameletus</i>           | 0.63 (0.63)  | 1.63 (1.63)    |
|  |               | Baetidae        | <i>Baetis</i>             | 13.62 (2.34) | 70.48 (9.54)   |
|  |               | Ephemerellidae  | <i>Drunella</i>           | 1.39 (0.79)  | 17.42 (7.88)   |
|  |               |                 | <i>Ephemerella</i>        | 3.84 (1.02)  | 32.25 (8.45)   |
|  |               |                 | <i>Serratella</i>         | 1.51 (0.72)  | 17.46 (8.28)   |
|  |               | Heptageniidae   | <i>Cinygmula</i>          | 8.46 (1.36)  | 37.72 (2.97)   |
|  |               |                 | <i>Epeorus</i>            | 2.59 (0.92)  | 37.21 (13.44)  |
|  |               |                 | <i>Rithrogena</i>         | 0.51 (0.32)  | 6.41 (3.99)    |
|  | Megaloptera   | Sialidae        | <i>Sialis</i>             | 0.05 (0.04)  | 0.72 (0.59)    |
|  | Oligochaeta   |                 |                           | 0.63 (0.51)  | 16.93 (13.82)  |
|  | Plecoptera    | Chloroperlidae  | <i>Kathoperla</i>         | 0.99 (0.35)  | 10.84 (3.97)   |
|  |               |                 | <i>Sweltsa</i>            | 0 (0)        | 0 (0)          |
|  |               | Nemouridae      | <i>Zapada</i>             | 0 (0)        | 0 (0)          |
|  |               | Paraleuctridae  | <i>Paraleuctra</i>        | 0.21 (0)     | 3.46 (0.19)    |
|  |               | Peltoperlidae   | <i>Yoraperla</i>          | 1.24 (0.84)  | 11.57 (7.91)   |
|  |               | Perlidae        | <i>Doroneuria</i>         | 0.43 (0.15)  | 10.88 (1.06)   |
|  |               | Perlodidae      | <i>Megarcys</i>           | 5.72 (1.64)  | 24.74 (3.89)   |
|  |               |                 | <i>Skwala</i>             | 0 (0)        | 0 (0)          |
|  | Trichoptera   | Brachycentridae | <i>Brachycentrus</i>      | 5.45 (2.96)  | 25.19 (11.27)  |
|  |               | Glossosomatidae | <i>Glossosoma</i> Larvae  | 0.05 (0.04)  | 0.54 (0.44)    |
|  |               |                 | <i>Glossosoma</i> Pupae   | 0.85 (0.44)  | 11.81 (6.6)    |
|  |               |                 | <i>Micrasema</i>          | 0.36 (0.2)   | 4.28 (2.26)    |
|  |               | Hydropsychidae  | <i>Arctopsyche</i>        | 0.23 (0.08)  | 7.48 (2.39)    |
|  |               | Limniphilidae   | <i>Eocosmoecus</i> Larvae | 0.1 (0)      | 2.39 (1.28)    |
|  |               |                 | <i>Eocosmoecus</i> Pupae  | 0.1 (0.09)   | 2.29 (1.87)    |
|  |               | Philopotamidae  | <i>Doliphoides</i> Larvae | 0.41 (0.12)  | 6.39 (2.31)    |
|  |               |                 | <i>Doliphoides</i> Pupae  | 0.05 (0.04)  | 1.31 (1.07)    |
|  |               | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.6 (0.12)   | 9.21 (1.33)    |
|  |               |                 | <i>Rhyacophila</i> Pupae  | 0.14 (0.09)  | 3.13 (2.07)    |
|  | Coleoptera    | Elmidae         | <i>Cleptelmis</i> Adult   | 1.62 (0.55)  | 13.17 (4.26)   |
|  |               |                 | <i>Cleptelmis</i> Larvae  | 11.63 (1.9)  | 64.83 (11.44)  |
|  |               |                 | <i>Lara</i>               | 0.26 (0.21)  | 4.38 (3.58)    |
|  | Diptera       | Athericidae     | <i>Atherix</i>            | 0.03 (0.03)  | 0.45 (0.45)    |
|  |               | Ceratopogonidae | <i>Bezzia</i>             | 0.98 (0.32)  | 14.62 (3.12)   |
|  |               | Chironomidae    | Larvae                    | 22.53 (3.37) | 114.34 (16.88) |
|  |               |                 | Pupae                     | 0.21 (0.1)   | 2 (1)          |
|  |               | Dixidae         | <i>Dixa</i>               | 0.05 (0.04)  | 0.82 (0.67)    |
|  |               | Simuliidae      | <i>Simulium</i> Larvae    | 11.49 (5.24) | 58.63 (27.1)   |
|  |               |                 | <i>Simulium</i> Pupae     | 0.89 (0.62)  | 4.38 (2.26)    |
|  |               | Tabanidae       | <i>Tabanus</i>            | 0.21 (0.12)  | 4.07 (2.35)    |
|  |               | Tipulidae       | <i>Hexatoma</i>           | 0.1 (0.09)   | 3.22 (2.63)    |
|  |               |                 | <i>Tipula</i>             | 0.28 (0.13)  | 5.09 (2.19)    |
|  | Ephemeroptera | Ameletidae      | <i>Ameletus</i>           | 0.05 (0.04)  | 0.68 (0.55)    |
|  |               | Baetidae        | <i>Baetis</i>             | 15.93 (1.81) | 87.68 (9.48)   |
|  |               | Ephemerellidae  | <i>Drunella</i>           | 1.1 (0.63)   | 19.11 (9.01)   |
|  |               |                 | <i>Ephemerella</i>        | 4.27 (0.94)  | 43.04 (7.04)   |

|        |               |                 |                           |                |                 |
|--------|---------------|-----------------|---------------------------|----------------|-----------------|
| Analog | Plecoptera    | Heptageniidae   | <i>Serratella</i>         | 0.83 (0.68)    | 10.42 (8.51)    |
|        |               |                 | <i>Cinygmula</i>          | 12.16 (3.6)    | 71.48 (11.46)   |
|        |               |                 | <i>Epeorus</i>            | 11.22 (5.25)   | 66.6 (31.19)    |
|        |               |                 | <i>Rithrogena</i>         | 2.36 (1.02)    | 24.17 (7.38)    |
|        |               | Oligochaeta     |                           | 0.49 (0.19)    | 9.99 (4.5)      |
|        |               | Chloroperlidae  | <i>Kathoperla</i>         | 1.26 (0.07)    | 15.2 (3.63)     |
|        |               |                 | <i>Sweltsa</i>            | 0.8 (0.65)     | 10.57 (9.18)    |
|        |               | Paraleuctridae  | <i>Paraleuctra</i>        | 0.23 (0.06)    | 2.98 (0.58)     |
|        |               | Perlidae        | <i>Doroneuria</i>         | 0.32 (0.09)    | 12.89 (3.57)    |
|        |               | Perlodidae      | <i>Megarcys</i>           | 4.13 (0.64)    | 19.31 (2.23)    |
|        | Trichoptera   | Brachycentridae | <i>Brachycentrus</i>      | 0.57 (0.39)    | 5.57 (3.47)     |
|        |               | Glossosomatidae | <i>Glossosoma</i> Pupae   | 0.47 (0.18)    | 5.48 (2.2)      |
|        |               | Limniphilidae   | <i>Eocosmoecus</i>        | 0.23 (0.06)    | 9.62 (2.25)     |
|        |               | Philopotamidae  | <i>Doliphoides</i> Larvae | 0.42 (0.09)    | 6.34 (1.69)     |
|        |               |                 | <i>Doliphoides</i> Pupae  | 0.1 (0.09)     | 2.5 (2.04)      |
|        |               | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.54 (0.07)    | 10.13 (1.4)     |
|        |               |                 | <i>Rhyacophila</i> Pupae  | 0.35 (0.09)    | 7.12 (1.85)     |
|        | Coleoptera    | Elmidae         | <i>Cleptelmis</i> Adult   | 2.72 (0.94)    | 23.66 (6.44)    |
|        |               |                 | <i>Cleptelmis</i> Larvae  | 11.22 (2.06)   | 58.32 (17.2)    |
|        |               |                 | <i>Lara</i>               | 0.28 (0.13)    | 4.73 (2.37)     |
|        |               | Diptera         | Athericidae               | <i>Atherix</i> | 0 (0)           |
|        |               |                 | Ceratopogonidae           | <i>Bezzia</i>  | 0.85 (0.38)     |
|        |               | Chironomidae    | Larvae                    | 14.9 (4.04)    | 55.27 (17.89)   |
|        |               |                 | Pupae                     | 0.13 (0.11)    | 1.02 (0.84)     |
|        |               | Dixidae         | <i>Dixa</i>               | 0.05 (0.04)    | 0.68 (0.56)     |
|        |               | Simuliidae      | <i>Simulium</i> Larvae    | 9.2 (2.24)     | 34.99 (11.01)   |
|        |               |                 | <i>Simulium</i> Pupae     | 0.1 (0.06)     | 1.36 (0.93)     |
|        | Ephemeroptera | Tabanidae       | <i>Tabanus</i>            | 0.24 (0.09)    | 5.24 (2.46)     |
|        |               | Tipulidae       | <i>Hexatoma</i>           | 0.1 (0)        | 5.32 (2.52)     |
|        |               |                 | <i>Tipula</i>             | 0.08 (0.06)    | 1.26 (1.03)     |
|        |               | Ameletidae      | <i>Ameletus</i>           | 0.47 (0.24)    | 7.06 (3.29)     |
|        |               | Baetidae        | <i>Baetis</i>             | 21.77 (9.64)   | 182.81 (112.05) |
|        |               | Ephemerellidae  | <i>Drunella</i>           | 0.76 (0.14)    | 15.99 (2.86)    |
|        |               |                 | <i>Ephemerella</i>        | 3.13 (1.54)    | 27.9 (10.35)    |
|        |               | Heptageniidae   | <i>Serratella</i>         | 1.93 (0.55)    | 28.16 (7.82)    |
|        |               |                 | <i>Cinygmula</i>          | 10.56 (3.12)   | 71.64 (11.37)   |
|        |               |                 | <i>Epeorus</i>            | 6.74 (0.4)     | 50.3 (5.98)     |
|        |               |                 | <i>Rithrogena</i>         | 6.96 (0.47)    | 46.56 (7.64)    |
|        | Oligochaeta   | Leptophlebiidae | <i>Paraleptophlebia</i>   | 0.21 (0.09)    | 2.96 (1.27)     |
|        |               |                 |                           | 0.69 (0.23)    | 17.27 (6.29)    |
|        | Plecoptera    | Chloroperlidae  | <i>Kathoperla</i>         | 2.04 (0.4)     | 20.93 (5.99)    |
|        |               |                 | <i>Sweltsa</i>            | 0.13 (0.11)    | 1.57 (1.28)     |
|        |               | Paraleuctridae  | <i>Paraleuctra</i>        | 0.29 (0.23)    | 1.99 (1.62)     |
|        |               | Perlidae        | <i>Doroneuria</i>         | 0.48 (0.01)    | 16.43 (1.79)    |
|        |               | Perlodidae      | <i>Megarcys</i>           | 3.9 (1.87)     | 21.05 (9.35)    |
|        |               |                 | <i>Skwala</i>             | 0 (0)          | 0 (0)           |
|        | Trichoptera   | Brachycentridae | <i>Brachycentrus</i>      | 1.76 (1.6)     | 11.03 (9.18)    |
|        |               | Glossosomatidae | <i>Glossosoma</i> Pupae   | 0.61 (0.06)    | 7.46 (0.95)     |
|        |               |                 | <i>Micrasema</i>          | 0 (0)          | 0 (0)           |

|         |         |               |                 |                           |              |                |
|---------|---------|---------------|-----------------|---------------------------|--------------|----------------|
| 2011    | Control | Coleoptera    | Hydropsychidae  | <i>Arctopsyche</i>        | 0.1 (0)      | 1.84 (0.31)    |
|         |         |               | Limniphilidae   | <i>Eocosmoecus</i>        | 0.17 (0.07)  | 5.21 (1.57)    |
|         |         |               | Philopotamidae  | <i>Doliphoides</i>        | 0.37 (0.08)  | 6.02 (1.83)    |
|         |         |               |                 | <i>Doliphoides</i> Pupae  | 0.13 (0.06)  | 2.4 (1.2)      |
|         |         |               | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.49 (0.21)  | 9.02 (4.04)    |
|         |         |               |                 | <i>Rhyacophila</i> Pupae  | 0.46 (0.16)  | 8.92 (3.16)    |
|         |         |               | Elmidae         | <i>Cleptelmis</i> Adult   | 0.88 (0.37)  | 7.6 (3.23)     |
|         |         |               |                 | <i>Cleptelmis</i> Larvae  | 11.83 (1.75) | 48.92 (9.68)   |
|         |         |               |                 | <i>Lara</i>               | 0.05 (0.04)  | 0.91 (0.74)    |
|         |         | Diptera       | Athericidae     | <i>Atherix</i>            | 0.21 (0)     | 3.88 (0.09)    |
|         |         |               | Ceratopogonidae | <i>Bezzia</i>             | 1.15 (0.46)  | 9.58 (0.5)     |
|         |         |               | Chironomidae    | Larvae                    | 12.65 (3.79) | 50.02 (23.36)  |
|         |         |               | Simuliidae      | <i>Simulium</i> Larvae    | 6.46 (3.21)  | 26.32 (12.5)   |
|         |         |               |                 | <i>Simulium</i> Pupae     | 0.3 (0.15)   | 3.17 (1.3)     |
|         |         |               | Tabanidae       | <i>Tabanus</i>            | 0.65 (0.55)  | 6.03 (3.67)    |
|         |         |               | Tipulidae       | <i>Hexatoma</i>           | 0.1 (0)      | 5.32 (0.46)    |
|         |         |               |                 | <i>Tipula</i>             | 0.23 (0.19)  | 4.41 (3.6)     |
|         |         | Ephemeroptera | Ameletidae      | <i>Ameletus</i>           | 0.35 (0.13)  | 5.52 (2.29)    |
|         |         |               | Baetidae        | <i>Baetis</i>             | 13.12 (4.56) | 70.69 (27.89)  |
|         |         |               | Ephemerellidae  | <i>Drunella</i>           | 0.82 (0.52)  | 12.03 (6.33)   |
|         |         |               |                 | <i>Ephemerella</i>        | 2.92 (1.15)  | 33.06 (11.42)  |
|         |         |               |                 | <i>Serratella</i>         | 0.36 (0.3)   | 4.22 (3.45)    |
|         |         |               | Heptageniidae   | <i>Cinygmula</i>          | 5.33 (0.88)  | 36.99 (1.74)   |
|         |         |               |                 | <i>Epeorus</i>            | 1.48 (1.3)   | 10.17 (7.78)   |
|         |         |               |                 | <i>Rithrogena</i>         | 0.73 (0.6)   | 8.41 (6.87)    |
|         |         | Oligochaeta   |                 |                           | 0.45 (0.13)  | 9.42 (3.42)    |
|         |         | Plecoptera    | Chloroperlidae  | <i>Kathoperla</i>         | 1.66 (0.53)  | 20.48 (4.55)   |
|         |         |               | Paraleuctridae  | <i>Paraleuctra</i>        | 0.13 (0.02)  | 2.84 (0.46)    |
|         |         |               | Peltoperlidae   | <i>Yoraperla</i>          | 1.17 (0.39)  | 9.54 (4.81)    |
|         |         |               | Perlidae        | <i>Doroneuria</i>         | 0.21 (0.04)  | 3.79 (0.25)    |
|         |         |               | Perlodidae      | <i>Megarcys</i>           | 3.04 (0.94)  | 11.65 (3.4)    |
|         |         | Trichoptera   | Brachycentridae | <i>Brachycentrus</i>      | 5.08 (3.08)  | 21.61 (7.73)   |
|         |         |               | Glossosomatidae | <i>Glossosoma</i> Larvae  | 0.23 (0.02)  | 2.85 (0.53)    |
|         |         |               |                 | <i>Glossosoma</i> Pupae   | 0.21 (0.06)  | 2.69 (0.81)    |
|         |         |               |                 | <i>Micrasema</i>          | 0.56 (0.56)  | 2.9 (2.9)      |
|         |         |               | Hydropsychidae  | <i>Arctopsyche</i>        | 0 (0)        | 0 (0)          |
|         |         |               |                 | <i>Hydropsyche</i>        | 0.1 (0.09)   | 2.35 (1.92)    |
|         |         |               | Limniphilidae   | <i>Eocosmoecus</i>        | 0.24 (0.07)  | 8.45 (3.72)    |
|         |         |               | Philopotamidae  | <i>Doliphoides</i> Larvae | 0.17 (0.1)   | 2.73 (1.34)    |
|         |         |               |                 | <i>Doliphoides</i> Pupae  | 0 (0)        | 0 (0)          |
|         |         |               | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.19 (0.08)  | 3.43 (1.32)    |
|         |         |               |                 | <i>Rhyacophila</i> Pupae  | 0.21 (0.06)  | 4.12 (1.38)    |
| Carcass |         | Coleoptera    | Elmidae         | <i>Cleptelmis</i> Adult   | 1.16 (0.48)  | 9.79 (4.04)    |
|         |         |               |                 | <i>Cleptelmis</i> Larvae  | 11.17 (0.66) | 51.35 (2.63)   |
|         |         |               |                 | <i>Lara</i>               | 0 (0)        | 0 (0)          |
|         |         |               |                 |                           |              |                |
|         |         | Diptera       | Athericidae     | <i>Atherix</i>            | 0.03 (0.03)  | 0.47 (0.55)    |
|         |         |               | Ceratopogonidae | <i>Bezzia</i>             | 0.78 (0.21)  | 11.11 (3.2)    |
|         |         |               | Chironomidae    | Larvae                    | 23.13 (6.19) | 114.91 (45.39) |
|         |         |               |                 | <i>Chironomidae</i> Pupae | 0.24 (0.13)  | 2.5 (1.27)     |
|         |         |               |                 |                           |              |                |
|         |         |               |                 |                           |              |                |
|         |         |               |                 |                           |              |                |
|         |         |               |                 |                           |              |                |
|         |         |               |                 |                           |              |                |
|         |         |               |                 |                           |              |                |

|        |               |                 |                           |              |               |
|--------|---------------|-----------------|---------------------------|--------------|---------------|
|        |               | Simuliidae      | <i>Simulium</i> Larvae    | 7.25 (2.83)  | 26.99 (9.54)  |
|        |               |                 | <i>Simulium</i> Pupae     | 0.37 (0.15)  | 4.32 (1.93)   |
|        |               | Tabanidae       | <i>Tabanus</i>            | 0.14 (0.03)  | 3.03 (0.52)   |
|        |               | Tipulidae       | <i>Hexatoma</i>           | 0.09 (0.05)  | 3.22 (1.99)   |
|        |               |                 | <i>Tipula</i>             | 0.05 (0.05)  | 1.09 (1.09)   |
|        | Ephemeroptera | Ameletidae      | <i>Ameletus</i>           | 0.49 (0.49)  | 5.43 (5.43)   |
|        |               | Baetidae        | <i>Baetis</i>             | 16.82 (2.48) | 82.06 (15.23) |
|        |               | Ephemerellidae  | <i>Drunella</i>           | 0.49 (0.16)  | 12.56 (3.94)  |
|        |               |                 | <i>Ephemerella</i>        | 5.91 (2.54)  | 45.75 (13.66) |
|        |               |                 | <i>Serratella</i>         | 12.95 (9.63) | 64.4 (24.56)  |
|        |               | Heptageniidae   | <i>Cinygmula</i>          | 4.52 (2.58)  | 27.48 (13.84) |
|        |               |                 | <i>Epeorus</i>            | 1.94 (0.4)   | 23.3 (1.81)   |
|        |               |                 | <i>Rithrogena</i>         | 0.28 (0.28)  | 3.67 (3.67)   |
|        | Oligochaeta   |                 |                           | 0.26 (0.26)  | 5.16 (5.16)   |
|        | Plecoptera    | Chloroperlidae  | <i>Kathoperla</i>         | 1.02 (0.6)   | 10.33 (5.26)  |
|        |               |                 | <i>Sweltsa</i>            | 0.14 (0.14)  | 1.9 (1.9)     |
|        |               | Paraleuctridae  | <i>Paraleuctra</i>        | 0.1 (0.1)    | 2.18 (2.18)   |
|        |               | Peltoperlidae   | <i>Yoraperla</i>          | 0.03 (0.03)  | 0.39 (0.39)   |
|        |               | Perlidae        | <i>Doroneuria</i>         | 0.24 (0.17)  | 8 (6.23)      |
|        |               | Perlodidae      | <i>Megarcys</i>           | 3.84 (0.71)  | 17.97 (1.87)  |
|        | Trichoptera   | Brachycentridae | <i>Brachycentrus</i>      | 2.77 (1.44)  | 13.57 (6.9)   |
|        |               |                 |                           |              |               |
|        |               | Glossosomatidae | <i>Glossosoma</i> Larvae  | 0.03 (0.03)  | 0.41 (0.41)   |
|        |               |                 | <i>Glossosoma</i> Pupae   | 0.27 (0.06)  | 3.34 (0.66)   |
|        |               |                 | <i>Micrasema</i>          | 0.07 (0.07)  | 1.14 (1.14)   |
|        |               | Limniphilidae   | <i>Eocosmoecus</i>        | 0.19 (0.06)  | 8.48 (3.18)   |
|        |               | Philopotamidae  | <i>Doliphoides</i> Larvae | 0.17 (0.09)  | 3.45 (1.77)   |
|        |               |                 | <i>Doliphoides</i> Pupae  | 0.02 (0.02)  | 0.39 (0.39)   |
|        |               | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.66 (0.16)  | 10.65 (2.55)  |
|        |               |                 | <i>Rhyacophila</i> Pupae  | 0.3 (0.06)   | 6.41 (1.26)   |
| Analog | Coleoptera    | Elmidae         | <i>Cleptelmis</i> Adult   | 2.68 (1.42)  | 17.81 (8.28)  |
|        |               |                 | <i>Cleptelmis</i> Larvae  | 8.09 (3.08)  | 41.98 (17.12) |
|        |               |                 | <i>Lara</i>               | 0.28 (0.09)  | 5.34 (1.46)   |
|        |               |                 |                           |              |               |
|        | Diptera       | Ceratopogonidae | <i>Bezzia</i>             | 1.03 (0.82)  | 6.81 (3.01)   |
|        |               | Chironomidae    | Larvae                    | 11.63 (7.46) | 54.85 (37.94) |
|        |               |                 | Pupae                     | 0.03 (0.03)  | 0.55 (0.55)   |
|        |               | Simuliidae      | <i>Simulium</i> Larvae    | 0.67 (0.63)  | 3.43 (3.01)   |
|        |               |                 | <i>Simulium</i> Pupae     | 0.03 (0.03)  | 0.42 (0.42)   |
|        |               | Tabanidae       | <i>Tabanus</i>            | 0.05 (0.05)  | 1.27 (1.27)   |
|        |               | Tipulidae       | <i>Hexatoma</i>           | 0.31 (0.16)  | 8.17 (4.33)   |
|        |               |                 | <i>Tipula</i>             | 0.12 (0.01)  | 3.44 (0.95)   |
|        | Ephemeroptera | Baetidae        | <i>Baetis</i>             | 10.28 (3.17) | 57.7 (11.53)  |
|        |               |                 |                           |              |               |
|        |               | Ephemerellidae  | <i>Drunella</i>           | 0.36 (0.2)   | 9.88 (5.63)   |
|        |               |                 | <i>Ephemerella</i>        | 2.08 (0.48)  | 23.39 (5.16)  |
|        |               | Heptageniidae   | <i>Cinygmula</i>          | 6.14 (1.2)   | 49.56 (5.41)  |
|        |               |                 | <i>Epeorus</i>            | 1.42 (1.26)  | 14.06 (11.29) |
|        |               |                 | <i>Rithrogena</i>         | 0.39 (0.45)  | 4.78 (5.53)   |
|        |               | Leptophlebiidae | <i>Paraleptophlebia</i>   | 0.19 (0.19)  | 2.7 (2.7)     |
|        | Oligochaeta   |                 |                           | 0.66 (0.17)  | 13.71 (3.47)  |
|        | Plecoptera    | Chloroperlidae  | <i>Kathoperla</i>         | 1.14 (0.33)  | 15.8 (3.7)    |

|             |                 |                           |             |             |
|-------------|-----------------|---------------------------|-------------|-------------|
|             |                 | <i>Sweltsa</i>            | 0.56 (0.5)  | 8.28 (7.58) |
|             | Paraleuctridae  | <i>Paraleuctra</i>        | 0.03 (0.03) | 0.66 (0.66) |
|             | Perlidae        | <i>Doroneuria</i>         | 0.09 (0.09) | 4.11 (4.11) |
|             | Perlodidae      | <i>Megarcys</i>           | 1.92 (0.8)  | 8.64 (4.68) |
| Trichoptera | Brachycentridae | <i>Brachycentrus</i>      | 0.89 (0.86) | 2.96 (2.67) |
|             | Glossosomatidae | <i>Glossosoma</i> Larvae  | 0.1 (0.1)   | 1.35 (1.35) |
|             |                 | <i>Glossosoma</i> Pupae   | 0.16 (0.04) | 2.03 (0.48) |
|             |                 | <i>Micrasema</i>          | 0.03 (0.03) | 0.31 (0.31) |
|             | Hydropsychidae  | <i>Arctopsyche</i>        | 0.17 (0.17) | 4.64 (4.64) |
|             |                 | <i>Hydropsyche</i>        | 0.03 (0.03) | 0.82 (0.82) |
|             | Limniphilidae   | <i>Eocosmoecus</i> Larvae | 0.12 (0.06) | 5.54 (2.88) |
|             |                 | <i>Eocosmoecus</i> Pupae  | 0.07 (0.07) | 4.5 (4.5)   |
|             | Philopotamidae  | <i>Doliphoides</i> Larvae | 0.17 (0.03) | 3.13 (0.67) |
|             |                 | <i>Doliphoides</i> Pupae  | 0.28 (0.18) | 6.22 (4.4)  |
|             | Rhyacophilidae  | <i>Rhyacophila</i> Larvae | 0.3 (0.08)  | 5.17 (0.91) |
|             |                 | <i>Rhyacophila</i> Pupae  | 0.17 (0.1)  | 3.6 (2.14)  |

Appendix 2b. Summary of resident fish biomass and density by treatment over years 2008-2011. RBT= Rainbow trout, BKT = Brook trout, SCP = Mottled sculpin

| Year | Treatment | Species | Biomass<br>g/m <sup>2</sup> (SE) | Density<br>#/m <sup>2</sup> (SE) |
|------|-----------|---------|----------------------------------|----------------------------------|
| 2008 | Analog    | BKT     | 0.46 (0.460)                     | 0.026 (0.026)                    |
|      |           | RBT     | 4.227 (1.605)                    | 0.256 (0.098)                    |
|      |           | SCP     | 1.193 (1.162)                    | 0.455 (0.453)                    |
|      | Carcass   | BKT     | 1.593 (1.593)                    | 0.043 (0.043)                    |
|      |           | RBT     | 4.769 (2.290)                    | 0.304 (0.159)                    |
|      |           | SCP     | 1.928 (0.495)                    | 0.307 (0.094)                    |
|      | Control   | BKT     | 1.386 (1.149)                    | 0.085 (0.063)                    |
|      |           | RBT     | 2.314 (1.408)                    | 0.241 (0.148)                    |
|      |           | SCP     | 1.297 (1.297)                    | 0.432 (0.432)                    |
| 2009 | Analog    | BKT     | 1.278 (1.278)                    | 0.043 (0.043)                    |
|      |           | RBT     | 4.561 (1.719)                    | 0.298 (0.088)                    |
|      |           | SCP     | 1.122 (1.023)                    | 0.383 (0.374)                    |
|      | Carcass   | BKT     | 1.957 (1.957)                    | 0.085 (0.085)                    |
|      |           | RBT     | 6.127 (3.038)                    | 0.340 (0.169)                    |
|      |           | SCP     | 4.254 (0.616)                    | 1.182 (0.064)                    |
|      | Control   | BKT     | 1.928 (1.676)                    | 0.077 (0.058)                    |
|      |           | RBT     | 1.920 (0.965)                    | 0.164 (0.096)                    |
|      |           | SCP     | 1.618 (1.618)                    | 0.546 (0.546)                    |
| 2010 | Analog    | BKT     | 0.963 (0.963)                    | 0.035 (0.035)                    |
|      |           | RBT     | 5.364 (3.075)                    | 0.300 (0.128)                    |
|      |           | SCP     | 1.008 (0.745)                    | 0.132 (0.089)                    |
|      | Carcass   | BKT     | 1.578 (1.310)                    | 0.077 (0.072)                    |
|      |           | RBT     | 3.880 (2.053)                    | 0.283 (0.163)                    |
|      |           | SCP     | 4.180 (1.244)                    | 1.178 (0.366)                    |
|      | Control   | BKT     | 2.394 (1.095)                    | 0.153 (0.041)                    |
|      |           | RBT     | 1.770 (0.858)                    | 0.164 (0.086)                    |
|      |           | SCP     | 1.628 (1.628)                    | 0.220 (0.220)                    |
| 2011 | Analog    | BKT     | 0.815 (0.815)                    | 0.026 (0.026)                    |
|      |           | RBT     | 2.474 (1.511)                    | 0.183 (0.067)                    |
|      |           | SCP     | 0.587 (0.491)                    | 0.205 (0.192)                    |
|      | Carcass   | BKT     | 1.198 (1.198)                    | 0.057 (0.057)                    |
|      |           | RBT     | 3.080 (1.683)                    | 0.164 (0.087)                    |
|      |           | SCP     | 3.203 (0.576)                    | 0.795 (0.151)                    |
|      | Control   | BKT     | 3.863 (3.294)                    | 0.153 (0.118)                    |
|      |           | RBT     | 1.050 (0.504)                    | 0.092 (0.036)                    |
|      |           | SCP     | 1.294 (1.294)                    | 0.280 (0.280)                    |

Appendix 2c. Summary of resident fish annual production. RBT= Rainbow trout, BKT = Brook trout, SCP = Mottled sculpin

| Year      | Treatment | Species | Annual production<br>g m <sup>-2</sup> yr <sup>-1</sup> (SE) |
|-----------|-----------|---------|--------------------------------------------------------------|
| 2008-2009 | Analog    | BKT     | 0.601 (0.601)                                                |
|           |           | RBT     | 5.595 (2.653)                                                |
|           |           | SCP     | 1.364 (1.358)                                                |
|           | Carcass   | BKT     | 1.452 (1.452)                                                |
|           |           | RBT     | 6.385 (3.106)                                                |
|           |           | SCP     | 1.032 (0.229)                                                |
|           | Control   | BKT     | 1.399 (1.265)                                                |
|           |           | RBT     | 2.072 (1.429)                                                |
|           |           | SCP     | -                                                            |
| 2009-2010 | Analog    | BKT     | 1.076 (1.076)                                                |
|           |           | RBT     | 7.246 (2.711)                                                |
|           |           | SCP     | 1.212 (1.172)                                                |
|           | Carcass   | BKT     | 3.518 (3.518)                                                |
|           |           | RBT     | 8.646 (3.981)                                                |
|           |           | SCP     | 3.750 (0.137)                                                |
|           | Control   | BKT     | 1.655 (1.445)                                                |
|           |           | RBT     | 1.524 (0.796)                                                |
|           |           | SCP     | -                                                            |
| 2010-2011 | Analog    | BKT     | 0.823 (0.823)                                                |
|           |           | RBT     | 7.544 (3.811)                                                |
|           |           | SCP     | 0.446 (0.296)                                                |
|           | Carcass   | BKT     | 3.027 (2.889)                                                |
|           |           | RBT     | 7.031 (3.681)                                                |
|           |           | SCP     | 3.776 (1.171)                                                |
|           | Control   | BKT     | 2.493 (1.423)                                                |
|           |           | RBT     | 1.501 (0.726)                                                |
|           |           | SCP     | -                                                            |

### **Chapter 3**

Heterogeneity of riparian habitats mediates responses of terrestrial arthropods to a  
subsidy of Pacific salmon carcasses

## **Abstract**

The transfer of nutrients and energy across habitat or ecosystem boundaries, or resource subsidies, is important in structuring biological communities. Variation in biotic and abiotic characteristics of patches receiving resource subsidies may mediate their effects, including responses by consumers; however, few studies have investigated this explicitly or the potential effects at broader spatial scales. To test the role recipient patches may play in mediating effects of a subsidy and consequences at larger reach scales, we conducted an experiment to evaluate changes in arthropod community composition and abundance in response to a subsidy of salmon carcasses in vegetated and un-vegetated riparian patches, where carcasses are frequently deposited by animals, and how these patterns in patches mediate responses at reach scales. Arthropod community composition differed between habitats, and salmon additions yielded strong positive changes in arthropod abundance among select families. Four dipteran families responded positively to additions of carcasses to riparian habitats, and effects were generally stronger in vegetated habitats. Salmon carcasses in un-vegetated habitats desiccated whereas in vegetated habitats they remained moist which likely facilitated rapid consumption. Of the five predatory arthropod families observed, only the coleopteran, Staphylinidae, increased in response to the salmon carcass subsidy, and only in vegetated habitats. Differences in effect size between habitats suggest selection of salmon carcasses by riparian arthropods changes with habitat context. Additionally, we detected significant increases in adult Calliphoridae biomass at reach scales, with the largest increases occurring at streams with more carcasses in vegetated patches. Our results show that the responses to the subsidy of salmon carcasses are not ubiquitous among

riparian arthropods, nor are they spatially homogenous. Rather, our findings demonstrate that spatial variation in recipient habitat can mediate the responses of primary and secondary consumers to a subsidy, with effects manifesting at broader spatial extents, highlighting an additional means by which landscape heterogeneity influences the dynamics of riverine food webs.

## **Introduction**

Characteristics and consequences of resource subsidies, the biologically or physically mediated transfer of nutrients and energy across habitat or ecosystem boundaries, have been investigated in a variety of settings over the past two decades (Polis et al. 1997, Baxter et al. 2005, Marczak et al. 2007, Richardson et al. 2010). The resultant findings, along with complementary theoretical advances (Loreau and Holt 2004, Leroux and Loreau 2008, Takimoto et al. 2009) have refined our understanding of the role subsidies play in the structure and function of communities and ecosystems, emphasizing the consequences of system openness (Polis et al. 2004). In particular, subsidies contribute to greater abundance, productivity, and diversity of organisms in recipient habitats (e.g., Nakano and Murakami 2001, Spiller et al. 2010, Savage et al. 2012), with responses that vary in magnitude and sign across landscapes (Marczak et al. 2007, Menge et al. 2003, Krenz et al. 2011). The latter suggests that context of habitats receiving subsidies matters, and indeed, spatial heterogeneity in subsidy magnitude, boundary conditions, or characteristics of recipient habitats have all been posited to play a role in mediating subsidy effects (Polis et al. 1997, Holt 2002, Anderson et al. 2008). However, few empirical investigations have explicitly examined how spatial

heterogeneity at small spatial scales mediates responses of consumers to subsidies and subsequent effects at broader spatial scales.

Ecosystems receiving subsidies are typically comprised of an array of habitat types or patches, defined at various scales as relatively homogenous areas differing from their surroundings, such that subsidy input occurs to patches of different character (Fig. 1). Patches may vary with respect to biotic (e.g., community composition) and abiotic (e.g., temperature, boundary characteristics; Cadenasso et al. 2004) factors that affect accessibility to a subsidy (Roth 2002, Gende et al. 2004, Selva et al. 2005) and how a subsidy is received or utilized (e.g., decomposed, consumed). Moreover, the structure and complexity of recipient patches can influence consumer-resource dynamics (Crowder and Cooper 1982, Denno et al. 2002). For instance, greater complexity is often associated with higher diversity or abundance of prey species (Bell et al. 1991), can mediate predator-prey interactions (Huffaker 1958, Crowder and Cooper 1982, Almany 2004), and may influence cascading effects across trophic levels (Schmitz et al. 2000, Grabowski et al. 2008). Indeed, both habitat patch quality (i.e., character) and quantity (i.e., dominance of patch type) may regulate the influences of subsidies on food webs in landscapes. Thus, investigation is required to address how habitat heterogeneity may mediate subsidy effects across spatial scales.

Variation in the effects of resource subsidies among habitat patches may also be influenced by a combination of the temporal character of subsidies and the traits of organisms using those habitats. For example, the duration of a subsidy's persistence within a recipient habitat may mediate responses of organisms across trophic levels (Ostfeld and Keesing 2000, Takimoto et al. 2009, Yang et al. 2010). Numeric responses

(e.g., increased production, aggregation) of organisms to subsidies are likely tied to the duration of availability (Fukui et al. 2006), but may also be influenced by life history and behavioral characteristics of consumers (Polis et al. 1996, Power and Rainey 2000). For instance, numeric responses to ephemeral subsidies may be constrained to organisms with short and rapid life histories (e.g., *r*-strategists) or behavioral attraction of longer-lived organisms (Yang et al. 2008). Moreover, the spatial extent of an organism's foraging may also affect its capacity to respond to a subsidy (Power and Rainey 2000). Subsidies that are pulsed in time or very patchy in space may occur only in a small portion of an organism's potential "resource shed," (sensu Power and Rainey 2000) and any effects will likely be influenced by attributes of the consumer, such as mobility and sensory abilities. However, studies are needed that explicitly investigate the potentially interactive roles of subsidy character and the traits of community members when evaluating the effects of resource subsidies.

The carcasses of salmon are a resource subsidy frequently trans-located to a mosaic of patch types. They provide a marine-derived nutrient and food resource not only for the freshwater habitats to which these animals return to spawn, but for many riparian and upland plants, arthropods, mammals, and birds (Helfield and Naiman 2001, Hocking et al. 2009, Quinn and Buck 2000, Quinn et al. 2009). Large piscivores, such as bears, frequently remove salmon from streams (Gende et al. 2004), feed on them, and then discard the carcasses across a range of vegetated and un-vegetated patches (e.g., cobble bars, grassy stream banks; Meehan et al. 2005) where they may be consumed by an array of animals. In particular, carcasses may be rapidly colonized and consumed by a diverse community of arthropods within hours to days (Hocking and Reimchen 2006,

Hocking et al. 2009). Stable isotope analyses indicate that a wide range of arthropods, encompassing numerous feeding guilds, utilize salmon-derived C and N (Hocking et al. 2009). The transfer of salmon carcasses to terrestrial environments provides a context within which to test how *in situ* arthropod communities of different habitats respond numerically (e.g., behaviorally, population increase) to a subsidy. It is likely that recipient habitat types vary in physical (e.g., temperature, exposure) and biological (e.g., traits of consumers present) characteristics that could affect the duration of availability and rate of utilization of such a subsidy by arthropods, but to our knowledge this has not been tested.

Here we present the results of experiments conducted at two spatial scales to investigate how patch type at small scales (in this case, tens of meters) mediates the response of a riparian arthropod community to a subsidy of Pacific salmon carcasses and, in turn, how composition of patches at larger scales (hundreds of meters) influence responses along entire stream reaches. We hypothesized that riparian patches differentially mediate the response of *in situ* communities of terrestrial arthropods to this subsidy, and that responses are further linked to the attributes of both the subsidy and consumers. Furthermore, we hypothesized that the composition of patch types along stream reaches influences responses to subsidies at this scale. Specifically, we predicted that salmon carcasses delivered to both un-vegetated and vegetated habitats would shift arthropod community composition. We expected that these changes would be driven by positive increases in primary consumers (saprophages) and secondary consumers (predators and parasitoids), but that responses would also be influenced by the intersection of arthropod traits (e.g., chemosensory) and carcass subsidy character. With

respect to the latter, we expected that salmon carcasses deposited in vegetated and un-vegetated patches would take on different characteristics during breakdown, thereby driving differences in arthropod responses. Moreover, we predicted that responses of arthropods would “scale” from patches to stream reaches, such that effects at the scale of stream reaches would be influenced most by the proportion of patches (vegetated vs. un-vegetated) with the strongest effects at the patch-scale.

## Methods

### *Study area and experimental design*

We evaluated our hypotheses by means of nested, manipulative field experiments, conducted in the North Fork of the Boise River drainage in central Idaho, USA. Surface geology is mostly granitic rock of the Idaho batholith. Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) are the dominant trees across the basin. Riparian zones are dominated by willows (*Salix* spp.), red-osier dogwood (*Cornus sericea*), and tall grasses (predominantly *Festuca* spp.). During the late-summer time frame of our experiment, the Boise basin is relatively warm (average daytime temperatures in August 2010 ranged from 28.3 to 30.6 °C) and dry (13.4 mm of rain in this period; U.S. Dept. of Agriculture, NRCS accessed 4-Aug-2011).

We nested a patch-scale experiment (described below) within the context of a larger, adaptive management experiment conducted from 2008 to 2011 in tributaries of the North Fork of the Boise River, Idaho, USA. The latter was aimed at testing the efficacy of mitigating for reductions of marine-derived nutrients accompanying the loss of Pacific salmon. One treatment was the application of salmon carcasses to streams that

historically received runs of salmon. Annually, salmon carcasses were added during the first week of August to Trail Creek (UTM: 11T 0629500 4861948), Little Beaver Creek (UTM: 11T 0618947 4853234), and Big Owl Creek (UTM: 11T 0617892 4860467), beginning in 2008. An additional three streams, Banner Creek (UTM: 11T 0616601 4871171), Beaver Creek (UTM: 11T 0618947 4853234), and Hungarian Creek (UTM: 11T 0617661 4852473) served as 500m control reaches. Treatments were applied to achieve 0.5 carcasses m<sup>2</sup> in 500-m reaches of each stream, values in the range of historic levels of salmon runs for this region (IDFG 1985). During summers 2008-2009, we observed that salmon carcasses were removed from streams, predominantly by black bears (*Ursus americanus*), and deposited on un-vegetated cobble bars as well as vegetated (typically dominated by grasses) patches within 1-2 m of the wetted stream edge.

The small-scale experiment was set within the larger experiment and required the artificial removal of salmon carcasses to specific patches (i.e., vegetated and un-vegetated). At the reach-scale, I allowed wildlife to naturally remove salmon carcasses from streams. During the reach-scale experiment, we counted the number of carcasses removed along each reach and noted in which patches they were deposited. At no point did wildlife introduce new salmon carcasses to our smaller, patch-scale plots.

At each of three carcass treated streams, we identified both un-vegetated and vegetated patches. Vegetated patches were principally composed of grasses approximately 0.2-0.5 m high growing on established soil, whereas un-vegetated patches were devoid of plants and characterized by cobble and gravel (sizes ranging from 4-14 cm in diameter), with sand filling interstitial spaces. At each of the three stream reaches

treated with carcasses, we established three treatment plots (i.e., control, submerged carcass, submerged carcass + removed carcass) 200-275 m apart, with each respective treatment containing both un-vegetated and vegetated patches. Controls (UR) were located upstream of treated reaches. We considered that the presence of submerged salmon carcasses in the stream might attract arthropods in riparian habitats, therefore to distinguish these effects from those caused by salmon carcasses removed to riparian habitats, we established treatment plots that were adjacent to stream reaches with submerged carcasses (SC), and compared them to similar plots to which salmon carcasses were added in riparian habitats (RC). For RC treatments, six carcasses of the same approximate length and mass were removed from each stream and placed within the respective vegetated (3 carcasses) or un-vegetated (3 carcasses) patches.

At the scale of each patch, we quantified the abundance of *in situ* arthropods using pitfall traps (8 cm width, 6 cm depth) deployed within 1 m of the wetted edge and 10–20 cm from salmon carcasses. Each pitfall trap was filled with ~3 cm of water and dilute soap to break the surface tension of the water. Four pitfall traps (subsamples) were deployed parallel to the stream within each patch (vegetated, un-vegetated) for each treatment (UR, SC, RC) for three collection periods of 7 days each. A fourth sampling was attempted after carcasses were largely decomposed, but in that period traps were destroyed by black bears (>65% trap damage). Samples were preserved in 70% ethanol until processed in the laboratory. Arthropods were identified to order and family and counted: Diptera (McAlpine et al. 1981); Aranaea (Ubick et al. 2005); Coleoptera, Hemiptera, Hymenoptera (Triplehorn and Johnson 2005). When different life stages were encountered, larvae were counted and analyzed independently of adults.

We expected the environment of the different habitats might mediate the rate of decomposition and consumption of carcass material, which could affect its persistence within the riparian zone. To evaluate potential differences in breakdown between habitats, as well as to track the physical character of the salmon carcasses, visual surveys were made daily for the first week, then weekly for the duration of the experiment, noting approximate percent of carcass consumed, integrity of fish tissue, exposure of bones, and putrefaction of tissue. Though we had originally expected we might need to replenish carcass treatments in the patch-scale experiment due to activities of animals like bears, we observed no sign of interference or alterations of the integrity or placement of the salmon carcasses by animals other than arthropods during the 3 weeks of that experiment.

To evaluate effects of the stream-reach scale treatments on arthropods in the adjacent riparian landscape, sticky traps were systematically deployed along both carcass (n=3) and control (n=3) streams. We chose different techniques for sampling arthropods at the two different scales in order to a) evaluate responses by a wider array of taxa and b) match sampling technique with the scale of treatments and mobility of taxa. We used sticky traps to evaluate responses at the stream-reach scale because they are designed to capture aerial insects that are more mobile than most taxa collected by pitfall traps, and that we expected would be more responsive to landscape characteristics integrated at this scale. At each stream, cylindrical sticky traps were suspended from fence posts 1.5m above the ground. Six alternating transects extended laterally (0, 5, 25m) from each stream for a total of 18 traps per stream. Traps were deployed for two-week intervals following treatment additions. Collected samples were covered in plastic wrap and

stored. Aerial arthropods were identified to family and counted. Abundance of taxa was summed across the 18 traps for each sample period.

### *Data analysis*

To evaluate our first hypothesis, we used multivariate techniques to identify potential differences in arthropod community composition in response to salmon carcass additions. Nonmetric multidimensional scaling (NMDS) of taxa relative abundance was used to visually evaluate differences in community composition between habitat types and plots (PC-ORD; McCune et al. 2002). For assessment at both habitat and plot levels, we used axis and stress scores generated from NMDS analysis. Infrequent or rare families were excluded from this data set (relative values <5%) to avoid distortion of the ordination results (Gauch 1982). Subsequently, we used multi-response permutation procedures (MRPP) to test for differences in community composition between habitat and plots using Sorenson Index as the distance metric (Mielke and Berry 2001). Correlations (Pearson's  $r$ ) with axis scores were used to identify which arthropod families drove observed patterns. We report three values for the MRPP analyses:  $\delta$ , the weighted mean within-group distance;  $A$ , the chance-corrected within-group agreement; and  $P$  value. Pairwise comparisons were generated from MRPP analysis to evaluate differences between treatment plots. We used a Bonnferoni correction to reduce the likelihood of a type I error when making multiple comparisons ( $\alpha$  of  $0.05 \div 3$  comparisons = 0.016). To evaluate numeric responses separately for families of saprophages, predators, and parasitoids with variable life history and foraging attributes, we performed a multivariate analysis of variance (MANOVA; PROC GLM; Scheiner 1993) to differentiate effects of

salmon carcasses located in-stream plus riparian salmon carcasses (RC) from salmon carcasses in-stream only (SC) and controls (UR). Significant effects were further analyzed with univariate repeated-measures analysis of variance to identify which arthropod families were responsible for changes in community structure (rmANOVA; PROC MIXED; O'Brien and Kaiser 1985). To determine if effect size varied between un-vegetated and vegetated patches (fixed factor), we compared families to one another that had responded significantly to salmon carcasses in RC plots. Comparisons between habitats of the effect size on arthropods were calculated as the difference between the mean of treated and control groups divided by the mean of control. Because capture efficiency of pitfall traps likely differs among arthropod taxa, we used the mean control in the denominator; thus an increasing denominator would lower effect size and *vice versa*.

To evaluate our second hypothesis, abundance of aerial insects collected on sticky traps was analyzed using repeated-measures analysis of variance. If significant treatment effects were observed, we compared stream specific responses to riparian habitat composition to identify whether specific patches might have a disproportionate impact on mediating subsidy effects at the reach scale. All data were square-root transformed to correct for heteroscedasticity. Analyses of patch and reach scale changes in abundance to treatments were conducted using SAS 9.2 (SAS Institute, Cary, North Carolina, USA).

## Results

### *Salmon carcass consumption and decomposition*

Arthropods were observed on the carcasses in deposited in both vegetated and un-vegetated habitats. Carcasses attracted saprophagic dipterans within hours of deployment. After the first 48 hours, we observed that salmon carcasses were more desiccated on un-vegetated bars in comparison to the salmon carcasses in vegetated plots. Subsequently, carcasses were consumed and decomposed faster in vegetated than in un-vegetated habitats. Salmon carcasses were reduced to skeletons 14-16 days in vegetated and 18-21 days in un-vegetated habitats.

### *Patch-scale arthropod community composition*

In the patch-scale experiment, assemblage composition of riparian arthropods collected in pitfall traps differed for both patches and treatments. The NMDS ordination of mean relative abundance yielded a 2-dimensional solution (47.2% of variation along Axis 1 and 43.4% along Axis 2; Fig. 2) and a stress score of 12.6. Whereas un-vegetated and vegetated habitats were in close spatial proximity, these habitat types were distinct from one another in arthropod community ordination space (MRPP,  $\delta = 0.43$ ,  $A = 0.1125$ ,  $P < 0.0001$ ), principally along Axis 1. As expected, the presence of salmon carcasses in both vegetated and un-vegetated habitats shifted arthropod community composition (MRPP,  $\delta = 0.41$ ,  $A = 0.1442$ ,  $P = < 0.0001$ ). Relative abundance of Drosophilidae, Sciaridae, Sphaeroceridae, and Staphylinidae were all positively correlated with scores on Axis 2 ( $r = 0.44, 0.76, 0.72, 0.69$ ; respectively). Additional pairwise comparisons via MRPP indicated that carcasses removed to riparian habitats explained this shift in

community composition (RC vs. SC,  $\alpha = 0.016$ ,  $P < 0.0001$ ; RC vs. UR,  $\alpha = 0.016$ ,  $P < 0.0001$ ; SC vs. UR,  $\alpha = 0.016$ ,  $P = 0.0247$ ) after correcting alpha for multiple comparisons ( $\alpha$  of  $0.05 \div 3$  comparisons =  $0.016$ ). Additionally, we detected no effect on the riparian arthropod assemblage of the presence of salmon carcasses submerged in-stream (SC).

#### *Patch scale arthropod abundance*

At the patch scale, the addition of salmon carcasses to both vegetated and un-vegetated habitats had a positive effect on the total abundance of arthropods (MANOVA,  $F_{3, 263} = 4.28$ ,  $P = 0.0057$ ). Arthropod families responded significantly to treatment versus control plots (MANOVA, Family  $\times$  Treatment,  $F_{42, 264} = 5.40$ ,  $P < 0.0001$ ). Five families responded positively to the presence of carcass in riparian habitats (Fig. 3). No families responded negatively to treatment additions. Consistent with our hypothesis, four dipteran saprophages positively responded to the presence of riparian carcasses (Calliphoridae larvae and adults of Drosophilidae, Sciaridae, Sphaeroceridae), as did one coleopteran predator (adult Staphylinidae), but no parasitoids (Table 1). Arthropod responses to treatments were sustained over the duration of our experiment (Table 1). We used these five taxa to evaluate whether patch type mediated effect size of the subsidy. Overall, effect sizes in vegetated patches were generally greater than in un-vegetated patches. Carcasses did not increase the abundance of adult Calliphoridae flies captured in pitfall traps during the experiment, but those present deposited eggs, and the larvae consumed carcass material. Because larval Calliphoridae were not collected in pitfall traps at in-stream (SC) or control (UR) plots, effect size was calculated as their

average abundance in vegetated minus average abundance in un-vegetated habitats, divided by their average abundance in un-vegetated habitats. Subsequently, the effect of riparian carcasses on larval Calliphoridae was 49 times greater in vegetated than in un-vegetated patches ( $t$ -test,  $P = 0.0007$ ; Table 2). In comparison to the control, responses to riparian carcasses by Sphaeroceridae were approximately 7-fold in vegetated patches, whereas they were 4-fold in un-vegetated patches. Similarly, abundance of Drosophilidae was greatest in vegetated patches with salmon carcasses, though the overall magnitude of effect was low in comparison to those on other taxa. The effect size for Sciaridae did not differ by habitat, with approximately 3.5 times greater abundance in treatment than control in both vegetated and un-vegetated habitats. Only 1 family, Staphylinidae, exhibited a significant patch by treatment interaction (rmANOVA,  $F_{2, 12} = 10.23$ ,  $P < 0.0026$ ). Staphylinidae responded strongly to the presence of salmon carcasses, but only in vegetated patches, where abundance was 4 times that of control plots (Table 2). The remaining five families were generally more abundant in vegetated versus un-vegetated patches, but showed no response to the presence of salmon carcasses: Anthomyiidae [Diptera], Braconidae and Formicidae [Hymenoptera], Lycosidae [Aranea], Cicadialidae [Hemiptera], Oribatidae [Oribatida] (Table 1).

#### *Riparian patch pattern and arthropod responses at the reach scale*

Riparian habitat along stream reaches was predominantly comprised of dense willows (50-70%), with lesser proportions of vegetated grasses (20-33%) and un-vegetated (10-16%) patches (Fig. 4A). Trail Creek had the greatest proportion of patches vegetated by grasses (33%), followed by Little Beaver Creek (27%), and Big Owl Creek

(19%). The removal of salmon carcasses from the stream to riparian habitat by wildlife ranged from 20 to 31 carcasses, with roughly two times more salmon delivered to grassy patches in Trail Creek than in the other two streams (Fig. 4B).

Consistent with our findings at the patch scale, total abundance of adult Calliphoridae increased in carcass treatments at the reach scale (Treatment,  $F_{1, 12} = 15.29$ ,  $P = 0.004$ ). Abundance increased both initially and four to six weeks after treatment additions on sticky traps along carcass treated streams in comparison to controls (Fig. 5, Time  $\times$  Treatment,  $F_{4, 12} = 6.82$ ,  $P = 0.002$ ). We observed a 6-fold increase immediately after carcass additions and a delayed 3.6 fold increase four to six weeks afterwards (Fig. 4). In accordance with our hypothesis that small-scale patch character might differentially mediate effects of subsidies at larger spatial scales, we observed that Trail Creek had roughly two times higher abundance of adult Calliphoridae in comparison to the other treatment streams. However, in contrast to the patch-scale results, Sphaeroceridae and Sciaridae (Treatment,  $F_{1, 12} = 0.01$ ,  $P = 0.972$ ) exhibited no significant response to carcass treatments at larger reach scales (Fig. 5). Braconidae (Treatment,  $F_{1, 12} = 0.02$ ,  $P = 0.8811$ ) exhibited no significant increase in abundance at either scale (Fig. 5). Though Staphylinidae were collected in pitfall traps, they were not present on sticky traps.

## Discussion

The results of our study show how spatial heterogeneity can influence and mediate consumer responses at differing spatial scales to an experimentally manipulated subsidy, providing empirical evidence to accompany a range of theoretical and

conceptual contributions that have focused attention on this possibility (Polis et al. 1997, Holt 2002, Anderson et al. 2008). Strong mediating effects of riparian habitat character on attributes of the salmon carcass subsidy and concomitant traits of terrestrial arthropods appeared to drive the patterns in responses we observed at the patch scale. Furthermore, patch characteristics (i.e. biotic, abiotic), the strength of effects within a given patch type, and the composition of patches within riparian habitats appeared to influence the magnitude of effect of subsidies at broader spatial scales among certain arthropods.

Patch character altered the physical traits of the salmon carcass subsidy, apparently rendering it less palatable to certain consumers, which in turn influenced the magnitude of its effect. Generally, the effects of salmon carcasses were greatest when they were added to vegetated habitats. Based on observations of their breakdown, salmon carcasses on un-vegetated cobble bars became desiccated (probably owing to more direct exposure to sunlight) whereas carcasses in vegetated patches remained moist. Consequently, though the quantity of the subsidy and its quality in terms of energy density were similar between habitats (Marcarelli et al. 2011), desiccation of fish tissue on cobble bars may have decreased its palatability for arthropods, thus constraining responses. For example, salmon carcasses placed in vegetated habitats elicited a response by Calliphoridae larvae nearly 50 times stronger than did those placed in un-vegetated habitats. Dew formation and shading by surrounding grasses likely maintained a wetter microclimate in these habitats, preventing desiccation and maintaining the subsidy in a form amenable for feeding by insect larvae. Similar effects have been observed in tropical habitats, where desiccation of reptile carcasses inhibited rates of consumption by arthropods in dry versus wet habitats (Cornaby 1974). Yet, results of our study explicitly

demonstrate how the effects of a resource subsidy may depend upon small-scale environmental context. Additionally, our results contribute to a growing body of literature that demonstrates how environmental variability in general can influence subsidy effects across spatial scales (Menge et al. 2003, Menge and Menge 2013).

We observed that salmon carcasses in riparian habitats caused increases in arthropod abundance among four saprophagic families and one predatory family over the duration of our experiment, and that in most cases the strength of response differed by patch type. Arthropod families collected around salmon carcasses in riparian habitats were similar to those described by Hocking et al. (2009) along salmon streams in coastal British Columbia. For example, both larval and adult Calliphoridae were collected during our experiment. Adult Calliphoridae flies can deposit 150-200 eggs per individual, such that colonization of carcasses by relatively few adults can lead to large numbers of larvae (Triplehorn and Johnson 2005). Salmon carcasses added to riparian habitats caused increases in three other dipterans, Drosophilidae, Sphaeroceridae, and Sciaridae, all of which likely fed directly on putrefied tissue and bacteria at advanced stages of decomposition. Though we did not collect Sphaeroceridae and Sciaridae larvae in our pitfall traps, we did observe their larvae on salmon carcasses among the larvae of Calliphoridae. We speculate that the higher abundance we observed of adult Sphaeroceridae, Sciaridae, and Drosophilidae was driven by behavioral attraction to decomposing salmon carcasses, given that we only collected adults of these families in our traps and that the duration of the experiment was unlikely to encompass full development for these taxa. Thus, responses by these taxa, which can forage at scales much larger than the extent of our patch-scale experimental plots, were probably due to

aggregation of adults, whereas the response by Calliphoridae at this scale was caused by colonization by a few adults and subsequent high densities of larvae. Moreover, riparian habitat type influenced the degree to which salmon carcasses caused increases in Sphaeroceridae and Drosophilidae, with both showing an apparent preference for carcasses in vegetated habitats.

Given positive responses to salmon carcasses in abundance of dipterans that might serve as prey, we were somewhat surprised to find that only one predator, beetles of the family Staphylinidae, responded positively, and it did so only in vegetated habitats. Staphylinidae have adept chemosensory abilities allowing them to detect and colonize carcasses (e.g., pig, human) in early stages of decomposition and prey on adult flies, their eggs and larvae and other arthropods (Gennard 2007). Such sensory abilities may effectively increase the size of their “resource shed” (sensu Power and Rainey 2000). In contrast, other predators and parasitoids we observed (e.g., Formicidae, Braconidae, Lycosidae, or Coccinellidae) may be similarly mobile but not have comparable capacity to detect and locate salmon carcasses. Alternative explanations may include the subsidy being too short-lived to elicit responses in these taxa, or that they were not as efficiently captured by our pitfall trap method. Previous studies have documented the presence of these arthropod predators and parasitoids along salmon streams, and isotopic shifts that suggest they incorporate C and N along salmon-derived pathways, but numerical responses to salmon carcasses have not been reported (Hocking and Reimchen 2006, Hocking et al. 2009). With respect to our observation of a response by Staphylinidae in vegetated but not in un-vegetated patches, we offer two potential mechanisms. First, dipterans responded more strongly to the presence of salmon carcasses in vegetated

versus un-vegetated habitats, thus increasing the abundance of potential prey for Staphylinidae. Second, because Staphylinidae tend to avoid direct exposure to sunlight and higher temperatures (Centeno et al. 2002), vegetated patches that provided cover and shade may have been preferred. Overall, response of the predator assemblage was limited to a predator with traits best fitted to utilizing the subsidy of carcasses and associated prey.

Effects at the patch scale, coupled with riparian habitat composition, translated to significant increases at the scale of stream reaches for select arthropods, which was consistent with our second hypothesis. The removal of salmon carcasses to the riparian zone had overall positive effects on the abundance of aerial adult Calliphoridae, however no effects were observed for Sphaeroceridae and Sciaridae, or Braconidae. Positive changes in abundance of Calliphoridae were observed through time, with initial (0-2 week) and lagged (4-6 week) increases closely tied to the life cycle of Calliphoridae, such that initial increases were driven by behavioral attraction and lagged responses by emergence of adults from soils. Given the advanced state of decomposition and loss of carcass material in both riparian and stream environments (S.F. Collins, personal observation), it is most likely that the lagged responses were principally demographic and not behavioral. Curiously, no treatment effect on adult Calliphoridae was observed at the patch scale, but was observed at the reach scale, suggesting attraction was principally driven by the overall magnitude of the carcass subsidy to a reach. Most likely, those flies nearest carcasses opportunistically utilized the available resource. Alternatively, the lack of response at the patch scale may reflect the poor capture efficiency of pitfall traps when

it comes to adult Diptera. Whereas we observed a treatment effect on Sphaeroceridae and Sciaridae at the patch scale, this response did not translate to the reach scale.

Composition of riparian habitats appears to have an important mediating influence on the magnitude of response to subsidies at reach scales. Generally, streams with a higher proportion of dense riparian willow and red osier dogwood had fewer carcasses removed, suggesting that certain patch types may inhibit or shield the removal of carcasses to adjacent habitats, which was principally achieved by black bears in our study area (S. Collins, personal observation). In contrast, grassy vegetated patches provide easier access for wildlife to remove carcasses, which were also associated with greater effect sizes in our patch scale analysis. Based on our findings, the number of carcasses does not solely influence the overall effect size, but consideration of the habitats to which they are removed is also required. Spatial heterogeneity of recipient habitats may have implications for insectivores that forage at even broader spatial scales, integrating energy garnered across a mosaic of arthropod productivity that may occur in the landscape.

Our findings highlight the role habitat heterogeneity may play in mediating effects of resource subsidies across spatial scales, pointing to the need for models and conceptual frameworks to encompass such spatial complexity. Though most models of food webs and resource subsidies treat recipient systems as homogenous (Loreau and Holt 2003), we observed that spatial context dictated bottom-up responses to a subsidy, with consequences across trophic levels and larger spatial scales. Some have called for a more spatially explicit framework to understand food webs and resource subsidies among reaches in networks of stream-riparian ecosystems (Power and Rainey 2000). Our findings echo this call and suggest spatial patchiness at smaller scales may be important

as well, posing a further challenge to predicting responses to subsidies using existing models. Future investigations of resource subsidies, both theoretical and empirical, should make such spatial heterogeneity an explicit focus in order to further understanding of food webs in landscapes.

Riparian zones are important for maintaining biodiversity (Naiman et al. 1993). Factors that degrade riparian habitats and microclimates may, in turn, influence the magnitude of responses of organisms to salmon carcass subsidies. Alterations to riparian habitats may influence light availability and the composition of riparian vegetation. These alterations may be naturally occurring or human-induced, such as wildfire, timber harvest, or road construction. Broader scale factors such as climate change may also structure and alter riparian habitats over longer time periods, ultimately influencing how riparian habitats mediate the effects of salmon carcass subsidies (Battin et al. 2007).

### **Acknowledgements**

This research was supported by Idaho Fish and Game and Idaho State University (GS10-05). We thank JB Johnson, University of Idaho, for assistance verifying and identifying arthropods collected during our research. We also thank RT Bowyer, JM Davis, P Lendrum, and G Emfield at Idaho State University, who reviewed and provided comments on early drafts, which greatly improved this manuscript.

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## Tables

Table 1. Results of the univariate rmANOVA analyses for six Orders and 11 Families of arthropods collected in pitfall traps from Trail, Big Owl, and Little Beaver Creeks during summer 2010. Bold numbers indicate significant effects ( $\alpha = 0.05$ ).

| <i>Order/family</i> | <i>Effect</i>     | <i>Ecological role</i> | <i>F</i> <sub>(Between, Within)</sub> | <i>P</i>      |
|---------------------|-------------------|------------------------|---------------------------------------|---------------|
| Hymenoptera         |                   |                        |                                       |               |
| Braconidae          | Patch             | Parasitoid             | 11.46 <sub>(1,12)</sub>               | <b>0.0054</b> |
|                     | Treatment         |                        | 2.17 <sub>(2,12)</sub>                | 0.1567        |
|                     | Patch × Treatment |                        | 0.16 <sub>(2,12)</sub>                | 0.8508        |
|                     | Time              |                        | 1.24 <sub>(2,24)</sub>                | 0.3061        |
|                     | Time × Treatment  |                        | 1.25 <sub>(4,24)</sub>                | 0.3153        |
| Formicidae          | Patch             | Generalist             | 20.49 <sub>(1,12)</sub>               | <b>0.0007</b> |
|                     | Treatment         |                        | 8.02 <sub>(2,12)</sub>                | <b>0.0061</b> |
|                     | Patch × Treatment |                        | 0.32 <sub>(2,12)</sub>                | 0.7330        |
|                     | Time              |                        | 2.86 <sub>(2,24)</sub>                | 0.0772        |
|                     | Time × Treatment  |                        | 0.87 <sub>(4,24)</sub>                | 0.4981        |
| Diptera             |                   |                        |                                       |               |
| Anthomyiidae        | Patch             | Saprophage             | 28.48 <sub>(1,12)</sub>               | <b>0.0002</b> |
|                     | Treatment         |                        | 5.54 <sub>(2,12)</sub>                | <b>0.0197</b> |
|                     | Patch × Treatment |                        | 1.78 <sub>(2,12)</sub>                | 0.2103        |
|                     | Time              |                        | 1.18 <sub>(2,24)</sub>                | 0.3251        |
|                     | Time × Treatment  |                        | 0.87 <sub>(4,24)</sub>                | 0.4965        |
| Calliphoridae adult | Patch             | Saprophage             | 8.46 <sub>(1,12)</sub>                | <b>0.0131</b> |
|                     | Treatment         |                        | 1.60 <sub>(2,12)</sub>                | 0.2414        |
|                     | Patch × Treatment |                        | 0.46 <sub>(2,12)</sub>                | 0.6442        |
|                     | Time              |                        | 0.18 <sub>(2,24)</sub>                | 0.8331        |
|                     | Time × Treatment  |                        | 0.43 <sub>(4,24)</sub>                | 0.7834        |
| Drosophilidae       | Patch             | Saprophage             | 0.25 <sub>(1,12)</sub>                | 0.6286        |
|                     | Treatment         |                        | 7.49 <sub>(2,12)</sub>                | <b>0.0077</b> |
|                     | Patch × Treatment |                        | 0.58 <sub>(2,12)</sub>                | 0.5771        |
|                     | Time              |                        | 5.69 <sub>(2,24)</sub>                | <b>0.0095</b> |
|                     | Time × Treatment  |                        | 0.29 <sub>(4,24)</sub>                | 0.8816        |
| Sciaridae           | Patch             | Saprophage             | 17.05 <sub>(1,12)</sub>               | <b>0.0210</b> |
|                     | Treatment         |                        | 19.85 <sub>(2,12)</sub>               | <b>0.0002</b> |
|                     | Patch × Treatment |                        | 0.35 <sub>(2,12)</sub>                | 0.7142        |

|                |                   |             |                         |               |
|----------------|-------------------|-------------|-------------------------|---------------|
|                | Time              |             | 0.42 <sub>(2,24)</sub>  | 0.6625        |
|                | Time × Treatment  |             | 0.03 <sub>(4,24)</sub>  | 0.9985        |
| Sphaeroceridae | Patch             | Saprophage  | 0.96 <sub>(1,12)</sub>  | 0.3475        |
|                | Treatment         |             | 13.08 <sub>(2,12)</sub> | <b>0.0010</b> |
|                | Patch × Treatment |             | 1.23 <sub>(2,12)</sub>  | 0.3271        |
|                | Time              |             | 0.11 <sub>(2,24)</sub>  | 0.8984        |
|                | Time × Treatment  |             | 0.85 <sub>(4,24)</sub>  | 0.5056        |
| Coleoptera     |                   |             |                         |               |
| Staphylinidae  | Patch             | Predator    | 29.49 <sub>(1,12)</sub> | <b>0.0002</b> |
|                | Treatment         |             | 20.85 <sub>(2,12)</sub> | <b>0.0001</b> |
|                | Patch × Treatment |             | 10.23 <sub>(2,12)</sub> | <b>0.0026</b> |
|                | Time              |             | 0.32 <sub>(2,24)</sub>  | 0.7291        |
|                | Time × Treatment  |             | 0.25 <sub>(4,24)</sub>  | 0.9046        |
| Aranaea        |                   |             |                         |               |
| Lycosidae      | Patch             | Predator    | 4.81 <sub>(1,12)</sub>  | <b>0.0486</b> |
|                | Treatment         |             | 0.02 <sub>(2,12)</sub>  | 0.9783        |
|                | Patch × Treatment |             | 0.30 <sub>(2,12)</sub>  | 0.7453        |
|                | Time              |             | 1.60 <sub>(2,24)</sub>  | 0.2217        |
|                | Time × Treatment  |             | 0.69 <sub>(4,24)</sub>  | 0.6059        |
| Hemiptera      |                   |             |                         |               |
| Cicadialidae   | Patch             | Herbivore   | 6.43 <sub>(1,12)</sub>  | <b>0.0262</b> |
|                | Treatment         |             | 2.28 <sub>(2,12)</sub>  | 0.1451        |
|                | Patch × Treatment |             | 0.70 <sub>(2,12)</sub>  | 0.5167        |
|                | Time              |             | 1.78 <sub>(2,24)</sub>  | 0.1903        |
|                | Time × Treatment  |             | 0.32 <sub>(4,24)</sub>  | 0.2183        |
| Oribatida      |                   |             |                         |               |
| Oribatidae     | Patch             | Detritivore | 7.08 <sub>(1,12)</sub>  | <b>0.0208</b> |
|                | Treatment         |             | 0.22 <sub>(2,12)</sub>  | 0.8062        |
|                | Patch × Treatment |             | 0.2 <sub>(2,12)</sub>   | 0.8205        |
|                | Time              |             | 1.58 <sub>(2,24)</sub>  | 0.2288        |
|                | Time × Treatment  |             | 2.13 <sub>(4,12)</sub>  | 0.1175        |

Table 2. Effect size of the five arthropod families collected in pitfall traps from Trail, Big Owl, and Little Beaver Creeks during summer 2010. Comparisons between habitats of the effect size on arthropods were calculated as the difference between the averages of treated groups and control groups divided by the control average. Because no Calliphoridae larvae were collected in control plots, effect size was calculated by subtracting mean un-vegetated from mean vegetated, and then dividing by average un-vegetated. Response ratio's were also calculated:  $\ln(RC/UR)$ .

| Family               | Habitat                       |          |                                        |              |                   |             |                               |        |                                        |              |                   |                |
|----------------------|-------------------------------|----------|----------------------------------------|--------------|-------------------|-------------|-------------------------------|--------|----------------------------------------|--------------|-------------------|----------------|
|                      | Vegetated                     |          |                                        |              |                   |             | Un-vegetated                  |        |                                        |              |                   |                |
|                      | Riparian Carcass<br>Mean (SE) |          | Upstream<br>Reference<br>Mean (SE, SD) |              | Response<br>Ratio | Effect Size | Riparian Carcass<br>Mean (SE) |        | Upstream<br>Reference<br>Mean (SE, SD) |              | Response<br>Ratio | Effect<br>Size |
|                      |                               |          |                                        |              |                   |             |                               |        |                                        |              |                   |                |
| Sciaridae            | 11.08                         | (1.38)   | 2.5                                    | (0.44, 0.76) | 1.48              | 3.43        | 7.81                          | (1.61) | 1.72                                   | (0.45, 0.79) | 1.51              | 3.54           |
| Sphaeroceridae       | 7.66                          | (0.59)   | 0.91                                   | (0.08, 0.14) | 2.12              | 7.42        | 4.44                          | (0.37) | 0.80                                   | (0.36, 0.63) | 1.70              | 4.55           |
| Drosophilidae        | 4.94                          | (0.86)   | 2.94                                   | (0.44, 0.63) | 0.51              | 0.68        | 3.83                          | (0.63) | 2.75                                   | (0.78, 1.36) | 0.33              | 0.39           |
| Staphylinidae        | 3.63                          | (0.19)   | 0.80                                   | (0.21, 0.37) | 1.50              | 3.54        | 0.58                          | (0.09) | 0.47                                   | (0.10, 0.17) | 0.21              | 0.23           |
|                      | Vegetated<br>Mean (SE)        |          | Un-vegetated<br>Mean (SE, SD)          |              | Response<br>Ratio | Effect Size |                               |        |                                        |              |                   |                |
| Calliphoridae larvae | 197                           | (121.08) | 4                                      | (2.30, 4)    | 3.89              | 48.25       |                               |        |                                        |              |                   |                |

## Figures

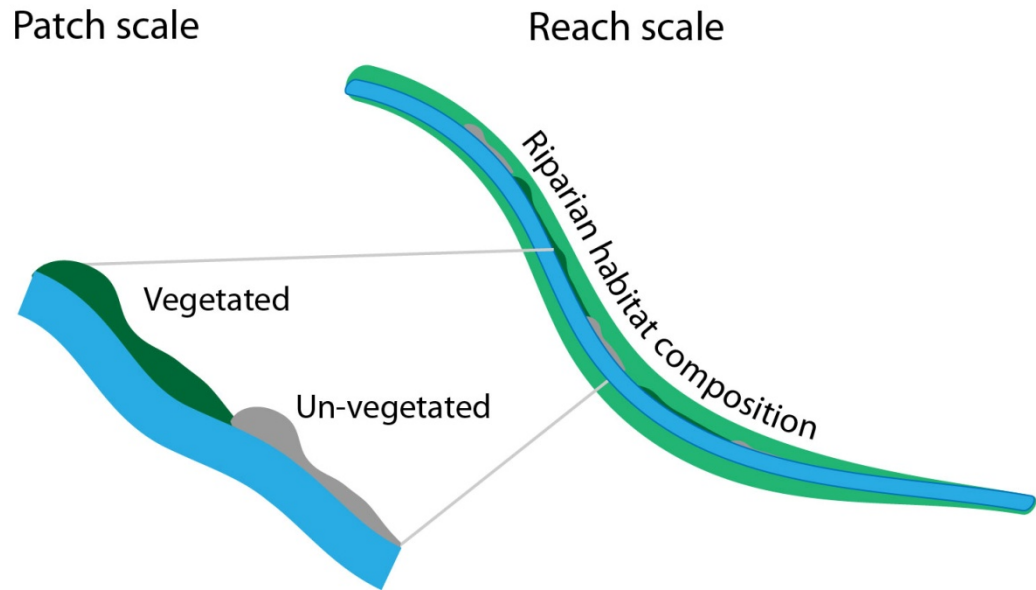


Figure 1. Fine-scale patches receive resource subsidies, yet often differ in biotic and abiotic characteristics. Such patches may vary in their ability to mediate consumer interactions with a subsidy, suggesting landscape composition may serve as an important intermediary between resource subsidies and broader scale effects.

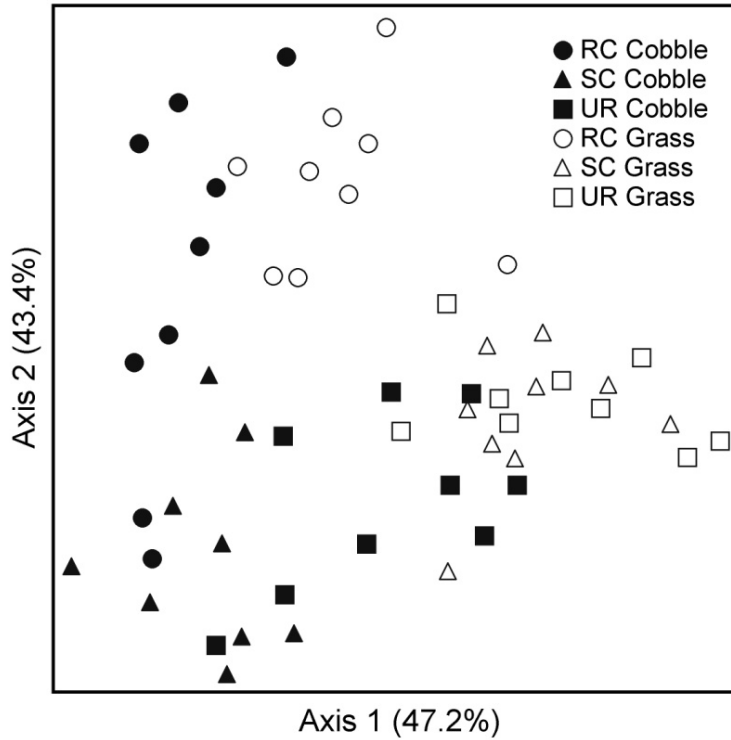


Figure 2. Arthropods were collected in pitfall traps at Trail, Big Owl, and Little Beaver Creeks during our summer 2010 experiment. NMDS ordination of mean abundance of arthropod families in vegetated and un-vegetated (grass, cobble) habitats and treatment plots (RC = Riparian carcass, SC = Stream carcass, UR = Upstream reference). A total of 16 families were included in the analysis. Axis 1 accounted for 47.2% of the variation and Axis 2 explained 43.4% of the variation in this NMDS ordination, with a stress score of 12.6. The presence salmon carcasses in both vegetated and un-vegetated habitats shifted the arthropod community composition in ordination space (MRPP,  $\delta = 0.41$ ,  $A = 0.1442$ ,  $P < 0.0001$ ). Pairwise comparisons generated from MRPP analysis indicated that carcasses removed to riparian habitats explained this shift in community composition (RC vs. SC,  $P < 0.0001$ ; RC vs. UR,  $P < 0.0001$ ).

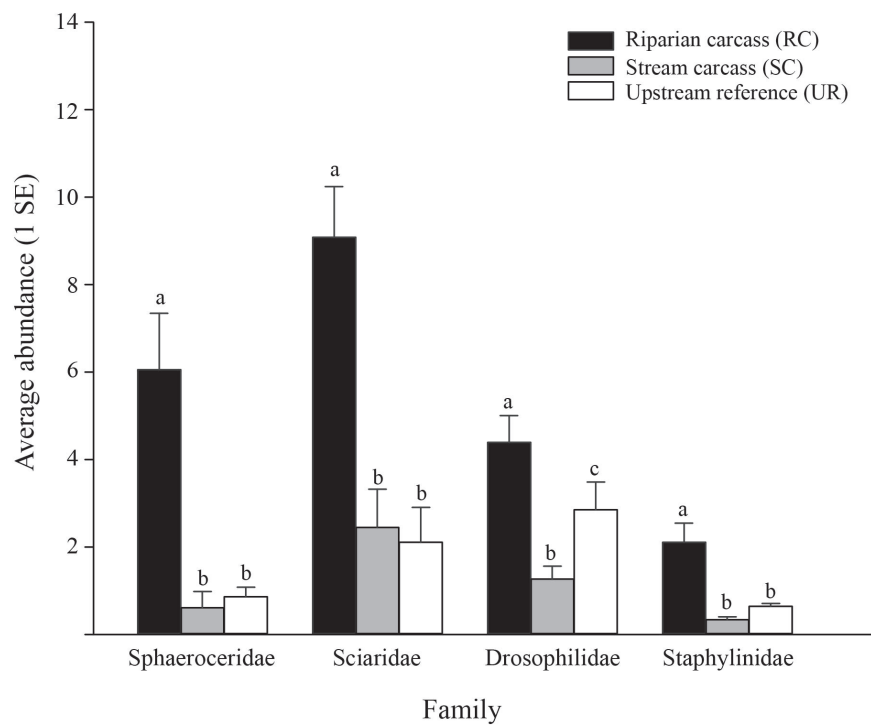


Figure 3. Average abundance of terrestrial arthropods collected in pitfall traps at treatment plots during summer 2010. Calliphoridae larvae were not collected in SC and UR plots. Error is  $\pm 1$  SE (n=3).

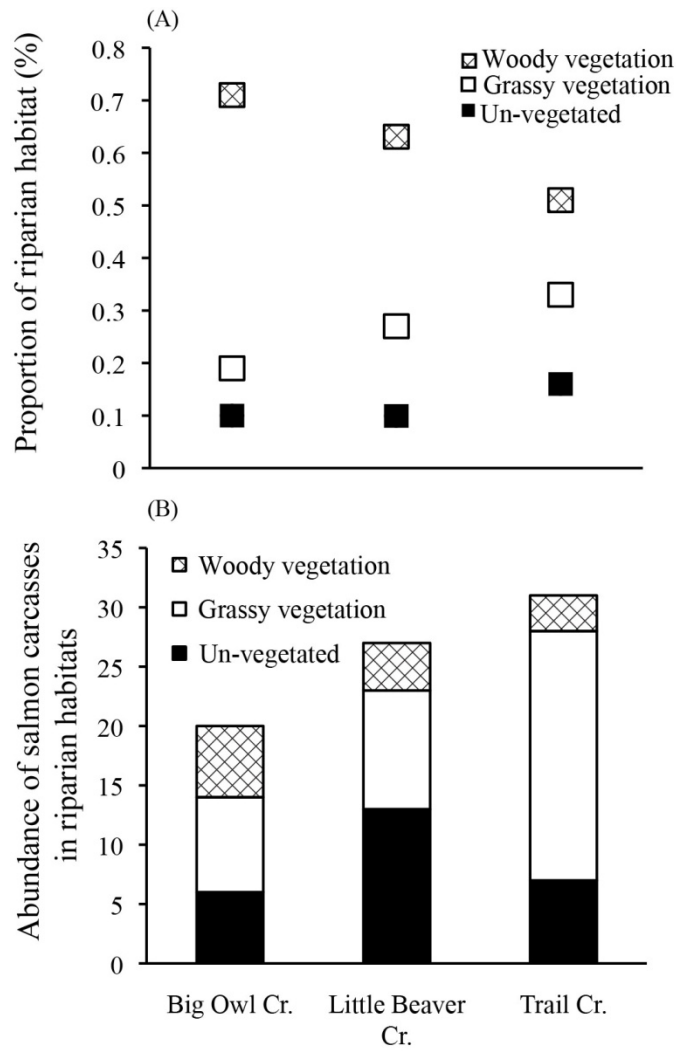


Figure 4. (A) Proportion of riparian patches and (B) abundance of salmon carcasses removed from treated streams to respective adjacent patches during summer 2010.

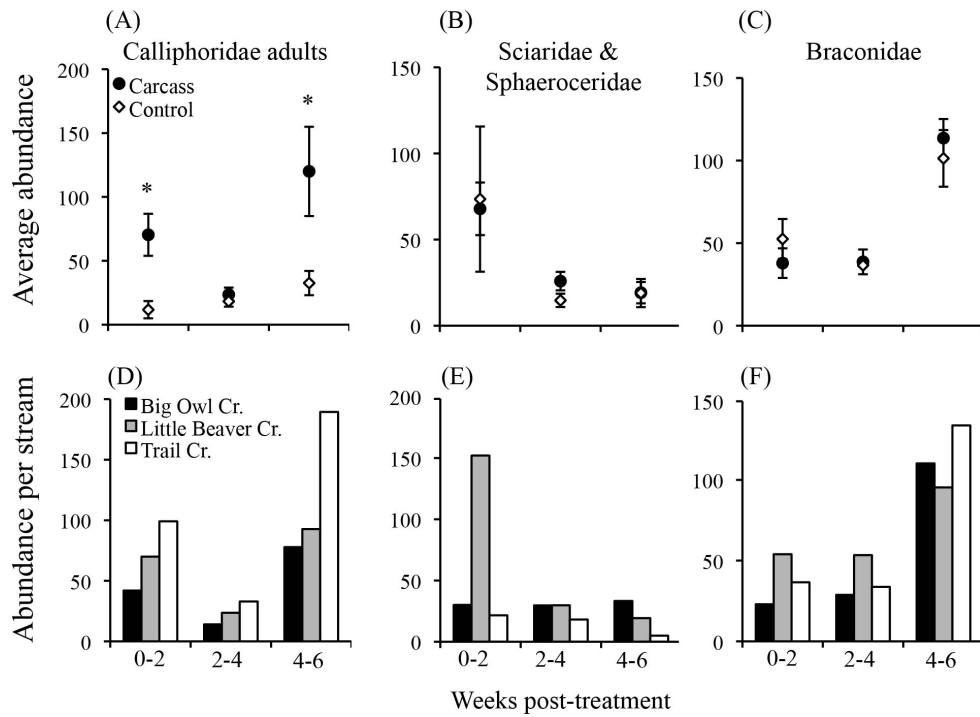


Figure 5. Treatment (A-C) and stream specific (D-F) abundance of Calliphoridae, Sphaeroceridae and Sciariidae, and Braconidae collected on sticky traps during summer 2010. Error is  $\pm 1$  SE. Asterisks indicate significant differences between treatment and control for specific time periods.

## **Chapter 4**

Direct and indirect responses of stream and riparian organisms to experimental subsidies  
of salmon are mediated by subsidy form and duration

## Abstract

Understanding the role of resource subsidies in food webs may require expanding from a simple donor-recipient framework to one that explicitly considers the effects of subsidy form, includes the potential for subsidies and their effects to propagate and feedback among multiple habitats, and provides a direct treatment of the mediating influences of temporal scale. Over four years we experimentally tested how the physical form of subsidies, either complex (carcasses of Pacific salmon) or simple (pelletized salmon tissue, referred to as “analog”), influenced direct and indirect responses by organisms across multiple time scales (weeks to years) within two linked, recipient habitats (streams and riparian zones). Salmon carcasses were frequently removed (typically by black bears) from streams to the wetted margins and riparian zones, whereas salmon analog was not. Salmon carcasses had both a greater array and magnitude of short-term ecological effects in comparison to analog. Over the duration of the experiment, fish consumption of benthic insects increased by 110-140% and 44-66% in carcass and analog treatments, respectively. Consequently, fishes efficiently cropped benthic insects, resulting in reduced average biomass of adult aquatic insects in the riparian zone, which indirectly reduced abundance of Tetragnathidae spiders and feeding activity of *Myotis californicus* and *yumanensis* bats in riparian habitats. Translocation of salmon carcasses to riparian zones increased terrestrial Diptera through behavioral attraction and greater emergence from riparian soils subsidized by carcasses. The activity of *M. thysanodes* and *evotis* bats increased at sites with more terrestrial Diptera, and, in a manner consistent with amplified apparent competition, there were corresponding declines in Araneidae spiders on which these bats also prey. Our experiment

demonstrated that the form of a subsidy determines the initial conditions in space (i.e., likelihood of dispersal among multiple recipient habitats) and through time (i.e., persistence of subsidy), and that, in turn, these constrain the type and magnitude of ecological responses to the subsidy.

## **Introduction**

Ecological theory regarding resource subsidies is guided by a donor-recipient paradigm, whereby the magnitude of a resource subsidy is controlled by conditions in the “donor” habitat and the subsidy has a range of potential consequences for population and community dynamics constrained to a recipient habitat (Polis et al. 1997, Polis et al. 2004, Holt 2004). Studies of subsidies have focused on responses in singular, recipient habitats, yet subsidies may be trans-located beyond an initial receiving habitat to those surrounding it, with attendant consequences there as well. The potential for such translocation, whereby multiple habitats are effectively subsidized by a shared donor habitat, may be determined by interactions between the physical form of the subsidy (i.e., dissolved, particulate, organism) and a range of processes, both biotic (e.g., dispersal of a subsidy by organisms) and abiotic (e.g., transport by wind or water). For instance, in forested watersheds large woody debris and forest litter subsidize headwater streams, but because of its form (e.g., complex and buoyant) it is ultimately transported by flow and subsidizes downstream habitats as well, from larger rivers, to estuaries and the near-shore ocean (Maser and Sedell 1994). Understanding the dynamics of food webs in heterogeneous landscapes may require consideration of how the form of a subsidy influences its extended spatial distribution and subsequent impacts.

Incorporating information about the physical form of a resource subsidy may allow for a better understanding of its effects. Subsidy forms range from simple nutrients to more complex organic structures such as detritus and living organisms (Polis et al. 1997). The consequences of resource subsidies within food webs are complex, in part, because of the diversity of organisms (e.g., microbes, vertebrate) affected and their roles within the ecosystem (Huxel et al. 2002). Subsidy form likely mediates which organisms and which trophic levels are directly influenced. For instance, plants utilize directly the nutrients from inorganic fertilizer added to a field, but herbivores do not. More structurally complex subsidies like seaweed detritus (Spiller et al. 2010), insects (Yang 2004), ungulate carcasses (Selva et al. 2005) and salmon (Wipfli et al. 1998) influence their local environment through decomposition, nutrient leaching, and direct consumption by organisms across trophic levels, and they may be distributed to multiple recipient habitats. The degree to which physical form of subsidies influences ecological responses has not been explicitly or experimentally addressed.

Subsidies of complex form may vary in the duration of their availability within a habitat and, in turn, this may constrain food web responses by influencing where a subsidy is delivered, how long the resource persists within habitat(s), and who benefits. Field experiments have demonstrated the importance of subsidies to food webs, however few have been conducted at temporal scales that encompass the potential for both short- and long-term responses (but see Slavik et al. 2004, Cross et al. 2006, Spiller et al. 2010). The duration of availability within receiving habitat(s) and the times over which subsidy effects manifest all influence the response of *in situ* (i.e., within receiving habitats) prey and predators (Sears et al. 2004, Spiller et al. 2010). For example, short-term availability

of a subsidy or its effects on prey may elicit only behavioral/aggregative responses of consumers because reproduction and a demographic response would require more time (Murakami and Nakano 2002, Sabo and Power 2002, Fukui et al. 2006). In contrast, a subsidy that persists longer may drive both behavioral and/or demographic responses by consumers. Such responses may have additional indirect effects on organisms in recipient habitat(s). For instance, a prey subsidy to a predator may amplify (apparent competition; Holt 1977) or alleviate (apparent mutualism; Abrams and Matsuda 1996) competition with *in situ* organisms that share that predator. Additionally, when predators are subsidized directly, top-down regulation can be strengthened, thereby suppressing *in situ* prey populations with potential cascading effects (Polis et al. 1997). However, such indirect effects are again dependent on the timescales of subsidy availability, whether predators can directly utilize the resource, and the relative efficiency of predators at consuming *in situ* prey (Takimoto et al. 2009, Spiller et al. 2010). The net outcome of subsidizing consumers by multiple direct and indirect food web pathways may depend on the overall strength of response of co-occurring bottom-up and top-down forces to subsidy additions (Borer et al. 2006). Such effects are often conceptualized as occurring within the confines of the recipient habitat, however if prey are mobile and link habitats, subsidy effects in one may propagate to others. Therefore, factors that mediate the strength of these linkages (e.g., predator efficiency) can potentially affect the sign of the relationship between consumers in adjacent habitats that share a common linkage.

Streams and their adjacent riparian zones have long served as an important model ecosystem for the study of flows of materials and organisms between habitats (Baxter et al. 2005). Annual returns of spawning Pacific salmon deliver marine-derived nutrients

and energy to streams and adjacent riparian habitats via removal by wildlife (Quinn et al. 2009), and emergence of aquatic insects (Francis et al. 2006), with positive effects on prey and predators in both habitats (for reviews see Cederholm et al. 1999, Gende et al. 2002), however less is known about how salmon subsidies influence linkages between these habitats (Chapter 1). The mechanisms by which these short-lived subsidies influence the structure of stream-riparian food webs may depend on the outcome of co-occurring bottom-up and top-down responses within aquatic (biofilm, insects, fishes) and riparian (insects, insectivores) food webs.

To investigate the direct and indirect effects of resource subsidies within stream-riparian food webs, we experimentally added salmon subsidies to streams in two stoichiometrically similar, but physically distinct, forms (salmon carcasses and pelletized salmon “analog”). As described previously (Chapter 2), salmon carcasses are translocated to riparian habitats by wildlife and analog pellets are not, indicating that differences in physical form can influence the distribution of a subsidy to multiple habitats. I evaluated the direct response of prey and predators in stream and riparian habitats to these subsidies, as well as the indirect effects within or across habitat boundaries. I hypothesized that the duration (short, long-term) of a subsidy’s availability and the timescales over which its effects are manifested influence whether direct responses by consumers are aggregative or demographic, and whether indirect effects on other species in the recipient food web are positive or negative. Based on differences in the physical form of experimental subsidies, I predicted that salmon carcasses and pelletized salmon analog would have similar effects (e.g., sign, magnitude) on consumers in aquatic habitats, but different effects on organisms in terrestrial habitats because only

salmon carcasses would be translocated to riparian areas. The previous predictions assume the primacy of bottom-up processes, however co-occurring top-down pressures can override bottom-up effects (Borer et al. 2006), therefore we predicted short-term effects of the subsidies would increase top-down controls by resident fishes, and indirectly decrease benthic insects upon which they prey. Additionally, we predicted terrestrial insect responses would be stronger at streams treated with salmon carcasses and have positive effects on insectivores in riparian habitats, effects that might feed back via input of these terrestrial arthropods to streams. We also expected that subsidy effects on benthic insects and fishes within aquatic habitats would propagate via changes in emergence of adult aquatic insects with attendant consequences in riparian food webs, such that resident fishes might indirectly affect terrestrial insectivores like spiders and bats that rely on such aquatic-derived prey.

## **Methods**

### *Study area & food web description*

Our experiment was conducted in the North Fork Boise River drainage in central Idaho, USA. The streams in our study are representative of those that would have received runs of Pacific salmon. Anadromous steelhead (*Oncorhynchus mykiss*) and Chinook (*O. tshawytscha*) salmon historically migrated to tributaries of the North Fork Boise to spawn, however the construction of dams along the migration corridor between 1906 and 1915 eliminated these fishes for the past century (NWPCC 2004). Surface geology across the basin is mostly granitic rock of the Idaho batholith. Upland forests are predominantly Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga*

*menziesii*). Willow (*Salix*), red-osier dogwood (*Cornus sericea*), and tall grasses (*Festuca*) are the dominant riparian vegetation.

The insect assemblage consisted of 7 Orders and 30 Families spanning aquatic and terrestrial habitats. Over the duration of our experiment we collected a total of 141,532 individual insect adults across nine streams. Aquatic insects comprised 70% of the abundance and 51% of the biomass of the aerial insects collected. Biomass of aquatic insects varied by three orders of magnitude, ranging from small-bodied Chironomidae midges to large bodied Limnephilidae caddisflies. Diptera and Hymenoptera were the dominant terrestrial arthropod Orders. In addition to arthropods, the fish assemblage consisted predominantly of three species, resident rainbow trout (*O. mykiss*), brook trout (*Salvelinus fontinalis*), and mottled sculpin (*Cottus bairdii*). There was no systematic distribution of these species by treatment in our experiment.

The insectivore taxa we studied included orb-weaving spiders, parasitoids, and bats, predators that range dramatically in the spatial extents over which they forage (i.e., their “resource sheds,” *sensu* Power and Rainey 2000). Two families of orb-weaving spiders were observed within the riparian zone, the horizontal orb-weaver Tetragnathidae and the vertical orb-weaver Araneidae. Tetragnathidae position their webs parallel to the surface of water to capture emerging aquatic insects, whereas Araneidae webs are vertical to capture both aquatic and terrestrial taxa (Sanzone et al. 2003, Iwata 2007). Additionally, the parasitoid Braconidae was the dominant Hymenopteran collected during our study. Nine bat species ranging in size and foraging strategies were observed at our study streams: Yuma myotis (*Myotis yumanensis*), California myotis (*M. californicus*), Western small-footed myotis (*M. ciliolabrum*), long-legged myotis (*M. volans*), little

brown myotis (*M. lucifugus*), fringed myotis (*M. thysanodes*), long-eared myotis (*M. evotis*), big brown bat (*Eptesicus fuscus*), and silver-haired bat (*Lasionycteris noctivagans*). Three of these species tend to forage above the surface of water and land (*M. yumanensis*, *californicus*, *lucifugus*), while also gleaning arthropods including spiders from vegetation (Brigham et al. 1992, Ober and Hayes 2008, Hagen and Sabo 2011).

### *Experimental design and treatments*

To test the hypotheses and predictions outlined above, we conducted a large-scale, multi-year, manipulative field experiment. To achieve this, we applied to sections of streams two marine-derived subsidies that are being increasingly used by managers to add nutrients to oligotrophic streams affected by the loss of Pacific salmon migrations. We used whole salmon carcasses that were pasteurized to alleviate concerns of spreading fish pathogens to unaffected basins (e.g., whirling disease, Compton et al. 2006), and pelletized, pasteurized fishmeal (referred to as ‘analog’; for description see Pearsons et al. 2007) that contains similar ratios of nitrogen and phosphorus, and is utilized by stream organisms (Wipfli et al. 2004). These treatments differ in their physical form, and because we anticipated that the ‘analog’ would not be removed to riparian habitats by wildlife, we expected that the contrast would allow us to distinguish how subsidy form mediates responses among aquatic and terrestrial organisms.

We used a randomized complete-block design in which 500-m long reaches at nine streams of the North Fork Boise drainage (located in central Idaho) with similar physical (e.g., discharge, substrate) and biotic (e.g., species assemblages) characteristics

were selected. Carcass loading rates were based on a target of 0.5 salmon carcasses / m<sup>2</sup> of wetted stream channel, chosen to reflect a high spawner density based upon historical data for streams of this region (IDFG 1985). We based analog loading rates to match P loads from salmon carcasses, which were 5.5 g P / m<sup>2</sup>. Treatments were applied annually during the first week of August for three consecutive years (2008-2010).

#### *Benthic insects*

Benthic insects were sampled annually (2009-2011) at all nine streams during July of each year. At each stream we randomly sampled seven riffle habitats with a Surber sampler (0.09 m<sup>2</sup>, 250 µm mesh size) to a depth of approximately 10 cm (Surber 1937). In the laboratory, insects were separated from detritus and measured to the nearest 0.5 mm. Biomass was calculated from taxon-specific, length-weight relationships (Benke et al. 1999).

#### *Consumption of benthic aquatic insects*

To estimate the annual consumption of benthic invertebrates by resident fishes, we used the trophic basis of production approach (Benke and Wallace 1980, Cross et al. 2011). Due to seasonal variability in aquatic insect prey, we used a constant assimilation efficiency of 0.75. Net production efficiency was 0.21 and 0.12 for age 0 and age 1+ to account for allometric relationships between fish consumption and growth with fish size (Donner 2011, Bellmore et al. 2013). For more detailed methods, please refer to the Methods sub-section “*Trophic basis of trout production and annual consumption of benthic invertebrates*” in Chapter 2.

### *Aerial insects*

I deployed 2430 sticky traps over three years to quantify aerial insect biomass within riparian habitats at each of the 9 streams from 2008 to 2010. Cylindrical sticky traps ( $0.104 \text{ m}^2$ ) were coated in resin and suspended from fence posts 1.3 m above the ground. At each stream, I established six lateral transects every 75-m on alternating sides of the stream and positioned traps at 0, 5, and 25 m from the stream, for a total of 18 traps per stream. Traps collected for 14 days and were replaced, ensuring continuous sampling during the experiment. Traps were deployed immediately post-treatment in summer 2008, with three sample periods spanning a total of six weeks. For 2009 and 2010, samples were collected for three pre- and three post treatment periods. In the lab, aquatic and terrestrial insects were identified to Order or Family, when possible, and counted. Subsets of individuals for each taxon were measured to determine average length. Length-weight regressions were used to estimate biomass for each Order and Family (Sabo et al. 2002; Appendix 4a).

### *Spiders*

Nighttime visual surveys (Kato et al. 2003) were conducted annually (2009-2011) to quantify the abundance of two dominant riparian spiders, the horizontal orb-weaver Tetragnathidae, and the vertical orb-weaver Araneidae, 10-m around stationary fence posts within the stream reach. A total of 60-m of stream reach was surveyed per stream per sample period. Lateral surveys (0 – 5-m) indicated 96% of Tetragnathidae and Araneidae abundance occurred within 1m of the wetted edge, so we sampled to 1m from

the water's edge and vertically to 2.5-m, on both sides of the stream. Riparian spiders were identified based upon spider morphological characteristics and web orientation (Ubick et al. 2005).

### *Bats*

Bat activity was acoustically monitored with Anabat SD1 bat detectors deployed at each of nine streams in locations chosen to reduce environmental feedback (Brigham et al. 1992). Two detectors were deployed for three night intervals at each stream. Bat activity was recorded during spring (May), summer (July) and late summer (August). Due to similarities of certain species, we partitioned echolocation calls into four phonic groups. Bat activity for each group was measured as the mean number of search calls per night, averaged across seasons to represent annual utilization of stream-riparian prey resources. Due to logistical constraints including limited quantities of recorders, five streams were sampled in 2009 and the remaining four were sampled in 2010.

### *Statistical analyses*

To evaluate the effect of subsidies in different recipient habitats (i.e., stream versus riparian), temporal changes of arthropods (aquatic and terrestrial) and fishes (consumption of benthic invertebrates) were evaluated using ANOVA with repeated measures, with treatment and sampling period as fixed factors. To determine the short-term effects of adult aquatic insects and terrestrially-derived invertebrate prey resources on trout production, we used ANOVA. To differentiate effects based on experimental subsidy form, *a priori* contrasts of carcass and analog subsidies and controls were

conducted for all main effects ( $\alpha = 0.05$ ). Over time, we distinguished responses by consumers as behavioral or demographic based upon knowledge of the organisms' life-history characteristics and behavioral traits. Emergence patterns of aquatic insects vary temporally, so covariance structures were calculated using the auto-regressive function (SAS, Proc Mixed, ar(1)), which assumes that samples taken closer together in time are more similar than samples further apart.

I used analysis of covariance (ANCOVA) with treatment as a fixed factor to evaluate changes in the sign of the relationship between consumption of benthic invertebrates by fish and either adult aquatic insect biomass or orb weaving spiders for 2009 and 2010. Sampling of bat activity across all nine streams occurred over two years, limiting our analysis to a simple linear regression between annual fish consumption and average seasonal bat activity. Because salmon subsidies can also influence terrestrial invertebrates (Hocking and Riemchen 2006), we evaluated relationships between terrestrial Diptera and bat activity. Additionally, certain bat species are adept at gleaning prey from vegetation, so we also evaluated whether bat activity influenced Araneidae abundance to identify potential apparent competitive or mutualistic relationships between terrestrial Diptera and Araneidae spiders. Outliers were removed only if their Grubbs value exceeded the critical value (Grubbs 1950).

## **Results**

### *Benthic insect biomass and consumption by resident fish*

Overall, treatment additions increased total benthic insect biomass in carcass streams (Treatment,  $F_{2,6} = 9.79$ ,  $p = 0.012$ ). Carcasses had the strongest effect (Carcass

vs. control,  $F_{1,6} = 18.46$ ,  $p = 0.005$ ; Fig. 1 A). Benthic insect biomass responses to analog treatments were highly variable and did not differ from carcass treatments or controls. The consumption of aquatic insects by resident fishes exhibited similar patterns. Overall, consumption of benthic insects was the strongest in carcass treatments (Treatment,  $F_{2,6} = 6.28$ ,  $p = 0.025$ ; Fig. 1 B).

#### *Aerial insect responses to subsidy additions*

We observed both short-term (weeks) and lagged (annual) increases in the biomass of aerial insects, but only by subsets of the terrestrial and adult aquatic insect assemblages. The most consistent effects were short-term (2-6 weeks following treatment additions) responses by aquatic midges (Chironomidae) emerging from streams, aggregations of terrestrial Diptera (Calliphoridae) that were attracted to treatment reaches, or Diptera emerging from soils. Overall, emergence of aquatic Diptera did not vary by treatment (Treatment,  $F_{2,6} = 3.49$ ,  $p = 0.098$ ), however select sample periods increased 71-154% in carcass and 43-115% in analog treatments in the weeks following additions during 2009 and 2010, relative to control (Treatment  $\times$  Sample  $\times$  Year,  $F_{27,54} = 2.94$ ,  $p < 0.001$ ; Fig. 2 A). Carcasses increased the overall biomass of terrestrial Diptera (Treatment,  $F_{2,6} = 5.28$ ,  $p = 0.047$ ) in the riparian zone. Additionally, short-term responses were observed for terrestrial Diptera during sampling periods after carcasses were added (Fig. 2 E). Terrestrial Diptera biomass increased 122-167% in carcass and 70-94% in analog treatments during 2009 and 2010 (Treatment  $\times$  Sample  $\times$  Year,  $F_{27,54} = 3.75$ ,  $p < 0.001$ ; Appendix 4b). We detected no overall (Treatment,  $F_{2,6} = 1.13$ ,  $p = 0.383$ ) or sample specific treatment effects for adult Ephemeroptera (Treatment

× Sample × Year,  $F_{27, 54} = 1.23, p = 0.258$ ; Fig. 2 B). Yet, prior to treatment application in summer 2009, adult Ephemeroptera biomass in analog streams was 122% greater than carcass and control streams. Overall, biomass of adult Plecoptera (Treatment,  $F_{2, 6} = 0.46, p = 0.654$ ) and Trichoptera (Treatment,  $F_{2, 6} = 1.97, p = 0.220$ ) did not respond to treatments (Fig. 2 C, D). Biomass of both adult Plecoptera (Treatment × Sample × Year,  $F_{27, 54} = 0.42, p = 0.991$ ) and Trichoptera (Treatment × Sample × Year,  $F_{27, 54} = 1.10, p = 0.377$ ) exhibited considerable temporal variability.

The consumption of benthic insect larvae by fishes affected patterns of adult insect biomass in riparian habitats (averaged across samples for 2009 and 2010). I observed a positive relationship between fish consumption and adult aquatic Diptera biomass in control streams, however the sign of this relationship was reversed in treatment streams. Increased benthic insect consumption by fishes resulted in decreased adult Diptera biomass in the riparian zone (ANCOVA, Consumption × Treatment,  $F_{1, 12} = 5.31, p = 0.004$ ; Fig. 4 A). Consumption of benthic insects by fishes did not reverse the sign of relationship with adults of Ephemeroptera, Plecoptera, or Trichoptera (ANCOVA, Consumption × Treatment,  $p > 0.05$ ), however treatment streams did deviate considerably from the positive relationships observed in control streams (Fig. 4 B-D, Appendix 4c – Table C2).

#### *Insectivore and parasitoid responses to treatments and fish consumption*

Neither Tetragnathidae (Treatment,  $F_{2, 6} = 1.32, p = 0.363$ ) nor Araneidae (Treatment,  $F_{2, 6} = 1.04, p = 0.432$ ) spiders exhibited any direct increases to treatment additions (Fig. 3 A, B). Such was the case for parasitic hymenopterans, principally

Braconidae, which also exhibited no changes in biomass relative to treatment additions (Treatment,  $F_{2,6} = 2.22, p = 0.189$ ; Fig. 2 F). Because fish influenced patterns in aquatic insect emergence, we evaluated the indirect responses by riparian spiders and parasitoids. Tetragnathidae exhibited a positive relationship with fish consumption in control streams, however the sign of the relationship reversed in treatment streams, with more insect consumption by fishes resulting in fewer spiders (ANCOVA, Consumption  $\times$  Treatment,  $F_{1,12} = 9.26, p = 0.004$ ; Fig. 4 E). This pattern was not observed for Araneidae, whom rely on both aquatic and terrestrial insects (ANCOVA, Consumption  $\times$  Treatment,  $F_{1,12} = 0.08, p = 0.924$ ; Fig. 4 F), or for Hymenoptera (ANCOVA, Consumption  $\times$  Treatment,  $F_{1,12} = 0.09, p = 0.919$ ; Fig. 4 G), which feed on a range of prey items.

We observed evidence for indirect effects of predation by fishes on the activity of select bat species within the riparian zone that were similar to those we observed for spiders. Like Tetragnathidae spiders, the activity of small-bodied *Myotis californicus* and *yumanensis* weakly declined in streams where the consumption of benthic insects by fish was high (adj.  $R^2 = 0.37, p = 0.061$ ; Fig. 5 A), after the removal of an outlier. Similarly, activity by *M. volans*, *lucifugus*, and *ciliolabrum*, which are slightly larger in body size, declined as consumption of benthic insects increased (adj.  $R^2 = 0.36, p = 0.068$ ; Fig. 5 D), again after the removal of an outlier. There were no relationships between fish consumption and activity by *Myotis thysaodes* and *evotis* ( $p = 0.635$ ; Fig. 5 B.), nor the large-bodied *Eptesicus fuscus* and *Lasionycteris noctivagans* ( $p = 0.217$ ; Fig. 5 C.).

Salmon subsidies influenced terrestrial flies and bat activity. We observed that the activity of *M. thysaodes* and *evotis* increased with terrestrial Diptera biomass, though the pattern was weak (adj.  $R^2 = 0.28, p = 0.082$ ). Likewise, the activity of *M. thysaodes*

and *evotis* (adj.  $R^2 = 0.34$ ,  $p = 0.051$ ) and *E. fuscus* and *L. noctivagans* (adj.  $R^2 = 0.65$ ,  $p = 0.008$ ) was negatively related with Araneidae spiders (Fig. 5). Additionally, activity of *Myotis californicus* and *yumanensis* declined with increased terrestrial Diptera biomass (adj.  $R^2 = 0.31$ ,  $p = 0.012$ ; Fig. 5).

## Discussion

The results of our large scale, multi-year experimental addition of salmon subsidies to streams demonstrate that the form of a subsidy mediates responses, including the potential for effects to propagate and feedback among more than one recipient habitat and the responses of organisms in these habitats across a hierarchy of time scales, all of which point to the need for a more complex treatment of resource subsidies in general. Though studies of resource subsidies are often framed within a donor-recipient paradigm (Polis et al. 1997, Polis et al. 2004, Holt 2004), our findings indicate that this may be too simplistic when interpreting their numerous potential direct and indirect effects. Differences in the biophysical form of the salmon carcasses and pelletized salmon “analog” subsidies added in our experiment affected their distribution beyond the initial recipient habitat (stream) to adjacent habitats (riparian zone). In turn, organisms in both habitats, ranging from an array of aquatic and terrestrial insects to fish, spiders and bats, responded numerically through aggregative and/or demographic processes in the weeks and years following treatment additions. These responses were the consequence of both direct and indirect effects of the subsidies, occurring both within and across recipient habitats. Alterations to the exchange of organisms between these recipient habitats that were mediated by subsidy form, such as the distribution of salmon carcasses to riparian

zones by bears, the emergence of adult aquatic insects, and the input of terrestrially derived insects to streams, had important consequences for the net effect of salmon subsidies in the stream-riparian food web.

Our findings show that the form of a subsidy can influence both the range of recipient habitats influenced (as opposed to a singular habitat) and the organism responses within these. Though resource subsidies are ubiquitous, they come in differing sizes and degrees of biophysical complexity (e.g., dissolved nutrients, leaf litter, whale carcasses; Polis et al. 1997). Conceptually, they are treated as similar, yet differences in form or quality determine which consumers can utilize these resources (Marcarelli et al. 2011). Our findings indicated that differences in form influenced the distribution of experimental marine subsidies beyond the stream habitat. Salmon carcasses were readily removed to adjacent riparian habitats by black bear and other mammals (Chapter 2, 3). In contrast, the analog subsidy was not removed due to its pelletized form. Both subsidies influenced behavioral responses of terrestrial Diptera by attracting organisms to the riparian zone, and in some cases responses to analogs were stronger. These properties of a subsidy are often not considered when evaluating ecological responses and are certainly not limited to subsidies of salmon. For instance, the nitrogen and lignin content of allochthonous leaf litter affects the rate of decomposition and release of particulate organic matter to streams (Melillo et al. 1982). Likewise, mobile predators and scavengers redistribute carcass material throughout the landscape (Wilmers et al. 2003, Schmitz et al. 2010).

Results of our experiment demonstrated that the duration of experimental subsidy availability determined whether responses of prey were behavioral or demographic in

aquatic and terrestrial environments. Recent theoretical and empirical studies have demonstrated that the timescales of subsidy inputs (i.e., duration of availability) are an important determinant of the mechanism of consumer responses (Sears et al. 2004, Takimoto et al. 2009, Spiller et al. 2010). Salmon subsidies persisted for roughly 4-6 weeks in the stream (S.F. Collins, *personal observation*) and 1-2 weeks in riparian habitats (Collins and Baxter, 2014). I observed increased biomass of terrestrial Diptera in both salmon carcass and analog treatments (which are not removed from streams) in the weeks immediately following treatment additions during 2009 and 2010, suggesting aggregation responses were driven by attraction to decomposing organic material in the stream. Though the analog subsidy was not removed from the stream, the release of chemical odor from decomposition appears to have attracted consumers with chemosensory abilities (Archer and Elgar 2003). Flies also colonized exposed carcasses that were either completely removed to riparian habitats or exposed in the wetted margins of the stream. Terrestrial Diptera larvae consumed carcasses, pupated in the soil and emerged as adults 4-6 weeks after treatment applications. I did not detect any increases in aquatic Diptera larvae from year to year (Chapter 2). However, emergence of adult aquatic Dipterans increased in the weeks following treatment additions. This pattern was principally driven by Chironomidae, which are small-bodied midges capable of producing multiple generations within a year. I speculate that both rapid life cycles of *r*-strategist Diptera and their behavioral traits allowed them to respond to the ephemeral resource and subsequently increase productivity within the duration when the subsidy was available (Yang et al. 2008).

I observed negative indirect effects of subsidies on *in situ* prey through shared predators in both aquatic and terrestrial environments, through mechanisms of apparent competition (Holt 1977, Abrams et al. 1998). These types of subsidy effects have been demonstrated elsewhere (Polis and Hurd 1996, Nakano and Murakami 2002, Spiller et al. 2010), though they have been limited to a singular recipient habitat. My findings indicate that resource subsidies have the potential to influence these types of interactions between organisms in multiple recipient habitats. Resident trout production (but not abundance) increased through multiple food web pathways including the direct consumption of subsidy material and indirectly through the consumption of invertebrates from the stream and terrestrial environments (Chapter 2). These multiple pathways of energy flow in the short-term contributed to increased annual production of trout and increased consumption of benthic invertebrates through time, resulting in apparent competition between salmon subsidies and *in situ* benthic prey. In the riparian zone, I detected apparent competition between terrestrial Diptera and Araneidae spiders through mutual predators, *Myotis thysanodes* and *evotis*. In this instance, the biomass of Diptera increased due to behavioral attraction and increased production (in carcass treatments). Biomass of terrestrial Diptera positively correlated with the activity of *M. thysanodes* and *evotis*, which tend to forage on terrestrial prey (Faure and Barclay 1994, Clare et al. 2011). The activity of *M. thysanodes* and *evotis* and Araneidae spiders were negatively correlated, which suggests potential predation by bats, as these bat species frequently glean arthropods from vegetation (Faure and Barclay 1994, Clare et al. 2011). Other bat species exhibited no patterns in relation to Araneidae spiders. These findings indicate

that subsidies can influence the potential for apparent competition between prey and predators in multiple habitats.

The results further point to indirect subsidy effects that extend across boundaries to influence organisms in adjacent habitats. I had predicted that strong bottom-up subsidy effects would propagate to riparian habitats through the emergence of aquatic insects, benefitting insectivores. These findings indicated that increased consumption of benthic invertebrates by stream fishes throughout the year resulted in a reduction in the mean biomass of adult aquatic insects in the riparian zone. In contrast, these relationships were positive between consumption of invertebrates by fish and the aerial aquatic insects in control streams. The change in the sign of the relationship was strongest for adult aquatic Diptera, but the trend was generally consistent (though weaker and not statistically significant) across other Orders as well. Curiously, the short-term increases in adult Chironomidae midges did not offset this relationship at the annual scale. By mediating emergence, subsidized fishes indirectly influenced the abundance/activity of Tetragnathidae spiders and *Myotis californicus* and *yumanensis* bats, all of which feed on adult aquatic insects (Brigham et al. 1992, Marczak and Richardson 2007, Hagen and Sabo 2011). Again, subsidized fish changed the sign of the relationship with Tetragnathidae spiders relative to the control, much like the patterns observed for adult insects. A similar negative relationship was detected for the activity of *Myotis californicus* and *yumanensis* bats, which also forage above the surface of water on aerial aquatic insects (Hagen and Sabo 2011). These findings are among the first to indicate that subsidized environments and increased productivity do not necessarily translate to positive responses among all organisms.

Measurements of bat activity revealed foraging patterns across years, however we could not determine the size of their populations. Additionally, other factors such as species-specific foraging activity and proximity to roosting habitats (Menzel et al. 2005) may also have influenced variability in bat activity but were not evaluated. The linear correlations between Diptera, Araneidae, and some bats demonstrate the patterns are present in some cases, however we lacked the power to test specific interaction effects. The responses of riparian organisms stemmed in large part from the interaction of subsidy form and bears (Reimchen 2000, Quinn et al. 2009). Regions with low bear populations may lack this crucial mechanism. These extended riparian responses proved important for both the productivity of fish and terrestrial organisms, and are not exclusive to our study (Wipfli et al. 1998, Hocking and Reimchen 2006, Scheuerell et al. 2007). When considering subsidy form, biotic factors can have substantive effects on the response of organisms. Interpretations of experimental outcomes would have varied had I limited focus to a single recipient habitat, however by accounting for how subsidy form influenced organism responses in multiple recipient habitats I identified how subsidies influenced relationships between fishes and seemingly far removed organisms such as bats.

The experiment used whole salmon carcasses that were pasteurized and an artificial salmon carcass analog. These subsidies have similar ratios of nitrogen and phosphorus (Wipfli et al. 2004), yet their immediate and extended effects through the food web varied, variation that we attribute to form. Either of these forms is likely to differ further from natural (i.e., unpasteurized) carcasses in other ways including rates of decomposition. Though seemingly obvious, there are considerable difference between an

inanimate mitigation tool and live, spawning salmon. Yet, from a policy perspective, a distinction is generally not drawn between forms because nutrients are considered the common currency, not the fish (see review and critique in Chapter 1). Nevertheless, pasteurized salmon carcasses, analog pellets, and inorganic fertilizers are being utilized with increased frequency as a means of mitigation on the basis that the nutrients themselves are of principal importance (Roni et al. 2002). Results of our experiment suggest otherwise.

Responses of organisms to salmon subsidies were not always positive. We observed that terrestrial insectivores that were reliant on aquatic insects declined, whereas insectivores that feed on terrestrially-derived prey increased. Managers should consider that the re-introduction of salmon-derived subsidies may not have immediate, positive effects that propagate through landscapes. Such subsidies influence both bottom-up and top-down processes in complex ways, and strong, direct effects may negatively influence other organisms within food webs by indirect means. Consequently, there is need for a more refined understanding of the complex ways that subsidies of salmon influence the structure of communities in aquatic and terrestrial habitats.

### **Acknowledgments**

This experiment was conducted in collaboration with K. Kavanagh, C. Robbins, J. Chandler, L. Hebdon, T. Wheeler, and A. Noble-Stuen. We are grateful to past and present members of the Stream Ecology Center at Idaho State Universities for their field, lab, and intellectual support, particularly R. Martin, A. Bell, H. Bechtold, J. Benjamin, J.R. Bellmore, C. Morris, J. Leuders- Dumont, J. Haddix, N. Tillotson, M. Pacioretty, and H. Harris. This project was funded and supported by Bonneville Power Administration

(2007-332-00), Idaho Power, the Idaho Department of Fish and Game, and the National Science Foundation--EPSCoR in Idaho (EPS-08-14387). The use of trade names or products does not constitute endorsement by the U.S. Government.

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## Figures

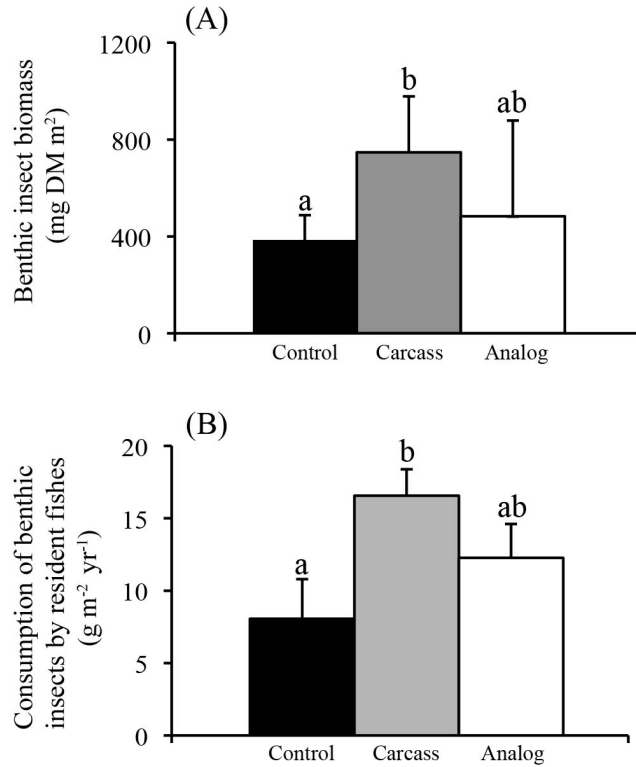


Figure 1. Effects of treatment additions on (A) standing crop biomass (mg DM m<sup>-2</sup>) of benthic insects and (B) the annual consumption of benthic insects (g m<sup>-2</sup> yr<sup>-1</sup>) by resident fishes in streams of the North Fork Boise River, ID, USA. Error bars are standard errors (n=3). DM = dry mass.

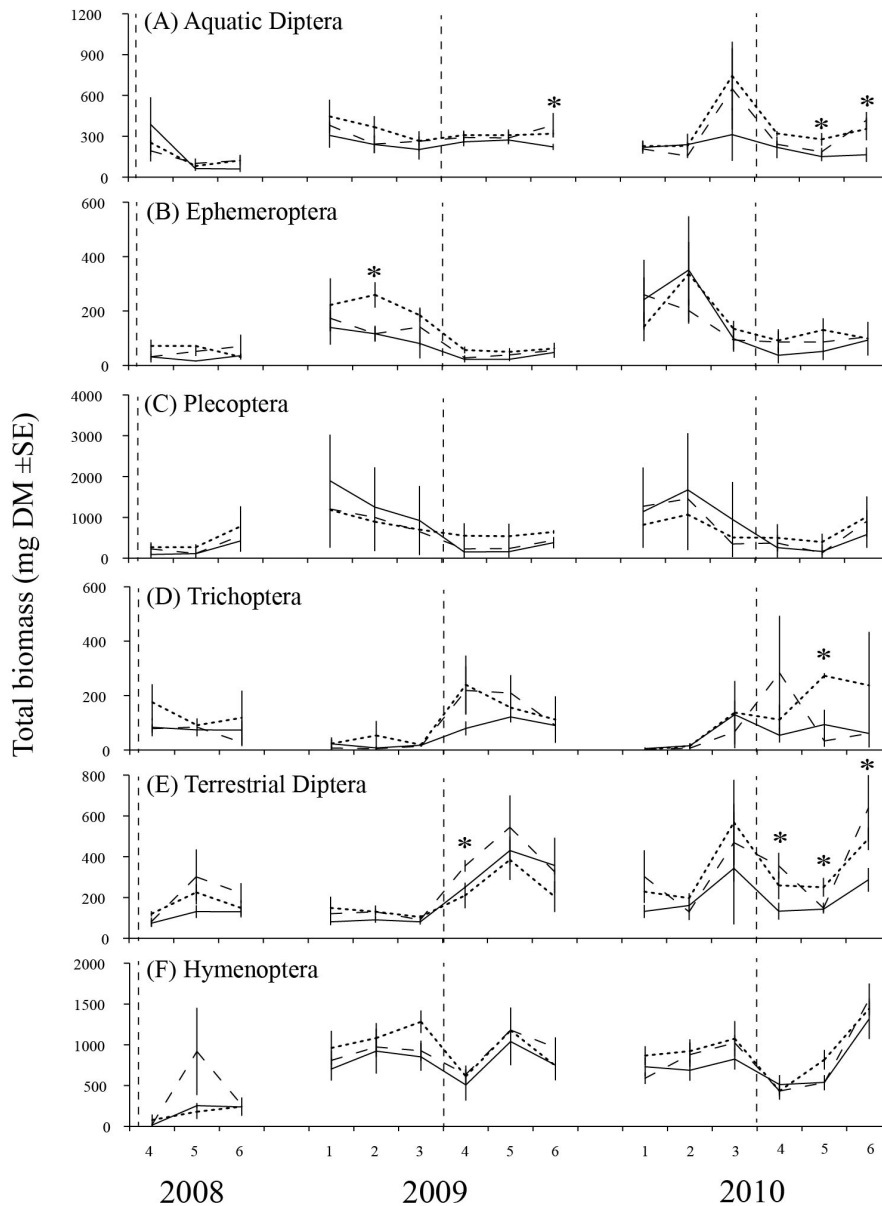


Figure 2. Effects of treatment additions on the total biomass of dominant aquatic and terrestrial insect Orders across three years. Insects were collected on sticky traps, which were deployed for 2-week intervals. Vertical dashed lines indicate between which samples annual treatments were added. Error bars are standard errors (n=3). Solid line = control, large-dashed = salmon carcass, small-dashed = analog pellet. Asterisks indicate significant treatment effects during specific sample periods. DM = dry mass.

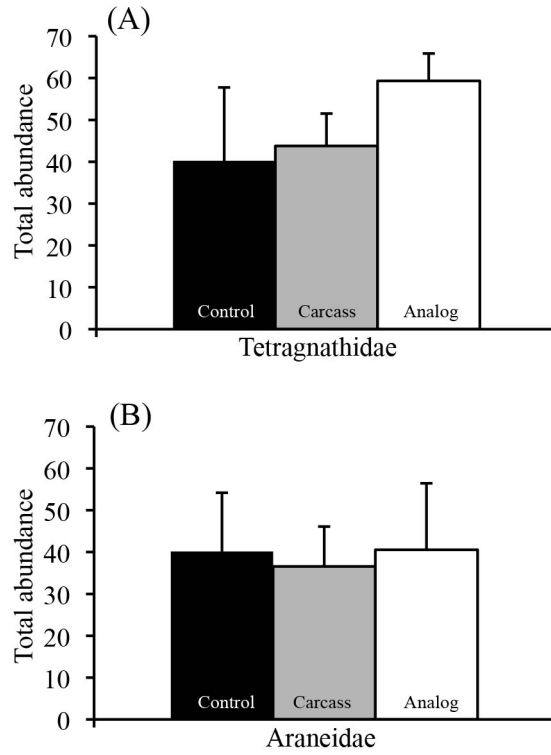


Figure 3. Overall effect of treatment additions on the total abundance of riparian spiders (A) Tetragnathidae and (B) Araneidae in riparian habitats of the North Fork Boise River, ID, USA. Error bars are standard errors (n=3).

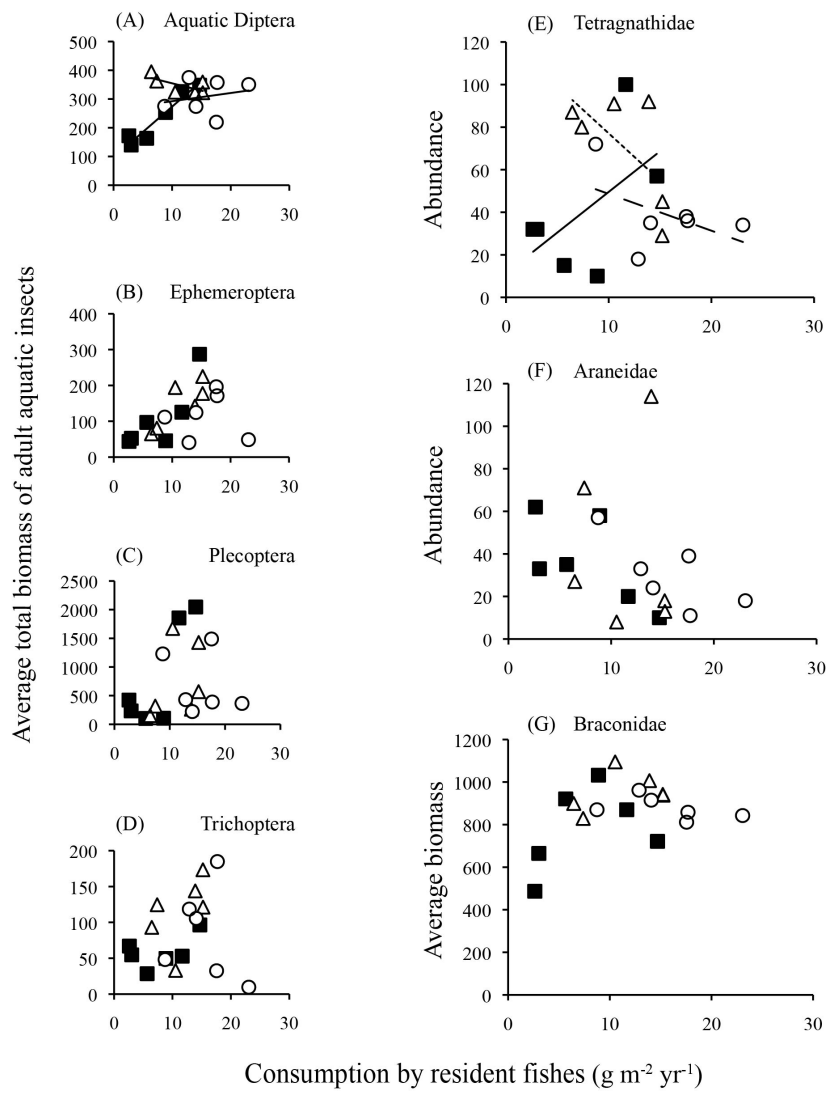


Figure 4. The relationships of the annual consumption of benthic insects by resident fishes and average annual biomass of (A) aquatic Diptera, (B) Ephemeroptera, (C) Plecoptera, (D) Trichoptera, and total abundance of riparian spiders (E) Tetragnathidae, (F) Araneidae, and parasitoid (G) Braconidae for years 2009 and 2010. Each point represents a stream by year combination. Squares = control, circles = salmon carcass, triangles = analog pellet

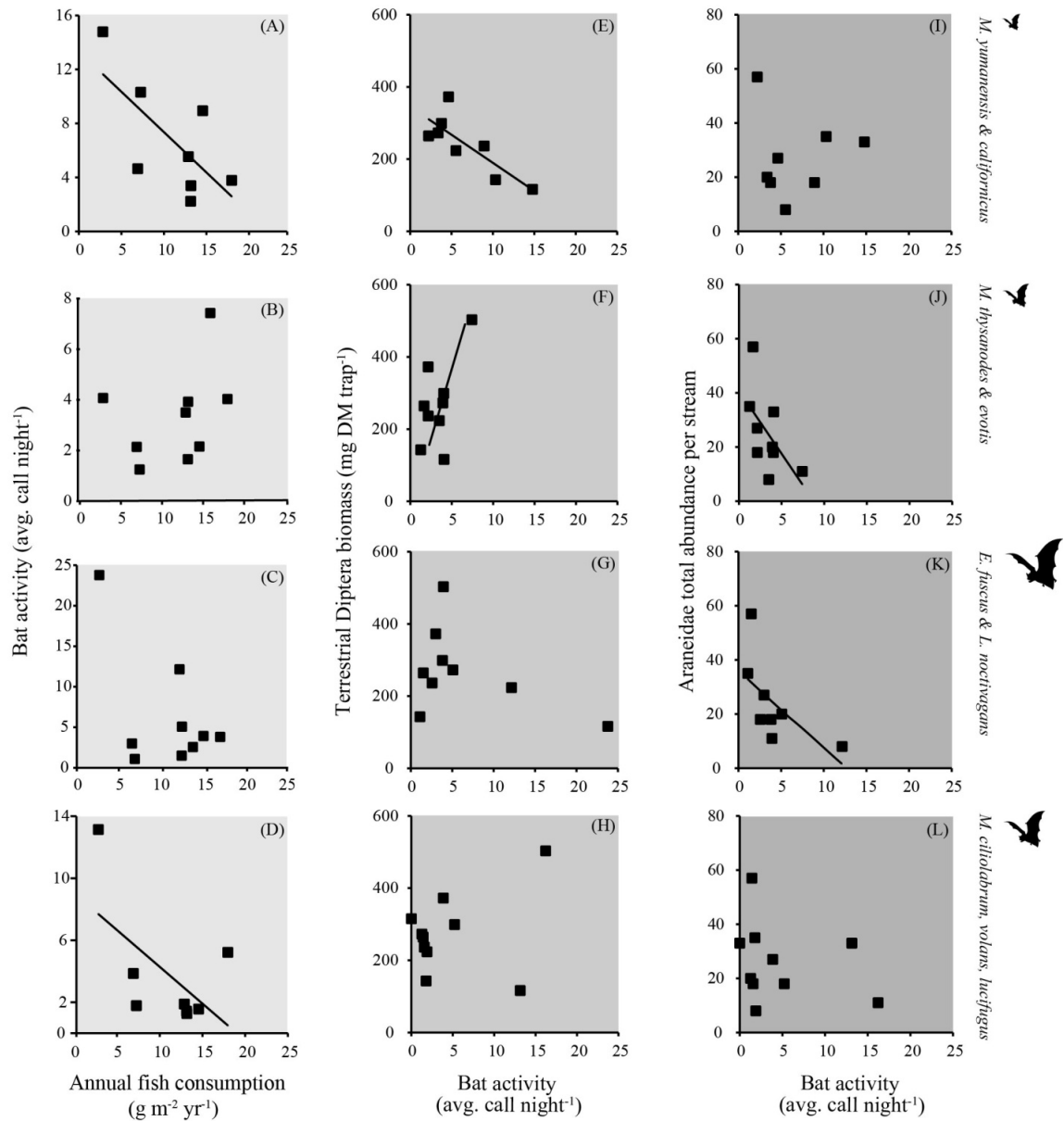


Figure 5. Mean bat activity versus the total annual consumption of benthic insects by resident fishes. Bat icons indicate the relative size of each phonic group. Mean bat activity versus the average biomass of terrestrial Diptera (left column), and total abundance of Araneidae (right column) at each stream.

1 Appendix 4a. Summary of length-mass coefficients used to estimate dry mass of aerial insects collected on sticky traps. Lengths of  
2 individual taxa were estimated using a digital micrometer.

| Origin      | Order         | Family          | Genera                                  | <i>b</i> | <i>a</i> | N   | Mean length<br>mm (SE) |        | Est. dry mass<br>(mg) |
|-------------|---------------|-----------------|-----------------------------------------|----------|----------|-----|------------------------|--------|-----------------------|
| Aquatic     | Ephemeroptera | Ameletidae      | <i>ameletus</i>                         | 2.49     | 0.014    | 14  | 6.69                   | (0.19) | 1.59                  |
|             |               | Heptageniidae   | <i>cinigmula, eporus, rhithrogenia</i>  | -        | -        | 21  | 7.26                   | (0.17) | 1.95                  |
|             |               | Ephemerellidae  | <i>ephemerella, drunella, seratella</i> | -        | -        | 74  | 7.80                   | (0.29) | 2.33                  |
|             | Plecoptera    | Baetidae        | <i>baetis</i>                           | -        | -        | 58  | 6.40                   | (0.11) | 1.42                  |
|             |               | Chloroperlidae  | <i>kathoperla, sweltsa</i>              | 1.69     | 0.26     | 152 | 6.00                   | (0.05) | 5.37                  |
|             |               | Paraleuctridae  | <i>paraleuctra</i>                      | -        | -        | 19  | 4.78                   | (0.12) | 3.65                  |
|             |               | Perlidae        | <i>doraneuria</i>                       | -        | -        | 1   | 11.50                  | na     | 16.13                 |
|             |               | Perlodidae      | <i>megarcys</i>                         | -        | -        | 25  | 11.65                  | (0.27) | 16.49                 |
|             |               | Nemouridae      | <i>zapada</i>                           | -        | -        | 65  | 4.76                   | (0.12) | 3.63                  |
|             |               | Peltoperlidae   | <i>yoraperla</i>                        | -        | -        | 10  | 7.12                   | (0.13) | 7.17                  |
|             | Trichoptera   | Glossosomatidae | <i>glossosoma, microsoma</i>            | 2.9      | 0.01     | 48  | 5.41                   | (0.08) | 1.34                  |
|             |               | Rhyacophilidae  | <i>rhyacophila</i>                      | -        | -        | 30  | 8.21                   | (0.39) | 4.48                  |
|             |               | Brachycentridae | <i>brachycentrus</i>                    | -        | -        | 44  | 4.13                   | (0.28) | 0.61                  |
|             |               | Limnephilidae   | <i>eocosmoecus</i>                      | -        | -        | 15  | 18.00                  | (0.89) | 43.68                 |
|             |               | Hydropsychidae  | <i>arctopsyche</i>                      | -        | -        | 23  | 10.50                  | (0.10) | 9.15                  |
|             | Diptera       | Chironomidae    | <i>orthocladinae, tanypodinae</i>       | 1.57     | 0.1      | 163 | 1.79                   | (0.06) | 0.25                  |
|             |               | Simuliidae      | <i>simulium</i>                         | -        | -        | 54  | 1.25                   | (0.04) | 0.14                  |
|             |               | Tipulidae       | <i>tipula, hexatoma</i>                 | -        | -        | 23  | 14.33                  | (1.07) | 6.54                  |
|             |               | Culicidae       | -                                       | -        | -        | 50  | 3.90                   | (0.19) | 0.85                  |
| Terrestrial | Diptera       | Tabanidae       | -                                       | 3.05     | 0.006    | 103 | 8.17                   | (0.16) | 3.64                  |
|             |               | Emphididae,     | -                                       | -        | -        | 76  | 5.54                   | (0.12) | 1.11                  |

|             |                |   |      |      |     |       |        |       |  |
|-------------|----------------|---|------|------|-----|-------|--------|-------|--|
|             | Tachinidae     |   |      |      |     |       |        |       |  |
|             | Calliphoridae  | - | -    | -    | 103 | 8.49  | (0.14) | 4.09  |  |
|             | Bombyliidae    | - | -    | -    | 31  | 9.78  | (0.36) | 6.29  |  |
|             | Sciaridae,     | - | 1.57 | 0.1  | 77  | 2.53  | (0.03) | 0.43  |  |
|             | Sphaeroceridae |   |      |      |     |       |        |       |  |
| Hymenoptera | Formicidae,    | - | 1.56 | 0.56 | 33  | 7.03  | (0.22) | 11.73 |  |
|             | Halictidae,    |   |      |      |     |       |        |       |  |
|             | Braconidae     |   |      |      |     |       |        |       |  |
| Neuroptera  | Raphidiidae    | - | 1.79 | 0.11 | 13  | 14.67 | (0.56) | 13.47 |  |

Appendix 4c. Results of ANCOVA evaluating the treatment effects and relationships between resident fish consumption of benthic insects and the biomass of adult aquatic insects collected on sticky traps, riparian spider abundance, and parasitic Hymenoptera biomass.

| Adult aquatic insects | Effect            | F    | P           |
|-----------------------|-------------------|------|-------------|
| Aquatic Diptera       | Consumption       | 2.5  | 0.14        |
|                       | Trt               | 6.73 | <b>0.01</b> |
|                       | Trt × Consumption | 5.31 | <b>0.02</b> |
| Ephemeroptera         | Consumption       | 3.73 | 0.08        |
|                       | Trt               | 0.64 | 0.54        |
|                       | Trt × Consumption | 0.92 | 0.42        |
| Plecoptera            | Consumption       | 0.82 | 0.38        |
|                       | Trt               | 0.75 | 0.49        |
|                       | Trt × Consumption | 0.86 | 0.44        |
| Trichoptera           | Consumption       | 0.18 | 0.67        |
|                       | Trt               | 0.86 | 0.44        |
|                       | Trt × Consumption | 0.95 | 0.41        |
| Insectivores          |                   |      |             |
| Tetragnathidae        | Consumption       | 9.76 | 0.012       |
|                       | Trt               | 1.54 | 0.266       |
|                       | Trt × Consumption | 6.99 | 0.014       |
| Araneidae             | Consumption       | 0.39 | 0.549       |
|                       | Trt               | 0.32 | 0.732       |
|                       | Trt × Consumption | 0.25 | 0.382       |

|            |                          |      |       |
|------------|--------------------------|------|-------|
| Braconidae | Consumption              | 3.09 | 0.112 |
|            | Trt                      | 3.27 | 0.085 |
|            | Trt $\times$ Consumption | 2.32 | 0.153 |

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## Summary and conclusions

The donor-recipient paradigm as an organizing framework proposes that surplus productivity in a donor ecosystem is transported through biotic or abiotic processes to a recipient habitat where it may have a range of population, community and ecosystem level consequences (Polis et al. 1997). Though not wrong *per se*, the simplicity of this framework may also be its weakness. Ecologists are now more explicitly integrating spatial heterogeneity and temporal dynamics into the study of food webs in landscapes. Despite the importance of variation in both space and time (Polis et al. 1996), there have been few attempts to examine the consequences of incorporating spatio-temporal variation for population dynamics, community structure, and ecosystem functioning (Holt and Barfield 2003). This framework assumes unidirectional flow from a donor to a singular recipient habitat and includes no consideration of the physical characteristics of the subsidy. In its present state, the donor-recipient paradigm has limited utility for predicting the effects of resource subsidies in spatially heterogeneous and temporally variable food webs.

The refinement of this framework requires consideration of the biophysical properties of the subsidy itself and how these properties influence its subsequent distribution in space. Resource subsidies come in all shapes and sizes, ranging from dissolved chemical compounds, to detritus, to living organisms (Polis et al. 1997), however there has been little consideration of how the biophysical complexity of a subsidy influences responses of organisms in space and through time. Physical characteristics may allow for abiotic (e.g., wind, flooding) or biotic (e.g., translocation by consumer) processes to redistribute the resource subsidy within the landscape.

Additionally, form can determine the duration of availability for consumers. For instance, some subsidies such as carcasses (carrion) are ephemeral because they are quickly consumed by scavengers and/or broken down by decomposition (Bartels et al. 2012), whereas others such as detritus can persist for longer periods of time (Spiller et al. 2010). Finally, form may determine the number of pathways into a food web (Chapter 2). For example, a structurally simple subsidy like ammonium is only available to microbes or plants. In contrast, a subsidy like that of deer carrion can release nutrients through an enrichment pathway and be directly consumed by organisms.

My dissertation builds upon the simple donor-recipient paradigm by considering how the biophysical properties of a subsidy influences the distribution of a subsidy beyond the initial recipient habitat, the consequences for organism responses among multiple habitats (including feedbacks between recipient habitats), and the timescales over which effects occur.

I found that subsidy form (i.e., salmon carcass vs. analog pellet) influenced the extent to which the subsidy was spatially distributed among habitats, and consequently the responses of organisms. First, salmon carcasses were readily removed from the stream to the wetted edges of the stream and to the riparian zone by wildlife, principally black bear. Terrestrial wildlife removed the pasteurized carcasses like natural salmon carcass (Helfield and Naiman 2001, Quinn et al. 2009), though I cannot discern whether the quantity of carcasses removed differs. Carcasses had a rigid enough structure that allowed for the translocation from the initial recipient habitat, the stream, to adjacent riparian habitats. In contrast, the analog pellet broke down and accumulated in depositional pools within the stream and was therefore was not removed to the land.

However, odor associated with the decomposition of both treatments crossed the boundary of the aquatic environment and attracted bears, flies, and other scavengers to the stream. The observed behavioral responses were due to olfactory traits of the organism and the chemical traits of the subsidy. These findings are likely not exclusive to salmon carcasses, as many organisms are capable of detecting decomposing organic material (Chen and Wise 1999).

I also observed that the duration of subsidy availability differed by form. In the aquatic environment, salmon carcasses persisted for approximately six weeks, whereas analog pellets were completely broken down and largely absent by about four weeks, with the remaining analog material mostly in depositional pool habitats. Availability of carcasses was even shorter in riparian habitats. Carcasses were reduced to skeletons after about 2-3 weeks, with a large portion of the muscle tissue consumed within the first week.

Finally, I found that effects were almost always strongest in salmon carcass treatments. Though the nutrient stoichiometry of the subsidies and the experimental loading rates were similar, the magnitude of responses differed. Overall, on the basis of physical form, salmon carcasses were distributed to more recipient habitats, persisted longer, and had the greatest impacts on consumer responses.

The biophysical properties of the carcass subsidy allowed for its distribution beyond the stream habitat to the adjacent terrestrial environment, in effect subsidizing multiple habitats. This is likely a characteristic of many resource subsidies, but one that has largely been unaddressed. My findings indicate that it is important in understanding responses that may manifest across habitats, and that short-term organism responses to

salmon subsidies can have strong impacts on the structure of consumers across trophic levels in linked stream-riparian food webs.

Salmon carcasses were the more complex subsidy and generally had the strongest direct and indirect effects on consumers in both habitats in comparison to analog treatments. The removal of carcasses from the stream takes away resources from the aquatic environment, however responses in terrestrial environments had beneficial impacts on stream organisms. Additionally, effect sizes were generally strongest in carcass treatments. This has been demonstrated in other settings as well (Janetski et al. 2009). There is the added benefit that more organisms across multiple habitats can utilize these subsidies as opposed to only aquatic organisms. The presence of salmon carcasses in the wetted stream margins and riparian zone established an initial set of conditions from which terrestrial consumers, principally Dipterans, responded. Response of Diptera further influenced the activity of select bat species. These positive responses of terrestrial arthropod prey also spilled over to the aquatic environment, resulting in increases in fish production.

The translocation of carcasses to the wetted margins of streams provided a pathway of energy flow to resident trout. Terrestrial maggots falling into the stream provided a feedback to aquatic habitats that had positive effects on the production of trout. This pathway was exclusive to salmon carcasses, as flies could not colonize analog material. However, both carcass and analog forms did attract adult Diptera to the riparian zone. The attraction and aggregation to stream reaches also resulted in more flies in the diets of stream fishes and increases in short-term fish production. It is likely that these flies are attracted to the water or exposed carcass or analog material (Greenberg 1990),

and subsequently washed into the stream where fishes consume them from the drift. My findings are consistent with others, indicating that inputs of terrestrial arthropods influenced by salmon subsidies are not exclusive to Idaho (Scheuerell et al. 2007, Denton et al. 2009). A key distinction, again influenced by the form of the subsidy, was the increased production of terrestrial Diptera that directly fed on exposed carcasses, pupated, and emerged from riparian soils. The two-fold processes of behavioral aggregation and increased production distinguish salmon carcasses from analog pellets that solely attracted adults from the surrounding landscape.

Where carcasses were distributed in the riparian zone had important consequences for the magnitude of response of select terrestrial arthropods in the weeks following carcass additions. Carcasses were predominantly transported from the stream to un-vegetated gravel and vegetated grassy patches within 1-2 meters of the wetted stream channel. Communities of terrestrial arthropods that were collected near carcasses were similar to others (Meehan et al. 2005, Hocking et al. 2009). These fine scale patches were small and often meters in area in relation to the stream reach that was 500 meters in length. Patches where carcasses were deposited mediated the strength of response of Diptera and a predatory Staphylinidae (Order: Coleoptera). Generally speaking, effects were greatest in vegetated patches where carcasses were readily consumed by Diptera larvae. Carcasses in un-vegetated patches became desiccated which likely limited the consumption efficiency of larvae. Additionally, predatory beetles (Family: Staphylinidae) exhibited clear habitat preference by choosing vegetated habitats, indicating that fine-scale patches can mediate bottom-up effects that extend to higher trophic levels. In addition, both the quantity of carcasses removed and the patch quality

influenced patterns of Diptera biomass at broader reach scales. Indeed, patterns of carcasses and their respective recipient patches may amplify or dampen subsidy effects. Stream reaches with more carcasses in vegetated patches had greater biomass of Calliphoridae adults, suggesting that characteristics of both the subsidy and fine-scale patterns of recipient patch habitat can influence responses at broader reach scales.

The variable responses I observed at fine patch scales may be nested within the context of larger scale climatic variability. The dry summer climate of Idaho contributed to the desiccation of salmon carcasses in un-vegetated patches, whereas those in vegetated patches remained moist. The distinction between patch type and subsidy effects may be relevant in arid regions of native salmon range, but coastal regions subject to more frequent precipitation may not experience similar mediating effects of patches. There are also other factors other than precipitation that may influence the palatability or breakdown of carcass material that I did not explore. My findings are consistent with others who reported spatially variable responses of organisms to subsidies in aquatic environments (Janetski et al. 2009, R  egg et al. 2012).

Salmon subsidies had positive short-term effects on stream biofilms, aquatic midges (Family: Chironomidae) and fishes. These findings were generally consistent with others (Wipfli et al. 2003, 2004, 2010, Janetski et al. 2009). Stream biofilms increased in the weeks following subsidy additions. Likewise, we observed strong short-term increases in the emergence of aquatic midges. These patterns indicate bottom-up pathways of energy flow through the food web. Additionally, trout directly consumed both treatment materials, however trout did consume more carcass than analog. My analyses indicate that trout directly consumed 3-5% and 4-11% of carcass and analog

material, respectively. Trout consumed more carcass material by weight than analog. The differences between the percentages consumed are influenced by the total quantity of subsidy material added to the streams. More carcass material was added than analog. The subsidy material not consumed by fishes was removed from the stream, directly consumed by benthic insects, or broken down and exported to downstream habitats (Rex and Petticrew 2008, Marcarelli et al. 2014).

Salmon subsidies are distributed in a spatially patchy fashion within watersheds. In addition to reach-scale effects which are often the focus, these materials are also exported to downstream habitats. In these downstream locations, carcasses are not removed to riparian habitats and maggots do not fall into the streams. Consequently, salmon productivity cannot benefit from the direct consumption of carcass material or consumption of terrestrial invertebrates. Fishes may behaviorally aggregate at reaches where carcasses are present. This movement may also alleviate predation pressure within the reaches where they once resided. The export of dissolved nutrients and particulate matter to downstream reaches may foster increased bottom-up production without top-down pressures. The potential for such a mosaic of ecological processes warrants exploration.

Organism responses to subsidies manifested at both weekly and annual timescales. The ecological processes affected by subsidy additions at short timescales greatly influenced the structure of stream and riparian food webs at annual scales and are consistent with ecological theory with respect to timescale hierarchies (Takimoto et al. 2009). The consumer responses addressed in the previous paragraphs occurred during the 0-6 weeks following annual treatment additions. These short-term effects influenced

energy flow to stream fishes, increasing their estimated production, which in turn increased consumption of benthic insects at longer time scales. Increased consumption further influenced annual patterns of adult aquatic insect biomass in the riparian zone. Alterations to patterns of insect emergence further influenced the indirect relationships with riparian insectivores, indicating that subsidy-driven effects within one habitat can influence the structure of consumers in an adjacent habitat. My findings challenge the conception that nutrient and energy additions result in positive effects that propagate throughout the food web. Instead, the efficient utilization of a subsidy and its effects on consumers in one habitat mediated the response of organisms in adjacent habitats.

Findings from my dissertation indicate that after multiple years of subsidy additions, populations (i.e., density, standing crop biomass) of resident trout did not increase, however their annual production did. I hypothesize that fish movement played an important role. More fish tissue was accrued through time, but was ultimately distributed throughout the river network. The increased fish production did not remain within our study reaches. Therefore, I did not detect responses in the density or standing crop biomass of stream fishes. Yet, I detected some responses of organisms across both aquatic and terrestrial habitats. The annual delivery marine-derived subsidies were important for stream-riparian food webs. This experiment indicates that subsidies of salmon impacted to productivity of fishes through multiple pathways instead of the strict bottom-up pathway.

### *Replacement and recovery?*

The replacement of nutrients and recovery of salmon populations are two distinct processes that are not always distinguished in nutrient mitigation efforts. This stems from how we treat salmon-derived nutrients and the power of the marine-derived nutrient paradigm. What is the relative strength of these nutrients in stabilizing or increasing populations of organisms in both aquatic and terrestrial environments? The potential for marine-derived nutrients additions to increase populations should be weighed against other factors that are limiting their recovery, including fishery harvest, climate change, and dams (NRS 1996, Budy et al. 2002, Battin et al. 2007, Naiman et al. 2012). Marine-derived nutrients are important, however if the effects of nutrient mitigation cannot overcome the larger impediments to salmon population growth, one must question the underlying rationale for nutrient mitigation. The overemphasis of the ecological effects of salmon nutrients and the predominance of the salmon-nutrient enrichment paradigm may actually undermine population recovery efforts by diverting resources and allowing other problems to persist that may, in truth, be limiting salmon populations (e.g., dams, degraded habitat conditions or food web interactions in mainstem rivers, etc.). If there is no evidence that nutrient additions increase salmon populations, then mitigation is not occurring. Simply put, if salmon were reduced, then mitigation efforts, to count as such, should return these numbers. However, if salmon are reduced to their chemical constituents, then mitigation is reduced to a mass balance equation. The use of nutrients as the “currency” for salmon mitigation ignores the suite of food web pathways influenced by the physical form of the mitigation tools and their overall effect sizes. From my findings, it is apparent that the salmon “analog” pellet is not analogous to

salmon carcasses. In turn, addition of salmon carcasses themselves may not serve as mitigation if they do not lead to increases in living salmon runs.

### *The practicality of pasteurization and large-scale implementation*

Pasteurizing the thousands of kilograms of carcasses for this experiment was difficult and time consuming. All told, our experiment treated 1.5 kilometers of stream (0.5 km  $\times$  3 streams) each year, or 4.5 kilometers in total. The time, effort, and resources necessary to accomplish this are worth discussing. Pasteurization is necessary to avoid the transmission of pathogens between affected and unaffected watersheds (Compton et al. 2006). This necessary precaution adds a suite of logistical issues that have to be dealt with. First, the salmon carcasses must be acquired from hatcheries. Still, there are only finite amounts of salmon carcasses available. We opted to freeze the carcasses until the initiation of the pasteurization process. These frozen carcasses take up space and have costs associated with freezer storage.

The salmon carcasses were pasteurized in a large propane oven that was mounted on a trailer. The carcasses were heated until the cranial cavity reached an internal temperature of 60°C and was maintained for 20 minutes. The carcasses were then removed to a freezer trailer where they were re-frozen until deployment. Each batch pasteurized about 150-200 kilograms of salmon, with a total of about two or three batches per day. A two or three person crew had to work approximately seven to ten days per year to pasteurize the quantities of salmon needed for our experiment. In addition to the cost of the cooking trailer, propane was another considerable expense.

Deployment required the use of a dozen or so vehicles to transport the material to the stream. Many of the streams were not located conveniently along the roadside. Programs that add carcasses should factor this in their logistics, as salmon spawning did not occur conveniently near the roadside either. Across the three years of treatments, there were between fifteen and thirty individuals actively transporting the salmon carcass and analog material to study streams. The pasteurized salmon in boxes were attached to backpacks and hiked into the wilderness. It was as fun as it sounds.

All told, the costs associated with pasteurizing salmon were considerable. Programs considering this approach should account for: the costs of obtaining the salmon, costs of storing/freezing salmon, costs of purchasing a cooking trailer or some alternative, the costs of propane or electricity, costs of labor throughout the process, the costs of deployment, and incidentals/consumables (i.e., storage boxes). On average, we added about 2400 kilograms of salmon carcasses per one kilometer of stream. If we were to pasteurize 400 kilograms per day, it would take a 2-3 person crew six days to pasteurize the salmon. Treating 10 kilometers, it would require 60 days of pasteurizing. Treating 50 kilometers with an estimated 120,000 kg of salmon carcasses would require a staggering 300 days, based on our approach. If the artificial additions of salmon carcasses were to resemble the magnitude and spatial distribution of a natural run of salmon, the costs of doing so would be considerable.

It appears that spatially scaling artificial enrichment to be more representative of a natural salmon run is unlikely. The use of inorganic fertilizers and analog pellets do not have to be pasteurized, however it is apparent from our investigations they do not have the same range of effects on organisms. Conveniently, another party does the processing

of these materials. Still, there are costs associated with the distribution of these materials to streams and rivers. Likewise, these alternative mitigation tools are expensive. Regardless of the mitigation tool used, it would require an immense amount of time, effort, and materials to mimic a salmon run in one basin, let alone many basins, for many years. Cost-benefit analyses should be conducted to account for these factors. The application of nutrients as a mitigation approach purports that a migration of salmon can be mimicked (Chapter 1), however engineered solutions for complex ecological problems are not always effective (Meffe 1992). My findings and experiences suggest that it may be infeasible to mitigate via nutrient additions for the loss of salmon at large spatial scales that are representative of natural spawning runs.

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