AN ABSTRACT OF THE THESIS OF

Megan E. Brady for the degree of Master of Science in Fisheries Science presented on September 14, 2020.

Title: Temporal Variation in the Prey Resource Portfolio of Juvenile Salmonids During Freshwater Rearing

Abstract approved:

Jonathan B. Armstrong

Freshwater rearing is a critical period in the life cycle of anadromous salmonids, known to produce carry-over effects mediating long-term growth and survival. Freshwater growth is primarily determined by food availability and temperature. While many species of salmon rear in freshwater for a full year or longer, most trophic ecology research is from a narrow window of time within the annual cycle. This work identified temporal biases in research, addressed gaps in understanding the trophic resources that support juvenile salmonids during key phases of freshwater rearing, and examined seasonal variability in asynchronous resource pulses and terrestrial-aquatic interactions. The first study in this thesis quantified temporal biases in the timing and duration of juvenile salmonid field research from the past 30 years. I found that across ecological topics, summer studies occurred 3x as commonly as winter studies and 57% of studies were focused on a single season. The second study in this thesis described the monthly variation in prey resources utilized by juvenile steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in the South Fork Skokomish River and its tributary Vance Creek in Hood Canal, Washington, USA. The results from this study suggest that stable *in situ* prey resources and ephemeral allochthonous prey resources create an asynchronous energy portfolio supporting juvenile salmonid freshwater rearing throughout the full annual cycle. Aquatic resources from the benthos and drift provided a relatively stable source of energy to juvenile salmonids year-round, but were most important during summer somatic growth, overwinter survival, and early spring prior to smoltification. Terrestrial subsidies contributed to fish diet over the course of spring, summer, and autumn; however, within the aggregate of terrestrial inputs, I found multiple ephemeral pulses of specific prey items. These ephemeral terrestrial invertebrates contributed heavily to fish diets and coincided with stressful developmental phases including smoltification in spring and lipid storage prior to the onset of winter: 66% of coho diet biomass in May came from rove beetles, 13% of coho diet biomass in October came from spiders, and 30% of steelhead diet biomass in October came from ground beetles. To an even greater extent, ephemeral marine subsidies provided energy to salmonids during a key development phase as they stored fat in preparation for overwinter survival. Multiple spawning events from three different species of salmon provided an extended resource pulse utilized by juvenile steelhead and coho with 61-96% of prey consumption during spawning months coming from marine subsidies. Moreover, despite the depressed size of salmon runs in this system, consumption of marine subsidies resulted in substantially larger rations than seen at any other point in the year. While summer research may be more common, the most interesting results from this field study came from spring and autumn. As salmon populations in the Pacific Northwest continue to decline, conservation and recovery

efforts could benefit from incorporating knowledge of temporal variability in the trophic resources that juvenile salmonids use throughout freshwater rearing.

Temporal Variation in the Prey Resource Portfolio of Juvenile Salmonids During Freshwater Rearing

by
Megan E. Brady

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented September 14, 2020
Commencement June 2021

Master of Science thesis of Megan E. Brady presented on September 14, 2020

APPROVED:

Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Megan E. Brady, Author

ACKNOWLEDGEMENTS

I want to express my sincere appreciation to Dr. Jonathan Armstrong, my major advisor, for mentoring me, collaborating with me, being my cheerleader, and pushing me to grow as a scientist, creative and critical thinker, writer, and person. I would like to thank my committee members Dr. Ivan Arismendi and Dr. Dave Lytle for their advice, support, and patience. Thank you to Katy Shelby for her help in getting this idea off the ground, loaning equipment, and spending time in the field with me. Thank you to Rob Endicott for coordinating rotary screw trap fish sampling. Thank you to my two field helpers: Lisa Brady and Peter Shaw. Thank you to Mitch Dennis for helping me navigate ESA permitting. Thank you to my financial supporters—my research wouldn't have been possible without generous funding from the National Science Foundation and the Fidalgo-San Juan Island Chapter of Puget Sound Anglers. Most of all though, I would like to thank my partner, Ty, for his outrageous optimism, unconditional support, database and R troubleshooting skills, and assistance in catching all the baby fish.

CONTRIBUTION OF AUTHORS

Dr. Jonathan Armstrong contributed to the study design, interpretation of results, and writing of this thesis and associated manuscripts. Dr. Ivan Arismendi and Dr. David Lytle contributed to the study design of the research presented in Chapter 3 and Appendix A. Katy Shelby contributed to the study design and field sampling for Chapter 3 and Appendix A. Andrew Chione contributed to data collection for the riverscape analysis portion of Chapter 2. Ty Garber, Lisa Brady, Rob Endicott, and Peter Shaw contributed to field sampling for Chapter 3 and Appendix A.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (Continued)

Page

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

CHAPTER 1. GENERAL INTRODUCTION

The continued decline of salmon (*Oncorhynchus* spp.*)* populations is one of the most important ecological, economic, and cultural issues in the Pacific Northwest, USA. Despite the billions of dollars spent on restoration efforts, salmon recovery largely remains an unmet goal and riverine habitat degradation persists (Bernhardt et al. 2005; Stranko et al. 2012). Recent work has identified two key knowledge gaps that impede restoration: temporal variation in energy flows to fish populations and biotic interactions between terrestrial and aquatic food webs (Naiman et al. 2012). Improved understanding of ecological interactions is likely essential to creating more effective restoration projects.

Are the constraints biotic or abiotic?

While physical characteristics of streams and habitat structure (e.g. pools, large woody debris, flow, substrate, temperature) have traditionally been identified as constraining factors to freshwater fish production, the abundance, quality, and temporal availability of food resources likely plays a significant role in determining carrying capacity and productivity within stream ecosystems (Bilby et al. 1996; Wipfli 1997; Rosenfeld 2003; Weber et al. 2014). Daily physical variations in habitat, such as river flow, combined with seasonal availability of food contribute to food supply and feeding rate for juvenile salmonids. Studies have shown a strong relationship between body size and survival in juvenile salmonids (Groot et al. 1995; Quinn and Peterson 1996), emphasizing the importance of improving foraging opportunities. Stable isotope analysis indicates that freshwater fishes rely on aquatic, terrestrial, and marine sources of food (Wipfli and Baxter 2010; Scheuerell et al. 2007). The magnitude of reciprocal subsidies between terrestrial and aquatic food webs are just beginning to be explored.

Bridging the energy gap with terrestrial inputs

The amount of energy needed to support juvenile fish populations is often much higher than the estimated contribution from autochthonous production within river systems, a phenomenon known as the Allen paradox (Allen 1951). Many studies have concluded that allochthonous energy from the riparian zone provides the remainder of fish energy budgets (Hynes 1970; Allan et al. 2003; Nakano et al. 1999b; Wipfli and Baxter 2010; Edwards and Huryn 1995). Therefore, prey availability is directly and indirectly shaped by riparian interactions.

Primary and secondary effects of allochthonous inputs

Allochthonous inputs of organic matter from riparian zones cross ecosystem boundaries, providing a vital source of energy to adjacent streams (Benfield 1996; Peterson and Cummins 1974; Wallace et al. 1997). These allochthonous inputs take two forms: secondary production from aquatic invertebrate shredders and direct inputs of terrestrial invertebrates that fall into the water as high energy prey available to predatory fishes, such as juvenile salmonids (Quinn 2005; Wipfli 1997; Baxter et al. 2005). Additionally, freshwater macroinvertebrates are essential for stream ecosystem functioning and energy flow within food webs (Polis and Winemiller 1996; Naiman and De'camps 1997; Cummins et al. 1995), breaking down leaves from coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM).

Impacts of terrestrial changes on aquatic habitats

Changes in riparian habitat can have cascading impacts through the terrestrial-aquatic interface. The effects of fire, deforestation, canopy composition and openness, anthropogenic habitat degradation (waves from large boats, dredging, land development, and pollution) and biological invasions have been shown to alter primary productivity, invertebrate composition and abundance, stream food web dynamics and prey available to predatory fish, temperature, flow and spawning and rearing habitat for fish (Mellon et al. 2008; Erős et al. 2012; Hladyz et al. 2009; Graca 2001; Arrington et al. 2002; Kaylor and Warren 2017; Mouton et al. 2012, Fierro et al. 2016; Hawkins et al. 1982). However, the effects of seasonal changes in riparian vegetation on aquatic food webs are still poorly understood (Baxter et al. 2005).

Temporal and ontogenetic diet shifts

Diet analysis of freshwater fish pinpoints important prey items and facilitates greater understanding of resource utilization based on size and ontogenetic niche shifts (Bisson 1978; Johnson et al. 2013; Werner and Gilliam 1984; Persson and Bronmark 2002; Steingrimsson and Gislason 2002). Gape and throat size influence ontogenetic niche shifts by determining the size of prey that can be swallowed (Armstrong et al. 2010; Johnson and Post 1996). The highly variable nature of stream habitats results in seasonal variation in food availability and fish growth rates (McCarthy et al. 2009).

Seasonal bias

Diet information is often recorded during summer, so less is known about how ephemeral and seasonally fluctuating *in situ* and allochthonous prey subsidies (aquatic, terrestrial, and marine) affect food availability and prey preference (Armstrong et al. 2010; Bridcut 2000; but see Bellmore et al. 2013). Recent work indicates that steelhead (*O. mykiss)* growth rate and population distribution varies seasonally, emphasizing the importance of year-round sampling (Tattam et al. 2017).

Forage vs drift feeding

Juvenile salmonids are often spatially segregated within river systems with feeding habits reflecting minimal overlap even for opportunistic feeders; for example, the diets of juvenile coho salmon (*O. kisutch*) often closely reflect the availability of prey in the drift whereas juvenile steelhead trout (*O. mykiss*) diets more closely resemble the availability of benthic prey (Johnson and Ringler 1980; Bilby et al.1998). However, in Hood Canal, WA, juvenile steelhead diets have been shown to shift from foraging behavior to more energetically efficient drift feeding, particularly in the winter (Wright 2010; Doctor-Shelby and Berejikian *In Draft*). Benthic macroinvertebrates dominated the winter diets of juvenile coho salmon, steelhead/rainbow trout, and cutthroat trout (*O. clarkii*) in Skokomish, WA with high diet overlap between mainstem and tributary habitats (Wright 2010). To add further complexity, aquatic invertebrates have varying rates of intentional drift, accidental drift, and drift distance (Rader 1997), making their accessibility to fishes as a prey resources somewhat difficult to predict. Terrestrial subsidies from flood pulses in winter may be a potentially important but underrepresented food source due to the difficulties of sampling in winter. Temporal and spatial shifts in primary and secondary production, prey availability, subsidy pulses, food demand, and predator diet preferences are important to understanding food web dynamics.

Terrestrial subsides

Aquatic systems are often subsidized by adjacent terrestrial inputs. Across-habitat prey fluxes with alternating subsidies emphasizes the reciprocal nature of seasonal shifts of available *in situ* and allochthonous prey inputs (Nakano and Murakami 2001; McCarthy et al. 2009; Wipfli and Baxter 2010). Peaks in terrestrial invertebrate abundance (summer) often corresponds with the seasonal low in benthic invertebrate availability as well as higher energetic requirements for fish due to the stress of elevated water temperatures (Cloe and Garman 1996; Dineen et al. 2007). Several studies have shown that terrestrial invertebrates are an important food source for stream fishes and may comprise 50-90% of total prey consumed by juvenile salmonids (Wipfli 1997; Nakano et al. 1999a; Kawaguchi and Nakano 2001; Dineen et al. 2007; Allan et al. 2003; Mason and MacDonald 1982; Nakano and Murakami 2001; Dunham et al. 2000; Garman 1991; Edwards and Huryn 1996; Hunt 1975; Li et al. 2016). Terrestrial invertebrate inputs to streams appears to increase with denser deciduous tree canopy (Cloe and Garman 1996; Nakano et al. 1999b). Terrestrial and aquatic invertebrates are produced directly adjacent to in-stream fish habitat, *in-situ*, and transported downstream from fishless headwaters, a phenomenon known as the River Continuum Concept where downstream communities benefit from upstream productivity (Wipfli and Gregovich 2002; Wipfli and Baxter 2010; Wipfli and Musselwhite 2004; Vannote et al. 1980).

Invertebrate drift and diel feeding habits of fish

Juvenile salmonids primarily feed during daylight hours in the drift (Quinn 2005; Forrester et al. 1994; Bisson 1978; Allan 1981). However, aquatic invertebrates tend to enter the drift at night while larger, more buoyant terrestrial invertebrates tend to drift during the day (Rader 1997; Nakano et al. 1999a; Allan 1978); but see recent work on horsehair worms manipulating their cricket hosts to be drawn to moonlight reflections on streams where they are eaten by trout (Sato et al. 2011). Furthermore, salmonid daytime feeding may not correlate with the density of invertebrates in the drift, but may show a preferred feeding window, although individual studies have identified conflicting preferred times including mid-morning (Angradi and Griffith 1990) as well as evening (Allan 1981). This may be highly variable temporally, spatially, and longitudinally for each species. This difference in diel availability and fish feeding times may result in greater contribution of terrestrial invertebrates to fish diets due to active foraging times (Baxter et al. 2005).

Marine subsidies

Upon migration to their natal streams to spawn, adult Pacific salmon transfer marine-derived nutrients to freshwater ecosystems (Bilby et al. 1998; Kline et al. 1997). Spawning salmon convey this high-energy food subsidy pulse to freshwater food webs directly as eggs and carcasses consumed by fish (Armstrong et al. 2010; Bilby et al. 1998; Denton et al. 2010) as well as indirectly with increased abundance of benthic aquatic invertebrates (Wipfli et al. 1998; Wipfli et al. 1999; Collins et al. 2016) and terrestrial invertebrates (Hocking et al. 2013). Eggs become available to juvenile salmonid consumption within the drift due to redd (nest) digging by adult salmon, especially when these redds are superimposed on other redds (Moore et al. 2008). Additionally, spawning adult salmon disturb the stream substrate, dislodging benthic invertebrates that are transported downstream in the drift (Moore et al. 2007). Marine resource subsidies, specifically eggs, from spawning sockeye salmon (*O. nerka*) have been shown to increase body size of juvenile coho salmon (Smits et al. 2016). Despite their ephemeral availability, salmon eggs can fuel more juvenile fish growth than benthic invertebrates due to their high energy value (Armstrong et al. 2010; Scheurell et al. 2007; Moore et al. 2008; Bilby et al. 1998; Bentley et al. 2012), large size relative to invertebrates, complete vulnerability, and superabundance (where salmon remain near their historical densities). If growth and survival of juvenile salmonids is increased due to high-quality energy subsidies, life-history traits and patterns that depend on early freshwater growth, such as migration timing and marine survival, may be altered significantly.

Benefits of larger size and the importance of marine-derived nutrients

Freshwater rearing is a critical time for juvenile salmonids. Faster growth and larger size improve chances of survival by reducing the effects of size-selective mortality through predation pressure and throat/gape size limits to food consumption (Sogard 1997). Freshwater growth in juvenile salmonids is primarily affected by temperature and food availability (Wipfli and Baxter 2010; Brett and Groves 1979). The eggs and marine-derived nutrients provided by carcasses of anadromous salmon subsidize freshwater ecosystems and can positively influence the body size of juvenile salmonids of different species (Nelson and Reynolds 2015; Wipfli et al. 2003; Bentley et al. 2012), with larger body size linked to earlier migration timing (Giannico and Hinch 2007). Faster growth may result in younger age-at-smoltification in anadromous salmonids with size thresholds triggering smoltification (Giannico and Hinch 2007; Irvine and Ward 1989). Larger fish size positively influences over-winter survival of juvenile coho (Quinn and Peterson 1996); but see Connolly and Petersen (2003) experiment where warm temperatures and limited food in winter negatively impact growth, condition, and fat storage more acutely in larger juvenile steelhead than smaller fish. There is evidence to suggest that energy-rich ephemeral prey subsidies, such as salmon eggs, may positively influence overwinter survival and push fish across the size thresholds for smoltification, resulting in younger outmigration (Näslund et al. 2015; Gende et al. 2002). The energy impact from spawning salmon has been found to persist after the resource pulse has disappeared, positively influencing juvenile coho growth rate and energy density 6 months after spawning (Rinella et al. 2012). Increased early life growth in freshwater has been shown to improve marine survival (Thompson and Beauchamp 2014), particularly in poor ocean condition years (Bond et al. 2008; Holtby et al. 1990). Higher adult return rates for Keogh River, British Columbia steelhead were correlated with larger smolt size and freshwater growth, emphasizing the importance of early growth to long-term survival (Ward et al. 1989).

Ephemeral egg subsidies

There is some evidence to suggest that carcasses from spawning salmon may positively influence the abundance (Bilby et al. 2002) and growth (Wipfli et al. 2003; Bilby et al. 1998) of juvenile salmonids due to enhanced aquatic food web productivity (Hicks et al. 2005). However, the effects of ephemeral resource pulses on life-history traits, such as age-at-smoltification or size-at-smoltification, in juvenile salmonids has not been extensively researched. Nelson and Reynolds (2015) found that spawning chum salmon density positively correlated to juvenile coho size and noted that spawner density was also associated with a higher proportion of the population classified as age 0, suggesting but not providing supporting evidence of earlier juvenile ocean migration. If fish growth is affected by marine subsidies, then the magnitude of this subsidy may alter the age-structure of juvenile anadromous fishes migrating downstream once they reach the size threshold for smoltification. The impacts of this ephemeral resource subsidy are poorly understood (Naiman et al. 2002). Some research indicates that increased spawner abundance is associated with increased stream productivity at lower trophic levels (including common prey items for fish) (Wipfli et al. 1998; Wipfli et al. 1999) as well as juvenile fish growth (Wipfli et al. 2003) possibly due to the ingestion of salmon tissue and eggs (Bilby et al. 1998). Marine resource subsidies from sockeye salmon may have resulted in higher growth rate of resident charr (*Salvelinus* spp.), however temperature differences make results unclear (Denton et al. 2010). Research by Wipfli et al. (2003) shows that coho salmon and resident cutthroat trout growth increased in the presence of pink salmon (*O. gorbuscha)* carcass additions and the juvenile fish maintained this accumulated body mass through winter. Overwinter survival of juvenile salmonids is largely dependent on body size (Groot et al. 1995). The growing season, and therefore survival, of freshwater fishes can be temporally extended through the addition of ephemeral food pulses, such as the return of spawning salmon in the fall and winter (Bilby et al. 1998; Wipfli et al. 1998). In many systems, this may be mediated by temperature constraints with maximum consumption rates declining in winter due to colder temperatures; however, in the mild winters of the Pacific Northwest, growth rates may not be as constricted if food is still available.

Loss of marine subsidies

Many salmon runs are now at only a very small fraction of their historic numbers due to loss and degradation of habitat as well as overharvest (Lichatowich 1999). Annual adult spawner returns on the Columbia River, once one of the most productive salmon rivers in the world, are only 1% of historic returns (Gresh et al. 2000). This sharp reduction in nutrient inputs may have significant impacts on future salmon returns through disruptions in this nutrient-feedback loop (Schindler et al. 2003). Loss of marine-derived nutrient subsidies from spawning population declines lowers the ability of freshwater habitats to support future generations of salmonids (Bilby et al. 1998). Moreover, pulses of resources may have varying effects in subsidized systems depending on the magnitude of the pulse (Anderson et al. 2008). Stable isotope analysis has shown that salmon make substantial nutrient contributions to freshwater and riparian ecosystems, however, the ecosystem consequences of these marine-derived nutrients are not fully understood (Naiman et al. 2002).

Maximizing resource pulses

While fishes may not be able to extend the temporal availability of resource pulses through storage, mobile consumers can exploit spatial variation to maximize foraging opportunities and increase growth during periods of high food abundance (Armstrong et al. 2016, Armstrong and Schindler 2013). Some fish, such as sculpins have coevolved to exploit this subsidy pulse during its short availability (Foote and Brown 1998). It is essential that fish maximize utilization of these short-lived yet energetically important resource pulses as these pulses tend to move through aquatic food webs faster than terrestrial food webs due to the importance of top-down controls and faster growth rates in aquatic systems (Nowlin et al. 2008).

Freshwater residence of juvenile salmon

Seasonal variations in prey availability and prey energy quality may affect juvenile salmonids with longer freshwater residence time more acutely than those with shorter residence time. Juvenile steelhead spend 2-4 years in freshwater before ocean outmigration while juvenile coho and Chinook (*O. tshawytscha*) typically spend 1 year in freshwater before smoltification (Quinn 2005). Chum and pink salmon spend even less time in freshwater as juveniles: 1-2 months (Quinn 2005). Shifts in prey availability may drive juvenile salmonid growth during freshwater residence.

Bioenergetics

Steelhead are often growth-limited by temperature but may be limited by food as well. It is often assumed that food availability for fish and fish growth rates are higher in summer than in winter, but recent work suggests this may not be true for *O. mykiss* (McCarthy et al. 2009, Doctor-Shelby and Berejikian *In Draft*). A bioenergetics model based on twice-yearly size sampling estimated juvenile steelhead consumption to be 22% of the maximum consumption in summer and 27% in winter; however, daily growth rate is higher in summer than in winter with an optimal growth rate at 12°C (Doctor-Shelby and Berejikian *In Draft*). But, since maximum consumption is temperature dependent, 20% in winter is much less food than 20% in summer but may result in greater growth due to decreased metabolic costs of colder winter temperatures. Furthermore, increases in diet energy density (such as from energy-rich salmon eggs) can have additional positive effects on size-selective mortality by raising the optimal growth temperature, a critical component of freshwater survival in the face of climate change (Beauchamp 2009). If juvenile salmon digestive capacity is limited by temperature in winter, having a high-energy prey item, such as eggs, could help mediate digestive constraints by increasing energy gains through high energy prey instead of making cuts to energetic costs.

Food webs for restoration

The temporal flux of seasonally available autochthonous and allochthonous inputs in stream systems can have individual level effects that lead to population level consequences such as growth, survival, and health (Sabo and Power 2002; Baxter et al. 2007; Nakano and Murakami 2001). Food webs are widely regarded as vital to understanding the needs of targeted species (Vander Zanden et al. 2003; Woodward and Hildrew 2002; Bellmore et al. 2013). Due to linked ecosystem processes and energy flow, ecosystem-based fishery management (EBFM) utilizing a food web approach that includes habitat and predator-prey interactions may be more effective in restoration monitoring rather than single species management (Pikitch et al. 2004).

Non-native plants in terrestrial-aquatic interactions

The availability of terrestrial prey and input of allochthonous subsidies to streams is determined by riparian composition (Naiman and De'camps 1997; Mason and MacDonald 1982; Edwards and Huryn 1996). Changes in nutrient content from inter- and intraspecific leaf litter variation have been shown to affect decomposition rates as well as the abundance and diversity of invertebrate colonization (Graca 2001; Kominoski et al. 2011; LeRoy et al. 2016; Hladyz et al. 2011; LeRoy and Marks 2006). Invasive plant species impact riparian zones by altering biodiversity, light availability, bank stability, terrestrial invertebrate composition and biomass, ecosystem processes like carbon cycling, and food web structure (Claeson et al. 2014; Ehrenfeld 2003). However, changes in aquatic ecosystem processes and invertebrate assemblages in detritus-based food webs due to the presence of terrestrial invasive plant species in riparian communities are poorly understood (Claeson et al. 2014; Hladyz et al. 2011; Naiman and De'camps 1997; Kennedy and Hobbie 2004). Introduction of non-native fish species often impacts native fish negatively by usurping prey (Baxter et al. 2004). However, the impact of invasive terrestrial plants on fish is largely unknown due to the unique characteristics of each invasive species (but see Fierro et al. 2016; Roon et al. 2016). Furthermore, the impact of human-driven changes in riparian corridors (deforestation, agriculture, land development) coupled with frequent natural disturbances from flooding provide an ideal opportunity for colonization by invasive plants that thrive in disturbed habitats.

Salmon recovery

Salmon recovery efforts have largely focused on the four Hs: habitat, hatchery, hydroelectric dams, and harvest (Naiman and Bilby 1998). Temporal and spatial food web dynamics should be added to that list (Naiman et al. 2012). In many systems, food, not the traditional metrics of stream characteristics, may be the limiting factor to carrying capacity and production of juvenile salmonids (Bellmore et al. 2013). Riparian management directly and indirectly influences fish productivity by altering the food supply available through aquatic and terrestrial food webs (Allan et al. 2003). Knowledge of terrestrial-aquatic food web linkages is essential to inform a science-based, ecosystems approach to restoring species of concern, such as Pacific salmonids.

Research objectives

The objectives of the proposed research are to 1) characterize temporal biases in ecological research that currently informs fisheries restoration and conservation, 2) determine the importance and temporal variation of terrestrial and aquatic invertebrates as prey resources for juvenile salmonids, 3) explore how aquatic-terrestrial linkages can inform salmon recovery and habitat restoration efforts, and 4) assess what effects invasive terrestrial plants have on aquatic food webs vital to juvenile salmonids.

References

Allan, J. D. 1978. Trout predation and the size-composition of stream drift. Limnology and Oceanography 23:1231-1237.

Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:183-192.

Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60:309-320.

Allen, K. R. 1951. The Horokiwi stream: A study of a trout population. Bullet of New Zealand Department of Fishery 10:1-231.

Anderson, W. B., Wait, D.A., and Stapp, P. 2008. Resources from another place and time: Responses to pulses in a spatially subsidized system. Ecology 89(3):660-670.

Angradi, T. R., and J. S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 47:199-209.

Armstrong, J. B., and D. E. Schindler. 2013. Going with the flow: Spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. Ecosystems 16:1429-1441.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445-1454.

Armstrong, J. B., G. T. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099-1122.

Arrington, D. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes "run on empty"? Ecology 83:2145-2151.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Nonnative stream fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656-2663.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2007. Invading rainbow trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. Oecologia 153:461-470.

Beauchamp, D. A. 2009. Bioenergetic Ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. American Fisheries Society Symposium 70, 2009.

Beauchamp, D. A., D. H. Wahl, and B. M. Johnson. 2007. Predator-Prey Interactions. Pages 765-842 in C. S. Guy and M. L. Brown, editors. 2007. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23(1):189-207.

Benfield, E. F. 1996. Leaf breakdown in stream ecosystems. Methods in Stream Ecology, 27:579-589.

Benke, A. C., A. D. Huryn, L. A. Smock, and B. J. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):1-17.

Berejikian, B. A., L. A. Campbell, and M. E. Moore. 2013. Large scale freshwater habitat features influence the degree of anadromy in eight Hood Canal *Oncorhynchus mykiss* populations. Canadian Journal of Fisheries and Aquatic Sciences 70:756-765.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308(5722):636–637.

Bilby, R. E., T. Bennett, and P. Roni. 2002. Utilization of nitrogen from spawning salmon by juvenile Chinook salmon and steelhead in two tributaries of the Columbia River. Report prepared for Bonneville Power Administration. BPA Contract #99-041-00. Pp 1-40.

Bilby, R. E., B. R. Franse, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 55:1909-1918.

Bisson, P. A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. Journal of the Fisheries Research Board of Canada 35:971-975.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242-2252.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pp 279-352 in Fish Physiology, vo 8. W.S. Hoar, D.J. Randall, and J.R. Brett, eds. New York: Academic Press.

Bridcut, E. E. 2000. A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. Hydrobiologia 427:83-100.

Canning, D. J., J. L. Randlette, and W. A. Haskins. 1988. Skokomish River comprehensive flood control management plan. Washington Department of Ecology, Report 87-24, Olympia, Washington.

Claeson, S. M., C. J. LeRoy, J. R. Barry, and K. A. Kuehn. 2014. Impacts of invasive riparian knotweed to litter decomposition, aquatic fungi, and macroinvertebrates. Biological Invasions 16(7):1531-1544.

Cloe, W. W., and G. C. Garman. 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36:106-114.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):e01248.

Connolly, P. J., and J. H. Petersen. 2003. Bigger is not always better for overwintering young-of-year steelhead. Transactions of the American Fisheries Society 132:262-274.

Cummins, K. W., C. E. Cushing, and G. W. Minshall. 1995. Introduction: an overview of stream ecosystems. In: River and Stream Ecosystems (eds C. E. Cushing, K. W. Cummins, and G. W. Minshall) pp 1-8. Elsevier, New York.

Denton, K. P., H. B. Rich Jr., J. W. Moore, and T. P. Quinn. 2010. The utilization of a Pacific salmon *Oncorhynchus nerka* by three populations of charr *Salvelinus* spp. Journal of Fish Biology 77:1006-1023.

Dineen, G., S. S. C. Harrison, and P. S. Giller. 2007. Seasonal analysis of aquatic and terrestrial invertebrate supply to streams with grassland and deciduous riparian vegetation. Biology and Environment: Proceedings of the Royal Irish Academy 107B(3):167-182.

Doctor-Shelby, K., and B. Berejikian. In Draft. Trophic dynamics and temperature interact to determine growth and age-at-smoltification in Hood Canal steelhead, *Oncorhynchus mykiss.*

Dunham, J. B., M. E. Rahn, R. E. Schroeter, and S. W. Breck. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. Western North American Naturalist 60:304-310.

Edwards, E. D., and A. D. Huryn, 1995. Annual contribution of terrestrial invertebrates to a New Zealand stream New Zealand Journal of Marine and Freshwater Research 29:467-477.

Edwards, E. D., and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. Hydrobiologia 337:151-159.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503-523.

Erős, T., P. Gustafsson, and L. A. Greenberg. 2012. Forest-stream linkages: effects of terrestrial invertebrate input and light on diet and growth of Brown Trout (*Salmo trutta*) in a boreal forest stream. PLoS ONE 7(5): e36462.

Fierro, P., L. Quilodrán, C. Bertrán, I. Arismendi, J. Tapia, F. Peña-Cortés, E. Hauenstein, R. Arriagada, E. Fernández, and L. Vargas-Chacoff. 2016. Rainbow trout diets and macroinvertebrates assemblages responses from watersheds dominated by native and exotic plantations. Ecological Indicators 60:655-667.

Foote, C. J., and G. S. Brown. 1998. Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 55:1524-1533.

Forrester, G. E., J. G. Chase, and W. McCarthy. 1994. Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. Environmental Biology of Fishes 39:301-311.

Garman, G. C. 1991. Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. Environmental Biology of Fishes 30:325-331.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems: Pacific salmon subsidize freshwater and terrestrial ecosystems through several pathways, which generates unique management and conservation issues but also provides valuable research opportunities. Bioscience 52:917-928

Giannico, G. R., and S. G. Hinch. 2007. Juvenile coho salmon (*Oncorhychus kisutch*) responses to salmon carcasses and in-stream wood manipulations during winter and spring. Canadian Journal of Fisheries and Aquatic Sciences 64:324-335.

Giles, N. 1980. A stomach sampler for use on live fish. Journal of Fish Biology 16:253-261.

Graca, M. A. S. 2001. The role of invertebrates in leaf litter decomposition in streams--a review. International Review of Hydrobiology 86:383-393.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25(1):15–21.

Groot, C., L. Margolis, and W. C. Clarke, editors. 1995. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Hafs, A. W., J. M. Niles, and K. J. Hartman. 2011. Efficiency of gastric lavage on age-0 brook trout and the influence on growth and survival. North American Journal of Fisheries Management 31:530–534.

Hatchery Scientific Review Group (HSRG). March 2004. Hatchery Reform Recommendations for the Puget Sound and Coastal Washington Hatchery Reform Project: Hood Canal. 62 p. Long Live the Kings, 1305 Fourth Avenue, Suite 810, Seattle, WA 98101 (available from www.hatcheryreform.org)

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63(6):1840-1856.

Hicks, B. J., M. S. Wipfli, and D. W. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oecologia 144:558-569.

Hladyz, S., K. Abjornsson, P. S. Giller, and G. Woodward. 2011. Impacts of an aggressive riparian invader on community structure and ecosystem functioning in stream food webs. Journal of Applied Ecology 48(2):443-452.

Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609-1612.

Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181-2194.

Hunt, R. L. 1975. Use of terrestrial invertebrates as food by salmonids. In: Coupling of Land and Water Systems (ed. A. D. Hasler) pp. 137-152. Springer-Verlag, New York.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnological Oceanography 41:243-252.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, 555 pp.

Irvine, J. R., and B. R. Ward. 1989. Patterns of timing and size of wild coho salmon (*Oncorhynchus kisutch*) smolts migrating from the Keogh River watershed on northern Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences 46:1086-1094.

Johnson, J. H., and N. H. Ringler. 1980. Diets of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) relative to prey availability. Canadian Journal of Zoology 58(4):553-558.

Johnson, J. H., J. E. McKenna, and K. A. Douglass. 2013. Movement and feeding ecology of recently emerged steelhead in Lake Ontario tributaries. Journal of Applied Ichthyology 29: 221-225.

Johnson, J. M., and D. M. Post. 1996. Morphological constraints on intracohort cannibalism in age-0 largemouth bass. Transactions of the American Fisheries Society 125:809-812.

Kaylor, M. J., and D. R. Warren. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. Ecosphere 8(6):e01845. 10.1002/ecs2.1845.

Kennedy, B. P., K. H. Nislow, and C. L. Folt. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. Ecology 89:2529–2541.

Kennedy, T. A., and S. A. Hobbie. 2004. Saltcedar (*Tamarix remosissima*) invasion alters organic matter dynamics in a desert stream. Freshwater Biology 49:65-76.

Kline, T. C., J. J. Goering, and R. J. Piorkowski. 1997. The effect of salmon carcasses on Alaskan freshwaters. Pages 179–204 in A. M. Milner, and M. W. Oswood, editors. Freshwaters of Alaska: ecological syntheses. Springer-Verlag, New York.

Kominoski, J. S., L. B. Marczak, and J. S. Richardson. 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. Ecology 92(1):151-159.

LeRoy, C. J., and J. C. Marks. 2006. Litter quality, stream characteristics, and litter diversity influence decomposition rates and macroinvertebrates. Freshwater Biology 51(4):605-617.

LeRoy, C. J., D. G. Fischer, W. M. Andrews, L. Belleveau, C. H. Barlow, J. A. Schweitzer, J. K. Bailey, J. C. Marks, and J. C. Kallestad. 2016. Salmon carcasses influence genetic linkages between forests and streams. Canadian Journal of Fisheries and Aquatic Sciences 73(6):910-920.

Li, J. L., W. J. Gerth, R. P. Van Driesche, D. S. Bateman, and A. T. Herlihy. 2016. Seasonal and spatial fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 73:1642-1649.

Lichatowich, J. A. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, District of Columbia, USA

Light, R. W., P. H. Alder, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81–85.

Mason, C. F., and S. M. MacDonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology 12:305-311.

McCarthy, S. G., J. J. Duda, J. M. Emlen, G. R. Hodgson, and D. A. Beauchamp. 2009. Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River watershed, California. Transactions of the American Fisheries Society 138:506-521.

Meehan, W. R., and R. A. Miller. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. Journal of the Fisheries Research Board of Canada 35:1359-1363.

Mellon, C. D., M. S. Wipfli, and J. L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. Freshwater Biology 53:2331-2343.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America, 4th edn. Kendall Hunt, Dubuque, IA.

Moore, J. W., D. E. Schindler, and C. P. Ruff. 2008. Habitat saturation drives thresholds in stream subsidies. Ecology 89(2):306-312.

Moore, J. W., D. E. Schindler, J. L. Carter, J. Fox, J. Griffiths, and G. W. Holtgrieve. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. Ecology 88:1278-1291.

Moore, M. E., B. A. Berejikian., and E. P. Tezak. 2010. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. Transactions of the American Fisheries Society 139:49-61.

Mouton, A. M., M. Buysse, M. Stevens, T. Van Den Neucker, and J. Coeck. 2012. Evaluation of riparian habitat restoration in a lowland river. River Research and Applications 28:845-857.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences 109(52):21201-21207.

Naiman, R. J., and H. De'camps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399-417.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98(1):155-170.

Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara. 1999a. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecological Research 14:351-360.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999b. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441.

Näslund, J., D. Aldvén, and L. Závorka. 2015. Eggs from anadromous adults provide marine-derived nutrients to Atlantic salmon and brown trout parr in late autumn – observations from a Swedish coastal stream. Environmental Biology of Fishes DOI 10.1007/s10641-015-0436-y

Nelson, M. C., and J. D. Reynolds. 2015. Effects of subsidies from spawning chum and pink salmon on juvenile coho salmon body size and migration timing. Ecosphere 6(10):209.

Nowlin, W. H., M. J. Vanni, and L. H. Yang. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. Ecology 89(3):647-659.

Persson, A., and C. Bronmark. 2002. Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. Oikos 97:272-281.

Peterson, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:343-368.

Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. Science 305:346–347.

Point No Point Treaty Council (PNPTC). 2015. Hood Canal steelhead management plan: 2014-2015. 19p.

Polis, G. A., and K. O. Winemiller. 1996. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press: Seattle, Washington.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Aquatic and Fisheries Sciences 53:1555-1564.

Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54:1211-1234.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz, and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Aquatic and Fisheries Sciences 69:73-84.

Roni, P., and A. Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. North American Journal of Fisheries Management 20:683-692.

Roon, D. A., M. S. Wipfli, T. L. Wurtz, and A. L. Blanchard. 2016. Invasive European bird cherry (*Prunus padus*) reduces terrestrial prey subsidies to urban Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 73:1-12.

Rosenfeld, J. S. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132: 953–968. doi:10.1577/T01-126.

Sabo, J. L., and M. E. Power. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860-1869.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336-343.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Sato, T., K. Watanabe, M. Kanaiwa, Y. Niizuma, Y. Harada, and K. D. Lafferty. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology 92(1):201-207.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52:1944-1956.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1(1):31-37.

Skokomish Indian Tribe and Washington Department of Fish and Wildlife (SIT and WDFW). 2017. Recovery Plan for Skokomish River Chinook 2017 update. Skokomish Indian Tribe, Skokomish, WA; Washington Department of Fish and Wildlife, Olympia, WA.

Smits, A. P., D. E. Schindler, J. B. Armstrong, M. T. Brett, J. L. Carter, and B. S. Santos. 2016. Thermal constraints on stream consumer responses to a marine resource subsidy. Canadian Journal of Fisheries and Aquatic Sciences 73:1661-1671.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129–1157.

Steingrimsson, S. O., and G. M. Gislason. 2002. Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxa, North-East Iceland. Environmental Biology of Fishes 63:417-426.

Stranko, S. A., R. H. Hilderbrand, and M. A. Palmer. 2012. Comparing the fish and benthic macroinvertebrate diversity of restored urban streams to reference streams. Restoration Ecology 20(6):747-755.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. Seasonal changes in spatial patterns of *Oncorhynchus mykiss* growth require year-round monitoring. Ecology of Freshwater Fish 26(3):434-443.

Thompson, J. N., and D. A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. Transactions of the American Fisheries Society 143:910-925.

Twomey, H. G., and P. S. Giller. 1990. Stomach flushing and individual Panjet tattooing f salmonids: an evaluation of the long-term effects on two wild populations. Aquaculture and Fisheries Management 21:137-142.

U.S. Fish and Wildlife Service (USFWS). 2011. Biological Sampling in the Skokomish River Basin, Washington: Army Corps of Engineers General Investigation. Fisheries Division, Washington Fish and Wildlife Office, Lacey, Washington.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in Lake Tahoe (California–Nevada) Basin. Ecosystems 6:274–288.

Vanderploeg, H. A., and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: Zooplankton grazing. Ecological Modelling 7:135–149.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

Washington Department of Natural Resources (WDNR). 1997. Washington State salmonid stock inventory: bull trout/Dolly Vardon. Olympia, WA.

Washington State Conservation Commission (WCC). 2003. Salmon and steelhead Habitat Limiting Factors: Water Resource Inventory Area 16: Dosewallips-Skokomish Basin. Olympia, WA.

Weber, N., N. Bouwes, and C. E. Jordan. 2014. Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. Canadian Journal of Fisheries and Aquatic Sciences 71(8):1158-1170.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393-425.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:1259-1269.

Wipfli, M. S. and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957-969.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. Fisheries 35(8):373-387.

Wipfli, M. S., and J. Musslewhite. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia 520:153-163.

Wipfli, M. S., J. P. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: Salmon carcasses increase growth rates of steam-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Woodward, G., and A. G. Hildrew. 2002. Food web structure in riverine landscapes. Freshwater Biology 47:777-798.

Wright, L. A. 2010. Winter feeding ecology of coho salmon (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*) in the Skokomish River, Washington. (Published master's thesis). The Evergreen State College, Olympia, Washington.

Young, M. K., R. B. Rader, and T. A. Belish. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. Transactions of the American Fisheries Society, 126:428-437.

CHAPTER 2. BEYOND SUMMER: REVIEW OF THE TEMPORAL ASPECTS OF JUVENILE SALMON ECOLOGICAL AND RIVERSCAPE STUDIES REVEALS THE NEED FOR YEAR-ROUND RESEARCH

Megan E. Brady, Jonathan B. Armstrong, and Andrew Chione

Abstract

In recent decades, fish ecologists have become increasingly aware of the need for spatially comprehensive sampling. However, a corresponding reflection on the temporal aspects of research has been lacking. We conducted a review of the seasonal timing and extent of sampling for the last 30 years of juvenile Pacific salmon and trout ecological research broadly and within the topics of habitat interactions, trophic ecology, and spatial distribution (n = 371 studies) as well as the emerging field of spatially continuous “riverscape” sampling (n = 38). We found that ecological research was biased towards summer (40% occurred during June-August) and the month of June in particular, at the expense of winter work (only 13% occurred during December-February). Riverscape studies were also biased toward summer (50% of studies) and against winter (9%). It was relatively rare for studies to encompass multiple seasons (only 43% of ecological studies but over 55% for riverscape studies) and most were shorter than 4 months (73% of ecological studies and 80% of riverscape studies). These temporal biases may cause researchers to overemphasize ecological phenomena observed during summer and limit our ability to recognize seasonal interactions such as carry-over effects. Full year and winter studies likely hold valuable insights for conservation and management.

Introduction

A key challenge in conservation is to understand how abiotic and biotic heterogeneity mediate the function of ecosystems and the survival of biota that inhabit these environments. This heterogeneity exists in both space and time, creating a shifting mosaic of physical and biological conditions that has significant ramifications for biota (Whited et al. 2007). Phenomena ranging from ontogenetic niche shifts (Werner and Gilliam 1984) to the stability of fisheries (Brennan et al. 2019) can only be understood by jointly considering interactions between space and time. However, because resources are limited and characterizing stream heterogeneity is a non-trivial task, it is often not feasible to study multiple dimensions of variation simultaneously. Indeed, many fundamental concepts in stream ecology are either spatially or temporally focused.

For example, spatial patterns of biota are often described with minimal reference to time. This applies to early work, such as the longitudinal zonation of fishes (Huet 1959), but also the River Continuum Concept (Vannote et al. 1980) and more contemporary emphasis on "riverscape" ecology (Fausch et al. 2002). Though time is recognized as the "fourth dimension" of the riverscape (Ward 1989), in practice, the suffix "scape" is typically used when working at large spatial extents of data, which often compounds the challenges of incorporating time.

Similarly, time is often considered independently in studies of both habitat and fish. Stream ecologists increasingly embrace a regime approach to characterizing temporal variation in habitat conditions, originating with the Natural Flow Regime (Poff et al. 1997), which considered the statistical distribution of conditions and metrics such as event magnitude, frequency, seasonal timing, predictability, duration, and rates of change. The regime concept is now applied beyond water quantity to include aspects of water quality (Poole and Berman 2001) (Caissie 2006), as well as physical attributes such as sediment, large wood, and abundance of pools (Beechie and Sibley 1997). In fisheries ecology, temporal variation is probably most commonly studied in the form of population dynamics, i.e., fluctuations in abundance typically described at an annual resolution. However, many important processes that may scale up to affect population dynamics (e.g. growth) play out at intra-annual timescales and relate to seasonality.

It is often recognized that short-term datasets can be inadequate because they fail to capture historical levels of productivity (i.e. the shifting baseline) or reveal coarser scale temporal patterning such as regime shifts (Mejia et al. 2019). Likewise, for cyclically patterned temporal variation, interpretations may be misleading if they are based on a limited portion of a cycle. For example, many fish switch between habitat types throughout the diel cycle (Neverman and Wurtsbaugh 1994) so only studying animals during daytime may fail to capture important habitats. Similarly, refuge habitat identified in summer may not represent refuge habitat for other seasons and stressors (Schlosser 1995). Riverine systems may exhibit extreme seasonal variation, with water temperatures ranging 20°C or more and flows varying 100-fold. This strongly affects not only fish and other aquatic organisms, but also the feasibility of field sampling. While a temperature logger can effectively collect data every day of the year, the cost and logistical challenges of sampling fish vary tremendously and can strongly govern when biological data are collected. Extrapolating from data that pertain to specific points in time can lead to misleading interpretations regarding how fish behave, the production capacity for ecosystems, and what locations or habitat types are important (Fraser and Metcalfe 1997; Bramblett et al. 2002). This is particularly problematic in the study of mobile organisms that undergo substantial physiological and ecological changes throughout their lifetimes, such as Pacific salmonids. The objective of this paper is to characterize the temporal attributes of fish ecology research to elucidate potential data gaps and guide future research.

Recent work on birds, amphibians, reptiles, and mammals found strong seasonal biases in field research (Marra et al. 2015), but analogous work on fish has been lacking. The assertion that winter fish ecology is an important, yet understudied portion of the research portfolio is not new (Huusko et al. 2007); however, no quantification of any inequity in research effort has previously existed. Here, we characterize the temporal aspects of Pacific salmon and trout ecology research from the last 30 years. We characterized patterns in the seasonal timing and duration of ecological field studies and considered how these patterns varied across three focal topics: fish-habitat interactions, trophic ecology, and spatial distribution. We then assessed whether spatially extensive sampling has come at the expense of time.

Methods

To determine whether and to what extent temporal biases are present in juvenile Pacific salmon and trout research, we conducted a literature review of 1) what months and seasons juvenile salmonid ecology research occurs, 2) the duration of studies, and 3) whether seasons were studied individually or if seasonal interactions were examined.

We reviewed 13 journals that commonly publish fisheries ecology research: *Canadian Journal of Fisheries and Aquatic Sciences, Ecology, Ecology of Freshwater Fish, Ecosphere, Ecosystems, Environmental Biology of Fishes, Freshwater Biology, Hydrobiologia, North American Journal of Fisheries Management, Oecologia, PLoS ONE, Science, and Transactions of the American Fisheries Society.* Using the Web of Science database, we performed searches within these journals using the following key words: “salmon,” “salmonids,” or “*Oncorhynchus*.” We then examined every article from the past 30 years, 1988-2017, and selected those that dealt with the ecology of juvenile *Oncorhynchus* species during freshwater residence. The juvenile life stages of fry, parr, and smolt were all included. We focused on juvenile Pacific salmon in freshwater because they are well-studied (providing us the power to detect trends in sampling) and they live in highly seasonal environments (which means an incomplete understanding of the annual cycle would be a problem and is thus important to test for). The past 30 years was chosen to characterize the current patterns of research. Only papers that presented original, ecologically-focused data were included, whether they were observational studies or experimental studies conducted in a natural environment. We did not include laboratory studies, reviews, or models not validated with field data.

Additionally, we identified "riverscape" studies that utilized spatially continuous sampling (Fausch et al. 2002). Using the Web of Science database, we performed searches within all peer-reviewed journals using combinations of the following key words: "riverscape", "spatially continuous", "longitudinal distribution", "Fausch et al. 2002", "salmon," "salmonids," and "*Oncorhynchus*." We then examined every article from the past 30 years, 1988-2017, and selected those that dealt with spatially continuous or riverscape-scale sampling of juvenile *Oncorhynchus* species during freshwater residence.

We classified each publication for both the ecological dataset and the riverscape dataset by the temporal aspects of data collection. First, we recorded the presence/absence of data collection in each month and season. We defined seasons meteorologically as aligned with the calendar months of June 1-August 31 for summer, September 1-November 30 for autumn, December 1-February 28 for winter, and March 1-May 30 for spring. Seasons were not defined by solstice or equinox to stay consistent with presence/absence within a single month. Studies may encompass more than one month, therefore the number of data points for these analyses are greater than the number of studies included in the review. Second, we quantified the frequency of the number of meteorological seasons (1-4) that were included in these studies to analyze temporal extent and consideration of inter-seasonal interactions (i.e., carry-over effects).

To explore whether temporal aspects of sampling differed among research areas, we classified each study into three focal areas: 1) fish-habitat interactions and the impact of habitat units and types on juvenile salmonid biology or behavior, 2) trophic ecology including fish diet, foraging, and food web structure, and 3) spatial distribution including movement and landscape-scale distribution. Studies examining fish growth and survival were often presented by researchers as a function of some aspect of one of the three focal areas identified and were classified accordingly. The temporal distribution and extent of sampling effort was then quantified both collectively and by research category. Each study was only classified into one of the three focal areas based on the main objective of the study. Studies that did not fall into one of these four main categories were classified as “Other” and included in overall analysis but not the subset analyses.

We tested for temporal biases using Pearson x^2-tests for temporal distribution and extent. Equal values would indicate that no bias exists, supporting the null hypothesis. While the test is objective, we acknowledge that the interpretation is subjective due to the assumptions that all months and seasons are equally important and present equal stresses, limitations, or opportunities for growth, fitness, and survival for juvenile salmonids.

We also acknowledge that phenology varies with latitude, elevation, and position in watershed, so the ecological conditions associated with a particular month or season may vary among locations (and thus among the studies in our paper). Thus, the implications of the temporal biases we observed may be somewhat context dependent.

Results

Monthly Temporal Distribution of Studies

At a monthly resolution across all ecological topics, we found that the most frequently represented month was 3-6 times more common than the least frequently represented month (Fig. 1). December was the least represented month across all topics, while the summer months of June, July, and August were most common among topics. The month of June had a significantly higher proportion of studies than the month of December at 14% and 3%, respectively.

Seasonal Temporal Distribution of Studies

Across all ecological topics, we found that 39-44% of studies occurred during summer while only 10-15% of studies occurred during winter (Fig. 1). There has been little change in the temporal distribution of research efforts with the proportion of winter studies remaining significantly lower than summer studies (Fig. 2).

Monthly Temporal Extent of Studies

At a monthly resolution across all ecological topics, we found that most studies had limited temporal extent across the annual cycle, with 71-75% of studies containing data from 4 months or less (Fig. 3). Less than 2-8% of studies across all topics encompassed data from all 12 months of the year.

Seasonal Temporal Extent of Studies

Across all ecological topics, we found that 48-63% of studies occurred during a single season while only 6-10% of studies encompassed field sampling from all four seasons (Fig. 3).

Only 43% of all studies collected data from multiple seasons and 73% of studies were shorter than 4 months. Again, there has been little change in the temporal extent of research efforts with the proportion of single-season studies remaining significantly higher than multi-season or year-round studies (Fig. 4).

Riverscape Studies

Analysis of riverscape studies revealed wider biases in temporal distribution at monthly and seasonal scales. The most frequently represented month was 8x more common than the least frequently represented month (Fig. 5). January and February were the least represented months, while June, July, August, and September were most common. Summer encompassed 50% of all juvenile Pacific salmon and trout riverscape studies while only 9% of studies occurred during winter (Fig. 5).

Monthly temporal extent was limited within riverscape studies as well. Spatially continuous studies were almost entirely conducted during a limited amount of time: 80% contained data from 4 months or less and only 3% of studies encompassed data from a full 12 months out of the year (Fig. 5). Seasonal extent for riverscape studies was the one metric that was more representative than the ecological studies we examined: 45% of riverscape studies occurred during a single season, 39% occurred over two seasons, 8% occurred over three seasons, and 8% occurred during all four seasons (Fig. 5).

Discussion

In our review of 371 ecological studies and 38 riverscape studies from the last 30 years of juvenile Pacific salmon and trout research, we observed strong biases in seasonal timing (distribution) and temporal extent. Within research topics where seasonality is particularly relevant, we observed the same general pattern of temporal bias; the period of summer was overrepresented in the study of fish-habitat interactions, trophic ecology, and spatial distribution. Below we discuss these temporal patterns of data collection and consider their potential causes and consequences.

Bias in Temporal Distribution of Studies

The most conspicuous pattern in the data was the lack of research during winter. For example, the month of December had less than one-quarter as many studies as that of June. Winter studies represented only 10-15% of total ecological research and 9% of riverscape studies. Winter may be tempting to overlook because it is generally a period of low biological activity in freshwater ecosystems. Winter is typically the coldest time of year, limiting the scope for growth and activity in aquatic poikilotherms. Further, winter is the darkest time of year, limiting primary productivity (Uehlinger 2006) and the foraging opportunity for visual predators (Fraser and Metcalfe 1997). Indeed, many stream-dwelling fishes tend to allocate energy to fat stores in anticipation of winter (Hurst and Conover 2003), suggesting it is generally a period of negative energy balance. Though juvenile salmonids may be less active in winter and not achieve substantial growth (Tattam et al. 2017), this does not mean that understanding winter ecology is not critical. If fish rely on summer and fall fat stores to survive winter, then any food intake during winter helps to minimize the need to deplete those stores. Identifying winter foraging opportunities, trophic pathways, and habitat use could provide insights into how fish survive during this time of year (Cunjak et al. 1987). For example, recent research exploring how environmental conditions influence fish interactions and movement has identified habitat not utilized outside of the winter months (McMeans et al. 2020). In many systems, winter survival is hypothesized to be a limiting factor to freshwater population productivity (Bustard and Narver 1975) and reducing winter mortality is often an objective of largescale restoration efforts (Cederholm et al. 1997). Understanding winter habitat use and foraging ecology could help improve our ability to increase overwinter survival.

The lack of winter research contrasted with the overabundance of summer studies. While emphasis on summer has benefits, such as an improved understanding of salmonid ecology during periods of climate stress, relying on summer-biased data could pose problems for conservation and management by violating assumptions of models. For example, species distribution models (SDM) are increasingly used in climate change adaptation and rely on the assumptions that a species occurs in all suitable habitats and that a species only occupies a portion of that suitable habitat due to constraining factors such as competition or predation (Guisan and Thuiller 2005). Developing such models from temporally biased data would be valid only if the focal species were sedentary and their habitat use did not vary over time. However, it's rarely possible to confirm that a species meets these criteria without having temporally representative data (i.e., you can't dismiss the possibility of winter habitat shifts without data on winter habitat use). Using data from a limited period of time can cause SDMs to erroneously dismiss critically important habitat. For example, Smeraldo et al. (2018) demonstrated that SDMs based on seasonally biased data failed to identify the habitats needed to support both hibernation and reproduction in bats. Defining climate refugia based on summer-biased data (Isaak et al. 2015) could similarly leave out critical overwinter habitats if fish exhibit seasonal movements and require multiple habitat types to complete the annual cycle. While summer heat stress may be the most vivid threat of a warming world, climate change may also make winter more challenging by increasing maximum flows (McCabe et al. 2007) or reducing ice cover (Huusko et al. 2007). The lack of winter studies in our analysis, and the emphasis on summer in both empirical studies and climate models (Isaak et al. 2015), suggests that winter may be a blindspot for climate change adaptation work on Pacific salmon.

Our current classification system for longitudinal fish zonation is largely based on summer sampling (Huet 1959). While recent decades have seen an emphasis on more spatially representative fish sampling (Angermeier and Smogor 1994) and a movement towards multiscale analysis of spatial distributions (Wiens 2002), this work tends to not be temporally representative. For example, spatially continuous “riverscape” sampling has been transformative for our understanding of salmonid spatial distributions (Fausch et al. 2002), yet our results confirm that virtually all of this work is conducted during summer or early autumn (Brenkman et al. 2012; Flitcroft et al. 2014). While longitudinal patterning is inherently relevant to lotic ecosystems (because they are linear networks), fish may also exhibit pronounced spatial patterning in lateral, and vertical dimensions (Favrot et al. 2018). In temperate regions of the Pacific salmon range, floodplains may only be connected and wetted during winter, so summer-biased sampling may hinder our ability to understand the significance of off-channel habitat use. Where summer and fall are the wet seasons (e.g., much of coastal Alaska), use of off-channel habitats may vary seasonally and require temporally extensive sampling to understand key dynamics. For example, the spatial patterning of juvenile coho salmon on a stream floodplain shifted over time, tracking shifts in water temperature (Armstrong and Schindler 2013) caused by fluctuating water levels. Use of temporary aquatic habitats by fish may be disproportionately important when they are available at the right place and time; however, research is lacking to capture this ephemeral aspect of fish ecology (Heim et al. 2019).

The distribution of juvenile salmonids among channel-unit scale habitat types (Bisson et al. 1982) may also vary among months and seasons. For example, Nickelson et al. (1992) found that juvenile coho primarily occupied backwater pools in spring, main-channel pools in summer, and alcoves and beaver ponds in winter. Distribution of juvenile salmonids in sub-habitats (e.g. riffles, pools, backchannel ponds) can also impact fish growth and fitness through energetic costs and benefits (Rosenfeld and Boss 2001). While fine-detail studies of fish distribution help identify quality salmonid habitat, our analysis demonstrates that this data implicitly favors summer habitat and devalues winter habitat.

Bias in Temporal Extent of Studies

While a bias against winter studies is seen in temporal distribution, a bias against full annual studies is seen in temporal extent. Studies examining all four meteorological seasons represented only 6-10% of total research. Research is heavily skewed toward shorter, single season studies: 73% of all studies capturing 4 months or less of data and 57% of studies focused on a single season in isolation. Within riverscape studies, 80% of research occurred during 4 or fewer calendar months. These patterns are similar to what Marra et al. (2015) found in their review, which did not include fishes. While there is increasing recognition of the value of long-term study (Lindenmayer et al. 2012), this usually means having multiple years or decades of data collection. Our review shows that there is also a lack of temporal extent in terms of the annual cycle. Lacking extent at this timescale leads to two issues. First, we are likely to temporally extrapolate and draw conclusions based on a subset of the year (as discussed above) and second, we will often lack the ability to identify interactions between different time periods, or carry-over effects (Marra et al. 2015).

Carry-over effects from one life stage or season can have significant impacts on fitness and survival of individuals and populations in subsequent seasons or life stages (Harrison et al. 2011). As climate change and increasing water demands make summer more stressful for salmon in regions such as the western United States, there is a strong need to understand how conditions during spring and fall mediate the effects of summer stress on freshwater rearing capacity. The ability of fish to survive negative energy balance during harsh summer conditions should depend on their ability to store energy in spring and rebuild energy stores in fall. For example, over-winter survival of juvenile salmon is often positively associated with larger body size at the onset of autumn (Holtby 1988). There is evidence that ephemeral food subsidy pulses, such as salmon eggs during the adult spawning season, can positively influence juvenile salmon growth rate and energy density as long as 6 months after this ephemeral resource pulse has disappeared (Rinella et al. 2012). Whether juvenile salmonids grow large enough to consume eggs depends on their emergence timing and early growth opportunities (Armstrong et al. 2010). Thus, small increases in the growth of fry during spring may determine whether marine subsidies benefit parr during fall, influencing overwinter survival and the size of smolts the following spring, which relates to subsequent marine survival (Thompson and Beauchamp 2014).

Sampling during multiple seasons is more likely to capture any carry-over effects that span pre-pulse, pulse, and post-pulse. Food availability, along with temperature, strongly affect fish growth rates with extreme variation in growth between seasons (Tattam et al. 2017; Myrvold and Kennedy 2019). Quantifying fish growth and food resources at multiple points in time are essential to avoid bias in assumptions and to identify ephemeral trophic pathways that could be disproportionately important during that season or in subsequent seasons. The lack of full annual cycle research on Pacific salmon has likely hindered our ability to recognize inter-seasonal carry-over effects, which may become increasingly important in the future.

A core concept in landscape ecology is that of habitat complementation and different patches of space functioning at different times (e.g., different lifestages or seasons) (Dunning et al. 1992; Schlosser 1995). The use of habitat by juvenile salmonids shifts 1) seasonally as river conditions such as temperature gradually change (Nickelson et al. 1992) 2) momentarily as a balance of energetic costs and benefits (Rosenfeld 2003), 3) ontogenetically as resource needs change (Werner and Gilliam 1984) and 4) ephemerally, such as during discrete events like floods or drought (Schlosser 1995). Without full annual studies, the effects of these stressors on fish (e.g. energetic costs, food availability, competition, predation) are poorly understood. Habitat restoration may be more successful if information is available to allow for targeting of the limiting life stage or limiting habitat in salmonid productivity (Roni et al. 2002). Identification of these productivity limitations is hindered by two kinds of error: an assumption of limitation and an assumption of importance. First, the assumption that winter is limiting to juvenile salmonid survival is problematic because without more winter studies we cannot validate this assumption or understand the mechanisms behind winter mortality or winter vulnerability. Second, if we assume that summer is more important because significant growth occurs in the summer months, we assume that summer sampling can characterize spatial distribution and habitat use. This is problematic because it hinders the ability to identify limitations to juvenile salmonid survival outside of spring through fall. It is well-established that the challenges faced by stream-dwelling fishes in winter are vastly different (Brown et al. 2011). In order to best protect the habitat supporting juvenile salmon and trout, more effort is needed to understand the importance of winter ecology.

Considerations

The seasonal bias of research could potentially be a product of two human limitations: environmental challenges and allocation of scarce resources. First, the summer months generally present the least challenging environmental conditions for human access to salmon-bearing habitat, particularly in the Pacific Northwest where a significant amount of Pacific salmon research takes place: low stream flow, warm temperatures, and minimal precipitation. Sampling fish in the winter months can be particularly challenging, as snow, ice, and high flow events limit safe access for researchers and lead to fish exhibiting behaviors that make them difficult to capture (e.g. winter concealment, nocturnality). Second, academic calendars create a seasonal bias towards summer field work by their very structure, allowing time for field work while classes are on break during summer. Field projects outside of academia also often follow a summer-intensive field season program due to the availability of field technicians who are often college students. Institutional hiring policies can further exaggerate these patterns. For example, at our institution students cannot work > 20 hours per week during non-summer months, and it costs ~30% more to hire seasonal assistants that are not students (due to the need for a temporary hiring agency). This makes non-summer field work considerably more expensive. Thus, a combination of environmental challenges, logistical hurdles, and institutional culture make field work more likely to happen in summer.

Conclusion

In recent decades, stream ecology has strongly emphasized the need for more spatially comprehensive sampling of fish (Fausch et al. 2002); however, the focus on space has often come at the cost of time. Mapping the entire riverscape can reveal rich, multiscale patterns, but efforts typically fail to reveal how these patterns shift over time. Fish may not occupy every meter of space available to them, but they do live in every second of time. Furthermore, phenomena such as floodplain dynamics (Whited et al. 2007), seasonal movement (Baldwin et al. 2002), portfolio effects (Schindler et al. 2015), resource waves (Armstrong et al. 2016), and thermoregulation (Wurtsbaugh and Neverman 1988) are driven by the interaction between spatial and temporal variation. We hope that our review encourages researchers to allocate more of their effort to understudied portions of the year, which likely hold valuable insights for conservation.

References

Angermeier, P. L., and R. A. Smogor. 1994. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. Canadian Journal of Fisheries and Aquatic Sciences 52:936-949.

Armstrong, J. B., G. T. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099-1112.

Armstrong, J. B., and D. E. Schindler. 2013. Going with the flow: spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. Ecosystems 16:1429-1441.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445-1454.

Baldwin, C. M., D. A. Beauchamp, and C. P. Gubala. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. Transactions of the American Fisheries Society 131:143-158.

Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitats in northwestern Washington streams. Transactions of the American Fisheries Society 126:217-229.

Bisson, P. A., J. L. Nielsen, R. A. Palmason., and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 in N. B. Armantrout (Ed.) Acquisition and Utilization of Aquatic Inventory Information. Symposium proceedings, October 28-30, 1981, Portland, Oregon. The Hague Publishing, Billings, MT.

Bramblett, R. G., M. D. Bryant, B. E. Wright, and R. G. White. 2002. Seasonal use of small tributary and main-stem habitats by juvenile steelhead, coho salmon, and dolly varden in a southeastern Alaska drainage basin. Transactions of the American Fisheries Society 131:498-506.

Brenkman, S. J., J. J. Duda, C. E. Torgersen, E. Welty, G. R. Pess, R. Peters, and M. L. McHenry. 2012. A riverscape perspective of Pacific salmonids and aquatic habitats prior to large-scale dam removal in the Elwha River, Washington, USA. Fisheries Management and Ecology 19(1):36-53.

Brennan, S. R., D. E. Schindler, T. J. Cline, T. E. Walsworth, G. Buck, and D. P. Fernandez. 2019. Shifting habitat mosaics and fish production across river basins. Science 364(6442):783-786.

Brown, R. S., W. A. Hubert, and S. F. Daly. 2011. A primer on winter, ice, and fish: what fisheries biologists should know about winter ice processes and stream-dwelling fish. Fisheries 36(1):8-26.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32(5):667-680.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389-1406.

Cederholm, C. J., R. E. Bilby, P. A. Bisson, T. W. Bumstead, B. R. Fransen, W. J. Scarlett, and J. W. Ward. 1997. Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. North American Journal of Fisheries Management 17:947-963.

Cunjak, R. A., R. Curry, and G. Power. 1987. Seasonal energy budget of brook trout in streams: implications for a possible deficit in early winter. Transactions of the American Fisheries Society 116:817-828.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6): 483-498.

Favrot, S. D., B. C. Jonasson, and J. T. Peterson. 2018. Fall and winter microhabitat use and suitability for spring Chinook salmon parr in a U.S. Pacific Northwest river. Transactions of the American Fisheries Society 147(1): 151-170.

Flitcroft, R., K. Burnett, J. Snyder, G. Reeves, and L. Ganio. 2014. Riverscape patterns among years of juvenile coho salmon in midcoastal Oregon: implications for conservation. Transactions of the American Fisheries Society 143:26-38.

Fraser, N. H. C., and N. B. Metcalfe. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. Functional Ecology 11:385-391.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8(9): 993-1009.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80(1):4-18.

Heim, K. C., T. E. McMahon, L. Calle, M. S. Wipfli, and J. A. Falke. 2019. A general model of temporary aquatic habitat use: water phenology as a life history filter. Fish and Fisheries 20:802-816.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Huet, M. 1959. Profiles and biology of western European streams as related to fish management. Transactions of the American Fisheries Society 88:155-163.

Hurst, T. P., and D. O. Conover. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84:3360-3369.

Huusko, A., L. Greenberg, M. Stickler, T. Linnansaari, M. Nykänen, T. Vehanen, S. Koljonen, P. Louhi, and K. Alfredsen. 2007. Life in the ice lane: the winter ecology of stream salmonids. River Research and Applications 23:469-491.

Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biology 21:2540-2553.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. A. Hoffman, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology 37:757-757.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

McCabe, G. J., M. P. Clark, and L. E. Hay. 2007. Rain-on-snow events in the western United States. Bulletin of the American Meteorological Society 88(3):319-328.

McMeans, B. C., K. S. McCann, M. M. Guzzo, T. J. Bartley, C. Bieg, P. Blanchfield, T. Fernandes, H. Giacomini, T. Middel, M. Rennie, M. Ridgway, and B. Shuter. 2020 (preprint).

Winter in water: differential responses and the maintenance of biodiversity. bioRxiV doi: https://doi.org/10.1101/849109.

Mejia, F. H., A. K. Fremier, J. R. Benjamin, J. R. Bellmore, A. Z. Grimm, G. A. Watson, and M. Newsom. 2019. Stream metabolism increases with drainage area and peaks asynchronously across a stream network. Aquatic Sciences 81:9.

Myrvold, K. M., and B. P. Kennedy. 2019. Seasonal variation in growth, consumption and growth efficiency in overwintering juvenile steelhead. Ecology of Freshwater Fish 00:1-15. https://doi.org/10.1111/eff.12526

Neverman, D., and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. Oecologia 98:247-256.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49(4):783-789.

Poff, N. L., D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47(11):769-784.

Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27(6):787-802.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz, and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Aquatic and Fisheries Sciences 69:73-84.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess, 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1-20.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953-968.

Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pool and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58(3):585-593.

Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13(5):257-263.

Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71-81.

Smeraldo, S., M. D. Febbraro, L. Bosso, C. Flaquer, D. Guixé, F. Lisón, A. Meschede, J. Juste, J. Prüger, X. Puig-Montserrat, and D. Russo. 2018. Ignoring seasonal changes in the ecological niche of non-migratory species may lead to biases in potential distribution models: lessons from bats. Biodiversity and Conservation 27:2425-2441.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. Seasonal changes in spatial patterns of *Oncorhynchus mykiss* growth require year-round monitoring. Ecology of Freshwater Fish 26(3):434-443.

Thompson, J. N., and D. A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. Transactions of the American Fisheries Society 143:910-925.

Uehlinger, U. 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. Freshwater Biology 51(5):938-950.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of North American Benthological Society 8(1):2-8.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393-425.

Whited, D. C., M. S. Lornag, M. J. Harner, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2007. Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. Ecology 88(4):940-953.

Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47(4):501-515.

Wurtsbaugh, W. A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333:846-848.

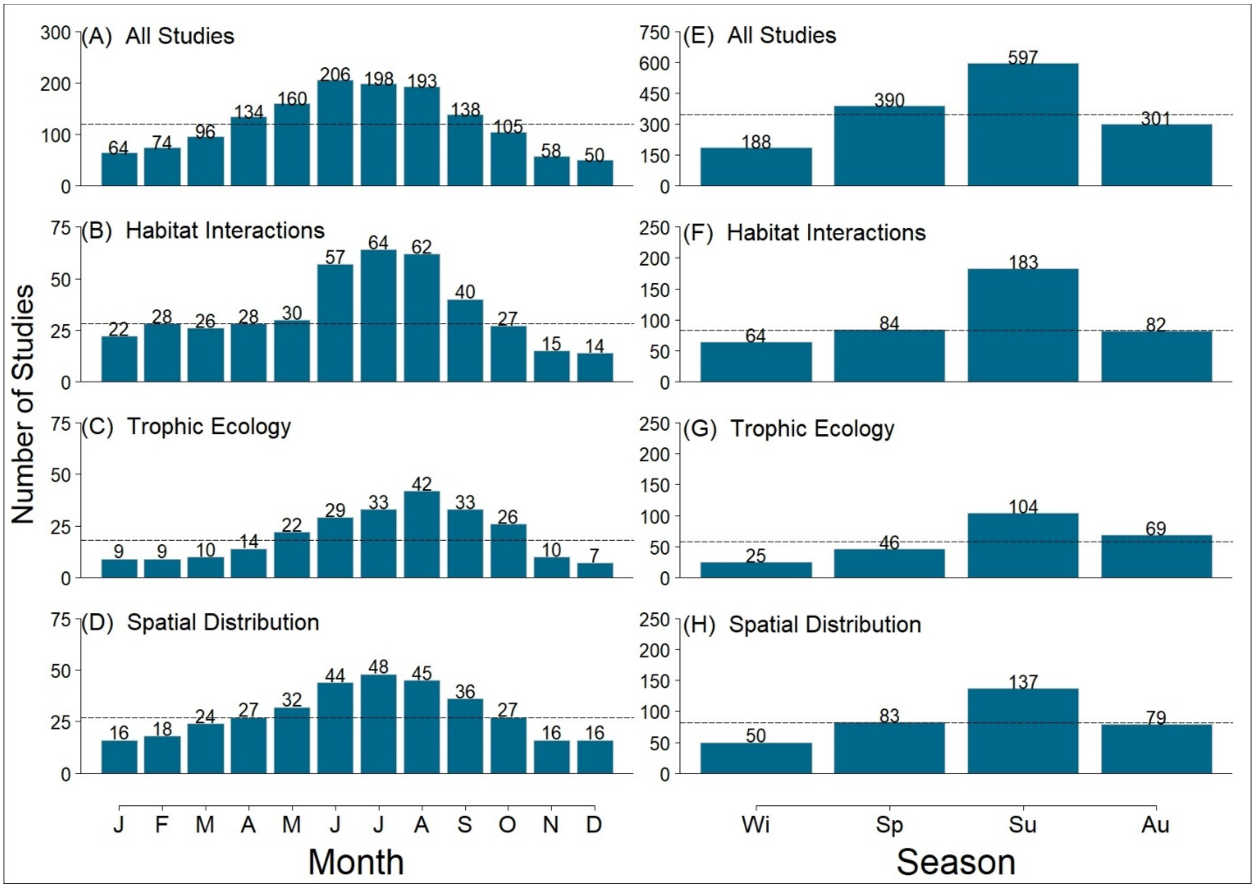


Figure 1. Temporal distribution of juvenile salmon ecology studies

Left column: monthly distribution of sampling effort for juvenile Pacific salmon and trout studies from 1988-2017 for (A) all studies (χ^2=289.58, $p < 0.0001$, n=1476, median=119.5), (B) habitat studies (χ^2=97.421, $p < 0.0001$, n=413, median=28), (C) trophic ecology studies (χ^2=78.131, $p < 0.0001$, n=244, median=18), (D) spatial distribution studies (χ^2=53.67, $p < 0.0001$, n=439, median=27). Right column: seasonal distribution of sampling effort for juvenile Pacific salmon and trout studies from 1988-2017 for (E) all studies (χ^2=243.39, $p < 0.0001$, n=1476, median=345.5), (F) habitat studies (χ^2=84.482, $p < 0.0001$, n=413, median=83), (G) trophic ecology studies (χ^2=56.295, $p < 0.0001$, n=244, median=57.5), (D) spatial distribution studies (χ^2=45.258, $p < 0.0001$, n=349, median=81). The number of studies for each month or season was calculated using presence or absence of research during that time frame. Dashed horizontal lines are data median. Studies may occupy more than one month or season. Seasons were defined meteorologically, but as whole months. Summer is defined as the months June, July, and August; Autumn is defined as the months September, October, and November; Winter is defined as the months December, January, and February; Spring is defined as the months March, April, and May.

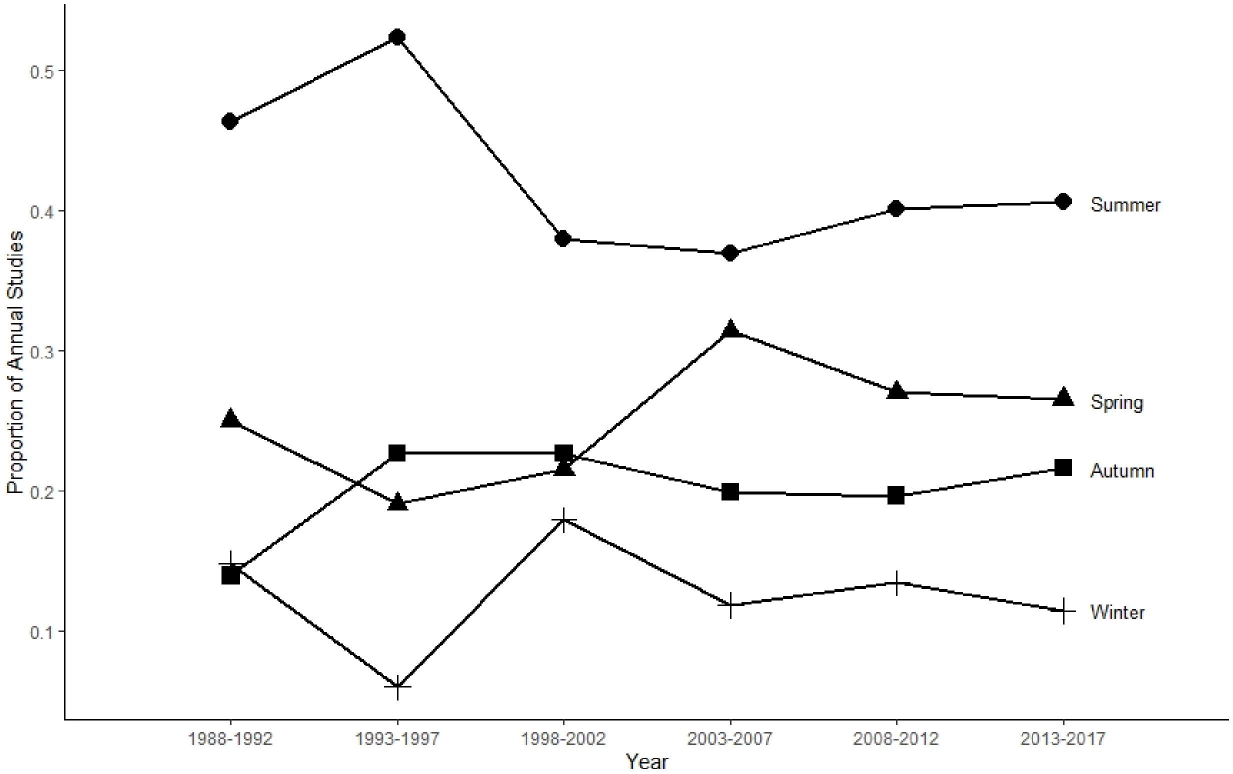


Figure 2. Seasonal study distribution over time
Change in the proportional temporal distribution (seasonal timing) of all studies published from 1988-2017 in 5-year increments.

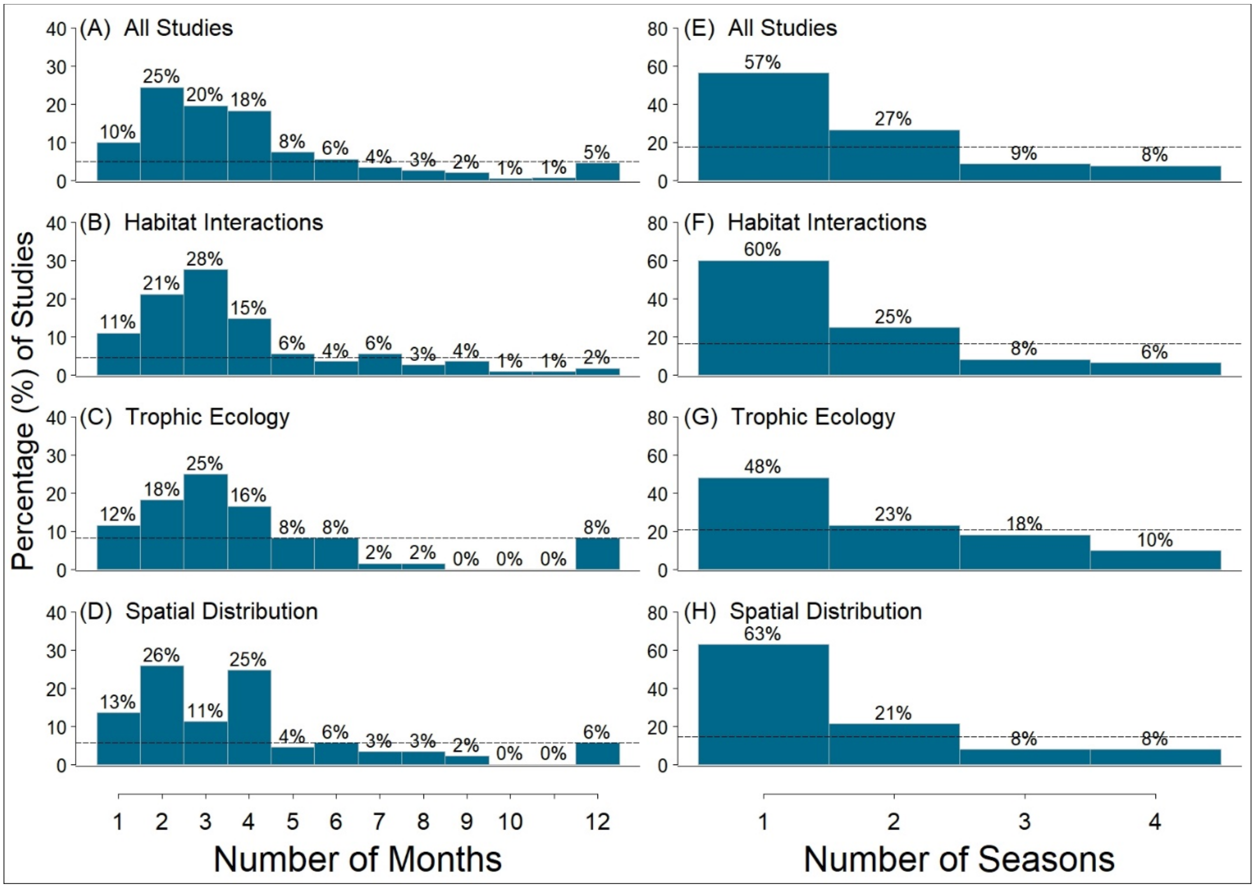


Figure 3. Temporal extent of juvenile salmon ecology studies

Left column: frequency of the number of months per calendar year (1-12) found in juvenile Pacific salmon and trout studies from 1988-2017 for (A) all studies (χ^2=670.07, p < 0.0001, n=371, median=5.1), (B) habitat studies (χ^2=173.55, p < 0.0001, n=108, median=4.6), (C) trophic ecology studies (χ^2=120.92, p < 0.0001, n=60, median=8.3), (D) spatial distribution studies (χ^2=173.01, p < 0.0001, n=89, median=5.1). Right column: frequency of the number of seasons per calendar year (1-4) found in juvenile Pacific salmon and trout studies from 1988-2017 for (E) all studies (χ^2=230.95, p < 0.0001, n=371, median=17.8), (F) habitat studies (χ^2=80.296, p < 0.0001, n=108, median=16.7), (G) trophic ecology studies (χ^2=19.6, p < 0.001, n=60, median=20.8), (H) spatial distribution studies (χ^2=72.573, p < 0.0001, n=89, median=14.6). The extent or duration was calculated by counting the total number of unique months (in a calendar year) that were included in each study and categorizing them by season as defined above. Data median is marked with a dashed horizontal line. Studies were only represented once at their greatest monthly extent and greatest seasonal extent.

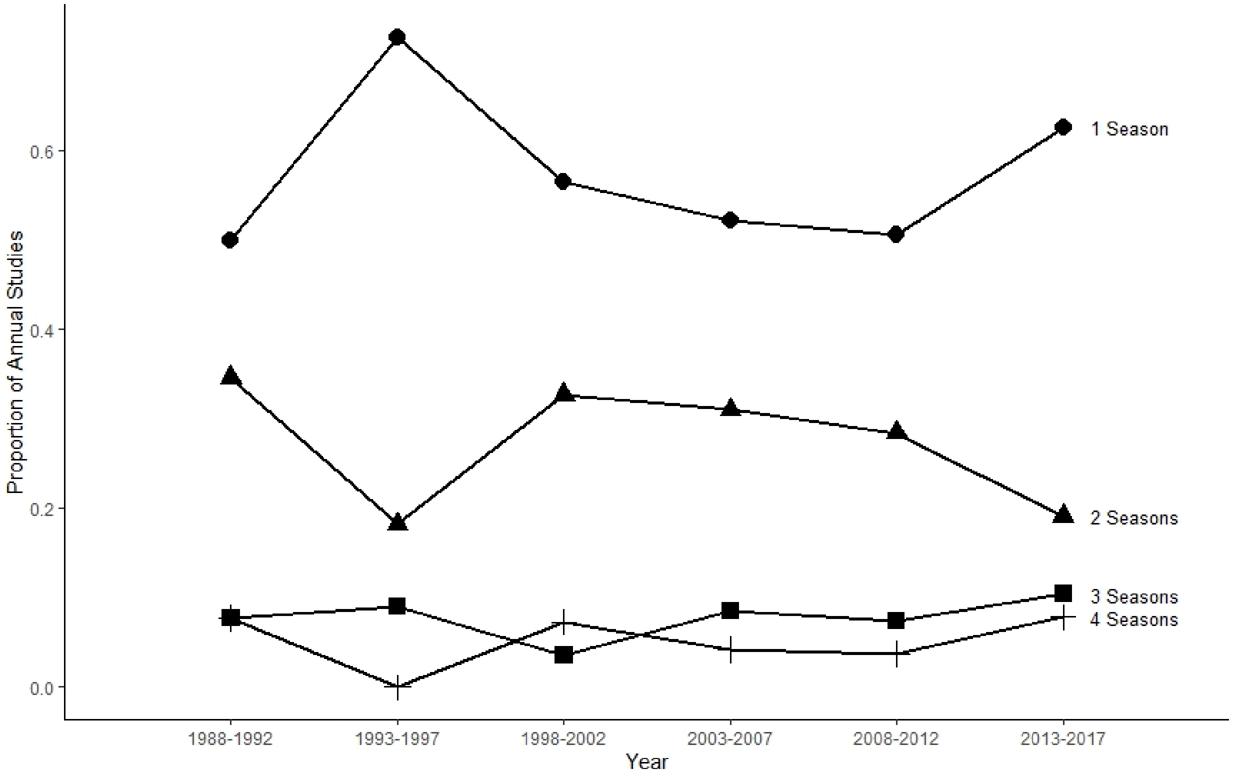


Figure 4. Seasonal study extent over time
Change in the proportional temporal extent (number of seasons included) of all studies published from 1988-2017 in 5-year increments.

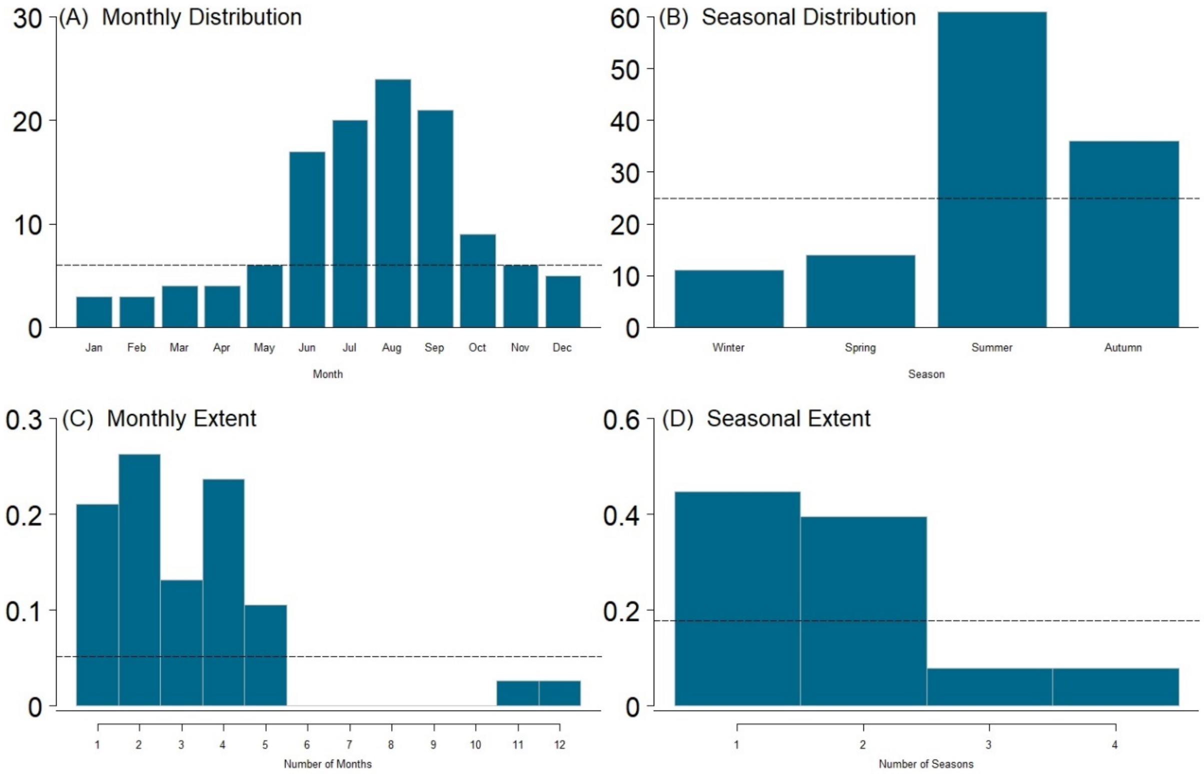


Figure 5. Distribution and extent of riverscape studies
(A) Monthly distribution of sampling effort for spatially continuous “riverscape” studies involving juvenile Pacific salmon and trout from 1988-2017 (χ^2=68.23, $p < 0.0001$, n=122, median=6); (B) seasonal distribution of sampling effort for riverscape studies (χ^2=52.885, $p < 0.0001$, n=122, median=25); (C) frequency of the number of months per calendar year (1-12) found in riverscape studies (χ^2=65.508, $p < 0.01$, n=38, median=2.6); (D) frequency of the number of seasons per calendar year (1-4) found in riverscape studies (χ^2=18, $p < 0.001$, n=38, median=23.68). The number of studies for each month or season was calculated using presence or absence of research during that time frame. Dashed horizontal lines are data median. Studies may occupy more than one month or season. Seasons were defined meteorologically, but as whole months. Summer is defined as the months June, July, and August; Autumn is defined as the months September, October, and November; Winter is defined as the months December, January, and February; Spring is defined as the months March, April, and May.

CHAPTER 3. ASYNCHRONOUS PREY RESOURCES CREATE A YEAR-ROUND ENERGY PORTFOLIO FOR JUVENILE SALMONIDS

Megan E. Brady and Jonathan B. Armstrong

Abstract

Juvenile salmonids (*Oncorhynchus* spp.) rearing in freshwater depend on a diverse portfolio of prey resources to support somatic growth, lipid storage, overwinter survival, and the parr-to-smolt transformation. While many studies have expanded our knowledge of juvenile salmonid trophic ecology, most of this effort has been focused on a narrow temporal scope that fails to capture variation in the importance of prey resources throughout the entirety of freshwater rearing. This study examined broad patterns in the contributions of aquatic, terrestrial, and marine trophic pathways to juvenile coho salmon (*O. kisutch*) and steelhead trout (*O. mykiss*) as well as specific sources of energy throughout the year in the South Fork Skokomish River and Vance Creek, Washington, USA. Prey resource availability and use by juvenile salmonids was evaluated by sampling invertebrates from benthic, drift, and terrestrial environments and then comparing those to juvenile coho and steelhead diets from corresponding monthly sampling events. The timing of peak and low productivity of each environmental source demonstrated asynchronous availability of prey resources. Juvenile salmonid diets exhibited temporal variation in quantity, composition, and selectivity. Aquatic resources supported fish during summer somatic growth, overwinter survival, and early spring prior to smoltification. Terrestrial input to fish diet was clearer at a monthly scale, contributing a large portion of fish diet in May during smoltification and October as fish switch from somatic growth to lipid storage in preparation for winter. Juvenile salmonids benefitted from interspecific variation in salmon spawning events

during autumn and early winter when lipid storage is essential before river flows increase, daylight decreases, temperatures drop, and food productivity declines. Despite the depressed state of salmon runs in this system, the largest diet rations of the entire year were observed in months where marine subsidies (e.g. eggs) contributed 61-96% of total biomass consumed by juvenile salmonids. We found that ephemeral subsidies were also responsible for the large ration sizes observed in May, with terrestrial rove beetles contributing 66% of coho diet biomass. Overall, our results indicate that a temporally diverse energy portfolio with asynchronous peaks in prey components supports juvenile salmonid foraging during each phase of freshwater rearing.

Introduction

Salmon conservation and recovery efforts have traditionally considered the four Hs: habitat, hatchery production, hydroelectric dams, and harvest (Naiman and Bilby 1998). However, more interest has recently been given to biotic interactions, including predation (Berejikian et al. 2016), competition (Thornton et al. 2017), and the trophic pathways that support juvenile rearing (Woo et al. 2019). There is increasing evidence that consideration of temporal and spatial food web dynamics is needed for more effective habitat restoration (Naiman et al. 2012). Indeed, in many freshwater systems, juvenile salmonid productivity may be more limited by food than physical stream characteristics (Bellmore et al. 2013; Weber et al. 2014). Further, while physical variables such as water temperature and velocity mediate energy costs and scope for growth, the energy budgets of fish are most sensitive to consumption rates (Bartell et al. 1986) and thus strongly influenced by food abundance. As salmon populations (*Oncorhynchus* spp.) continue to decline in much of their native range, examining the trophic resources that support juvenile salmon during key phases throughout the year is vital to conservation and recovery efforts.

The food available to stream dwelling fish derives from multiple trophic pathways (Allen 1951; Hynes 1970; Allan et al. 2003). Aquatic prey resources provide a significant source energy source for fish (Brett et al. 2018) and can come from both *in situ* productivity or subsidies flushed downstream from (often fishless) headwater streams (Wipfli and Gregovich 2002; Rosenfeld and Raeburn 2009). Diversity within *in situ* invertebrate production comes from the physical habitat preferences of invertebrates such as differences in invertebrate communities found in drift versus benthic environments (Johansen et al. 2010) or the benthic invertebrates found within pools versus those found in riffles (Brown and Brussock 1991). Several studies have shown that terrestrial invertebrates are also an important food source for stream fishes and may comprise 50-90% of total prey consumed by juvenile salmonids (Wipfli 1997; Nakano et al. 1999a; Kawaguchi and Nakano 2001; Dineen et al. 2007; Mason and MacDonald 1982; Nakano and Murakami 2001; Li et al. 2016). Terrestrial invertebrates are often more energy dense than aquatic invertebrates (Cummins and Wuycheck 1971) and can be a key prey subsidy to aquatic systems at times when aquatic productivity is at its lowest (Nakano et al. 1999b). Variation in terrestrial invertebrate subsidies to streams appears to be a function of seasonality (Nakano and Murakami 2001; Dineen et al. 2007) and the characteristics of riparian vegetation (Naiman and De'camps 1997; Mason and MacDonald 1982; Cloe and Garman 1996; Nakano et al. 1999b). Marine-derived nutrients comprise a third trophic pathway supporting fish. Marine subsidies vary in their type, e.g., kelp subsidies to estuaries versus anadromous fish migrations, and within each type there may be finer levels of variation. For example, rainbow trout were shown to exploit population-level variation in sockeye salmon subsidies to streams, thereby extending an ephemeral resource pulse (Ruff et al. 2011). Marine subsidies in the form of salmon eggs are 2-3 times more energy dense than benthic invertebrates and capable of fueling greater fish growth than benthic or terrestrial invertebrates despite their short period of availability (Armstrong et al. 2010; Scheurell et al. 2007; Moore et al. 2008; Bilby et al. 1998; Bentley et al. 2012). Juvenile salmon may exploit each of these resources at different points in time. A key challenge is understanding how this trophic diversity affects the potential for watersheds to rear salmon. Here, we consider how trophic diversity is patterned in time and how fish consumption integrates temporal diversity.

Most trophic pathways exhibit temporal variation in the foraging opportunity they present to fish. Some trophic pathways, such as marine subsidies from spawning anadromous fish, may occur as pulses that last a month or less at small spatial extents. In contrast, aquatic production may occur year-round but exhibit seasonal patterning. The effect of temporal variation on consumers depends on the level of asynchrony in variation. If component parts vary asynchronously, then the aggregate is more stable over time, a phenomenon known as the Portfolio Effect (Schindler et al. 2015). There is increasing interest in how asynchrony among trophic resources stabilizes consumer energy gains (Schindler et al. 2015; Armstrong et al. 2016; McMeans et al. 2016). Population diversity in the timing of salmon returns can extend the portfolio of resources available from a single species of salmon from weeks to months (Schindler et al 2010) or even longer when multiple species of salmon spawn at sequential or minimally overlapping dates. Similarly, variation in the emergence timing of aquatic insect species can extend the availability of resource subsidies with sequential adult phases (Uno and Pneh 2020). While some resource pulses come during the peak growing season for fish, other ephemeral resource pulses come at the tail ends of the growing season, thus extending growth opportunity and allowing fish to achieve greater body size before winter, aiding in overwinter survival (Bilby et al. 1998; Wipfli et al. 1998; Groot et al. 1995). Greater growth in freshwater has also been shown to have carry-over effects, positively correlating with increased marine survival (Thompson and Beauchamp 2014; Ward et al. 1989), particularly in years with poor ocean conditions (Bond et al. 2008; Holtby et al. 1990). While the full importance of ephemeral resource pulses to juvenile salmonid survival is not well-researched, the asynchrony observed in resource pulse timing likely helps to stabilize foraging opportunities.

Resource heterogeneity creates more stable foraging opportunities than dependence on any single prey item (Schindler et al. 2015; Deacy et al. 2017). If overwinter survival of juvenile salmonids is influenced by body size, as research suggests (Groot et al. 1995), then extending the growing season through asynchronous prey resources is important. Yet, we do not have a firm understanding of how asynchronous and ephemeral prey availability varies throughout juvenile salmonid freshwater residence. While a diverse portfolio of prey resources can mediate risk through variation in energy availability, it does not consider how predator needs change over time or how important diversity is at different energetic phases. For example, fish energy budgets vary seasonally (Cunjak et al. 1987; Post and Parkison 2001). The warmer temperatures of spring coupled with high food resource availability initially act as a catalyst for greater growth rates, but as temperatures continue to warm, metabolic costs rise as well with energy no longer going primarily toward growth but rather toward meeting high daily basal metabolic needs (Jones et al. 2002; Dockray et al. 1996). The energetic needs during the primary somatic growth phase (Limm and Marchetti 2009; Elliott 1982) that allows fish to grow large enough to eat large prey (Jaecks and Quinn 2014; Armstrong et al. 2010) or evade predators (Biro et al. 2005) is different from the energetic needs and metabolic activity that occurs during the parr-smolt transformation

(McCormick and Saunders 1987) and still different from the needs of fish during the building of fat stores for winter that aid in overwinter survival (Bull et al. 1996; Cleary et al. 2012; Berg and Bremset 1998). Likewise, the prey resources that support these unique phases of energetic needs are not homogenous.

While there is much interest in how trophic pathways or subsidies combine to support salmonids (Wipfli and Baxter 2010; Schindler et al. 2015; Bellmore et al. 2013), our understanding has been limited by a lack of comprehensive data. Many studies have provided insights into components of the full resource portfolio (Ruff et al. 2011; Scheurell et al. 2007) or the importance of allochthonous inputs (Cloe and Garman 1996; Wipfli 1997); however, virtually none of these encompass the full annual cycle (but see Nakano and Murakami 2001). During the last 30 years, 39-44% of all juvenile salmonid field research occurred during summer while only 10-15% of studies occurred during winter with 73% of studies spanning fewer than 4 months per calendar year (Brady et al. *In draft*). Possibly the most likely prey resources to be ignored by temporally narrow sampling are ephemeral sources only available to fish during a limited window of time.

Year-round research is needed to understand how the energy that fuels growth, accumulation of fat stores, physiological changes, and behavior varies over time. Here, we used the South Fork Skokomish River and Vance Creek in Washington, USA to examine year-round utilization of prey resources by juvenile steelhead trout (*O. mykiss*) and coho salmon (*O. kisutch*) combined with year-round availability of aquatic, terrestrial, and marine prey resources that contribute to a temporally variable energy portfolio. The purpose of our study was to answer the following questions: 1) how do prey composition and biomass vary across time within benthic, drift, and terrestrial sources, 2) how do juvenile steelhead and coho diets compare to the availability of prey across time, and 3) at what temporal and taxonomic resolutions are important prey items captured in samples?

Methods

Study System

The Hood Canal is an 80-km fjord that comprises one of the four sub-basins of Puget Sound, Washington, USA. Puget Sound steelhead (*O. mykiss*) have been listed as threatened under the Endangered Species Act (ESA) since 2007 and populations continue to decline despite greatly reduced fishing mortality associated with commercial, recreational, and tribal fisheries (Moore et al. 2010).

This study examined the South Fork Skokomish River (Figure 6), one of eight control and supplemented rivers in the larger Hood Canal steelhead Project (HCSP), and its largest tributary, Vance Creek. The HCSP is a 17-year study led by the National Oceanic and Atmospheric Administration (NOAA).

The South Fork Skokomish River is a 44.2 km long (37.0 km anadromy limit) river originating in the Olympic Mountains and flowing into the southwest side of Hood Canal. It is a rain-dominant stream with an elevation of 1646 m, mean annual water temperature of 8.1°C, and mean annual flow of 20.95 m3s-1 (Berejikian et al. 2013). Tidal influence extends up the mainstem Skokomish River to the confluence of the South Fork and North Fork (Canning et al. 1988). A rotary screw trap operated by NOAA is located at river mile 1.8, one mile upstream from the confluence of the South Fork Skokomish and Vance Creek.

Anadromous populations of steelhead and coho rear as juveniles in the study river. Chinook (*O. tshawytscha*) are present in low numbers in the South Fork Skokomish and are largely regarded as hatchery strays and not a viable population. The South Fork Skokomish historically supported pink salmon, spring Chinook, and early run summer chum; however, these populations have been extirpated (WDNR 1997).

Average annual winter steelhead spawner escapement between 1986 and 2014 to the Skokomish (South Fork, North Fork, tributaries, and mainstem combined) is 503 per year (PNPTC 2015). The majority (81.3%) of outmigrating steelhead in the South Fork Skokomish are age-2 smolts with an average length of 167.8 mm. Age-1 (FL=156.8mm) and age-3 (FL=185.3 mm) steelhead smolts represented a small portion of average annual outmigration, 2.2% and 16.2% respectively (Doctor-Shelby and Berejikian *In Draft*). Peak juvenile downstream migration is in late April and early May. South Fork Skokomish steelhead spawn in mid-March to mid-May with juvenile emergence in mid-July.

South Fork Skokomish coho are abundant and currently not listed under the ESA. They typically spawn in October-January, emerge in early March to late July, and outmigrate as age-1 smolts (WCC 2003), with peak outmigration occurring from mid-May to late-June (USFWS 2011). Peak spawning activity for coho is estimated at mid-December to early January (Weitkamp et al. 1995). Coho escapement is not as closely monitored as the other species as they are considered a healthy population, but typically ranges averages at least 2,000 spawning adults in the Skokomish Basin (WCC 2003). Vance Creek is a particularly important stream for coho productivity.

The Hood Canal has both ESA-listed “threatened” summer chum and non-listed fall chum. Peak live count of summer chum in the lower mainstem Skokomish River is estimated at 1600 fish in late August and September (SIT and WDFW 2017). Fall chum are abundant in the Hood Canal rivers as they don’t rely as heavily on freshwater as other species of do (Quinn

2005). The fish found spawning in the Skokomish are a mix of hatchery and natural origin fish. Annual fall chum escapement to the Skokomish River (includes South Fork, North Fork, mainstem, and tributaries) ranges between 926 and 1913 per year (HSRG 2004). Spawning typically occurs during November-January in the lower South Fork Skokomish River and Vance Creek (HSRG 2004) with juvenile emergence peaking in mid-February. The outmigrating chum fry average 42mm fork length (USFWS 2011).

A very small number of Chinook spawn in the South Fork Skokomish. Despite not having a sustainable population, any Chinook found in the Skokomish Rivers are considered part of the ESA-listed “threatened” Puget Sound Chinook. Annual average (1999-2016) natural origin escapement is calculated based on a combination of the South Fork Skokomish, North Fork Skokomish, and the mainstem Skokomish River and is estimated at 390 per year (SIT and WDFW 2017). Spawning typically occurs September-October with peak emergence in January-mid February (SIT and WDFW 2017).

Collection was done under Washington State Department of Fish and Wildlife Scientific Collection Permit, Endangered Species Act (ESA) Section 10(a)(1)(A) permits from NOAA and USFWS for pacific fish/invertebrate research, and Oregon State University Institutional Animal Care and Use Committee approved Animal Care and Use Proposal (IACUP).

Data Collection

We sampled fish diets and food availability every month to characterize temporal patterns. Specifically, we identified, counted, and measured all prey items in fish stomachs, and potential macroinvertebrate prey items in the stream drift, the benthos, and terrestrial fallout.

Invertebrate prey resources

On the first day that fish were sampled each month and in the same reaches, we collected environmental samples of available invertebrate prey resources from benthic, drift, and terrestrial sources.

Benthic. Benthic macroinvertebrates were collected with a Surber sampler. Five riffle substrate samples and five pool substrate samples (Johnson et al. 2013) were collected each month. A standard Surber sampler (D-frame net) with a 12in x 12 in area and 500 µm mesh size was used. The substrate was disturbed for 30 seconds at each collection site to a depth of one inch. Samples were collected working downstream to upstream to reduce impacts of substrate disturbance on subsequent samples. The samples were sieved to remove detritus and inorganic matter and then preserved in 70% ethanol.

Drift. To assess the availability of prey for juvenile salmonids in the water column during active foraging times (Baxter et al. 2005), three replicate drift nets were deployed across a riffle section of the river directly above a pool where juvenile fish have been sampled, lowered just above the stream bottom. Drift sampling occurred on the first day of fish sampling each month. The nets were deployed twice for 30 minutes (n=6 per month) between dawn and dusk (Wipfli and Gregovich 2002) to collect floating aquatic and terrestrial invertebrates at the same time as stomach content samples were obtained. Net contents were sieved (500 µm) and preserved with 70% ethanol.

Terrestrial. Fallout traps were deployed for 24 hours monthly to quantify the input of terrestrial invertebrates into the river system from specific terrestrial plant species. Traps to collect falling terrestrial invertebrates were placed on the stream bank, underneath six species of plants common in the riparian area: bigleaf maple, red alder, Sitka willow, vine maple, Bohemian knotweed, and Himalayan blackberry. Knotweed plants die back in the winter and, therefore, were not sampled during the months of December-May when the traps would only collect invertebrates from nearby vegetation of other species. Ten replicate traps were deployed for each of the plant species each month. Each trap was filled with approximately 1 liter of water and a small amount of dish detergent to break surface-water tension. Invertebrates were collected and preserved in 70% ethanol for later identification.

Environmental samples of invertebrates were counted and classified as terrestrial (e.g. ants, spiders), aquatic (e.g. mayfly nymphs, midge larva), or marine (e.g. salmon eggs) in origin. Invertebrates were identified to family or species where possible (Merritt et al. 2008) with life stage (larvae, pupae, adult) noted. Invertebrates were measured to the nearest millimeter to calculate dry mass based on published length-mass regressions (Sabo et al. 2002; Sample et al. 1993; Benke et al. 1999). Salmon eggs were dried and weighed to create a diameter-weight regression. Adult forms of invertebrates that emerged from aquatic larval stages were classified as aquatic.

Juvenile steelhead trout and coho salmon

A total of 229 natural-origin juvenile steelhead and 530 coho were sampled between August 2018 and December 2019. A portion of the fish sampled in April and May were collected using an 8-foot diameter rotary screw trap that is operated daily from April 1 to June 1 on the South Fork Skokomish River by NOAA and the Skokomish Indian Tribe. All other monthly fish were collected fish using either a stick (beach) seine or minnow traps baited with cured salmon eggs. Cured eggs were contained in perforated bags and inaccessible to fish for consumption. Summer fish collection occurred at dusk to capture peak daily stomach fullness (Beauchamp et al. 2007). Winter fish collection occurred at dawn, as fish are more active at night during the winter (Roni and Fayram 2000).

Snorkel observations were conducted immediately prior to seining, river flow permitting, to minimize impact to non-target species and simultaneously identify appropriate sites with target species present. Two people made multiple passes of the sample location using a hand-held 30-foot knotless nylon mesh seine to collect fish present. Up to 50 individuals each from steelhead and coho were sampled each month.

Fish were anesthetized with Tricaine methanesulfonate (MS-222) at a ratio of 5 ml:1 gallon of water and measured to the nearest mm by fork length (FL), followed by taking a caudal fin clip and performing gastric lavage. River conditions and fish presence dictated sample locations. Previous research has found that diet, weight, and length for coho salmon are not significantly different between the habitat types (pools, tributaries, riffles) in the Skokomish River, likely due to fish mobility (Wright 2010). Stomach contents were removed by gastric lavage, a non-lethal sampling method (Twomey and Giller 1990; Giles 1980) shown to remove 90-100% of fish stomach contents (Light et al. 1983; Meehan and Miller 1978; McCarthy et al. 2009) with very low mortality and handling effects (Hafs et al. 2011). Only salmonids >60mm FL were sampled due to size requirements for safe and effective gastric lavage. Diet contents were flushed onto a clean coffee filter, washed into whirlpaks, and preserved in 70% ethanol. Fish were placed in an aerated bucket, processed, and released after full recovery (generally within 15 minutes of collection) in a low-flow section of the stream with adequate in-stream cover. Preserved diet samples were counted and classified as terrestrial (e.g. ants, spiders), aquatic (e.g. mayfly nymphs, midge larva), or marine (e.g. salmon eggs) in origin. Invertebrates were identified to family or species where possible (Merritt et al. 2008) with life stage (larvae, pupae, adult) noted. Recently ingested, intact invertebrates were measured to the nearest millimeter to calculate dry mass based on published length-mass regressions (Sabo et al. 2002; Sample et al. 1993; Benke et al. 1999). Salmon eggs were dried and weighed to create a diameter-weight regression. Adult forms of invertebrates that emerged from aquatic larval stages were classified as aquatic.

Data Analysis

Invertebrate prey resources

Monthly and seasonal proportions and sums of mass were calculated for each of the prey items (by order and species) found in each of the environmental samples (benthic pool, benthic riffle, drift, and terrestrial).

Juvenile steelhead trout and coho salmon

Monthly and seasonal mean fork length and length frequencies were calculated for each fish species and graphed to track fish size at a cohort-scale over time. Fish mass was calculated using length-weight regressions (Roni 2000).

Monthly and seasonal diet proportions and sums of mass were calculated for each of the prey items found in fish gut contents by order and source (aquatic, terrestrial, marine). Fish rations were calculated as prey resource biomass (by order and source) then divided by fish biomass, grouped by month.

Feeding selectivity

To determine if fishes are exhibiting preference or avoidance of prey items, selectivity was calculated using Vanderploeg and Scavia's electivity index (Vanderploeg and Scavia 1979):

$$E_i = \frac{\left[W_i - \left(\frac{1}{n}\right)\right]}{W_i + \left(\frac{1}{n}\right)]} \text{ where } W_i = \frac{r_i/p_i}{\Sigma r_i/p_i}$$

r_i = proportion of taxon i in the diet

p_i = proportion of taxon i in the environment

n = number of kinds of food items

where E_i represents the relative proportion of a prey item in the diet compared to the proportion of a prey item found in the environment, with values 0 to -1 indicating avoidance and values 0 to +1 indicating preference or selection.

Results

Invertebrate prey resources

Benthic. Benthic invertebrate productivity in pools was highest in August (574.77 mg/m^2) (Fig. 7) with the largest contributing invertebrate orders consisting of Decapoda (30%), Ephemeroptera (27%), and Trichoptera (20%) (Fig. 8a). Benthic invertebrate productivity in pools was lowest in February (6.96 mg/m^2) (Fig. 7) with the largest contributing invertebrate orders consisting of Diptera (51%) and Plecoptera (35%) (Fig. 8a).

Benthic invertebrate productivity in riffles was highest in April (477.23 mg/m^2) (Fig. 7) with the largest contributing invertebrate orders consisting of Plecoptera (79%) and Trichoptera (14%) (Fig. 8b). Benthic invertebrate productivity in riffles was lowest in January (2.03 mg/m^2) (Fig. 7) with the largest contributing invertebrate orders consisting of Coleoptera (36%), Diptera (31%), and Plecoptera (28%) (Fig. 8b).

Autumn benthic biomass was comprised primarily of Plecoptera in pools and a mixture of Trichoptera and Plecoptera in riffles. Winter benthic biomass primarily consisted of Trichoptera in pools and Plecoptera in riffles. Spring benthic biomass for pools was similar to winter, but riffles more closely resembled the summer assemblage. Diptera were found in larger proportion in pools than riffles in summer, winter, and spring; however, in autumn, Diptera were more abundant in riffles (Fig. 8c-d)

Drift. Invertebrate productivity in the drift was highest in April (735.01 mg/30 minutes/270m^3) (Fig. 7) with the largest contributing invertebrate orders consisting of Trichoptera (68%) and Ephemeroptera (15%) (Fig. 9a). Invertebrate productivity in the drift was lowest in December (1.14 mg/30 minutes/270m^3) (Fig. 7) with the largest contributing invertebrate orders consisting of Plecoptera (42%) and Trichoptera (40%) (Fig. 9a). At a seasonal resolution, Trichoptera was a major component of drift in every season: 85% in summer, 80% in autumn, 38% in winter, and 62% in spring (Fig. 9c).

Drift samples consisted almost entirely of aquatic invertebrates; at no point in time was terrestrial input into the drift greater than aquatic contribution. Trichoptera were the largest contributors to drift invertebrate biomass during all seasons with the exception of winter, when a single salmon egg was found in the drift sample and the mass of this single egg outweighed aquatic invertebrate biomass.

Terrestrial. Invertebrate productivity among terrestrial vegetation in the riparian zone was highest in September (647.08 mg/97m^2) (Fig. 7) with the largest contributing invertebrate orders consisting of Hymenoptera (40%), Lepidoptera (32%), and Trichoptera (17%) (Fig. 10). Terrestrial invertebrate productivity was lowest in December (0.00%) (Fig. 7) when the weather was dominated by snow and ice and no invertebrate were collected (Fig. 10).

Terrestrial invertebrate samples showed large amounts of Hymenoptera in summer, Araneae in autumn, Plecoptera in winter (January in particular), and Coleoptera in late winter-spring.

Juvenile steelhead trout and coho salmon

Fish rations. The average weight of prey resources ingested per weight of fish varied widely from month to month. Juvenile coho average rations were highest in September (0.211 mg prey/g of fish) followed by December (0.163 mg prey/g of fish) (Fig. 11a). Coho rations were lowest in February (0.0.019 mg prey/g of fish) and January (0.02 mg prey/g of fish). Juvenile steelhead average rations were highest in September (0.514 mg prey/g of fish) and November (0.348 mg prey/g of fish). Steelhead rations were lowest in March (0.002 mg prey/g of fish) and July (0.01 mg prey/g of fish (Fig. 11b); no prey items were found in the stomach contents of the sole steelhead collected during the month of January. The average weight of marine prey items in fish rations first peaked in September for both coho (0.146 mg/g of fish) and steelhead (0.365 mg/g fish) and then again in December for coho (0.133 mg/g of fish) and November for steelhead (0.335 mg/g of fish) (Fig. 11c-d). Terrestrial rations were greatest in May and June for coho (0.061 mg/g of fish and 0.031 mg/g of fish, respectively) and September and May for steelhead (0.073 mg/g of fish and 0.04 mg/g of fish, respectively) (Fig. 11c-d). Aquatic rations were greatest in September (0.076 mg/g of fish) and April (0.057 mg/g of fish) for steelhead and August (0.087 mg/g of fish and June (0.079mg/g of fish) for coho (Fig. 11c-d).

Trophic pathways. Broad sources of energy (marine, terrestrial, aquatic) varied in coho diet proportion by month (Fig. 12b) and season (Fig. 13b). Marine contribution to total coho diet showed up in September (61%) and December (89%), corresponding with spawning times for

Chinook salmon (September) and chum or coho salmon (December) (Fig. 12b). At a seasonal resolution, marine resources were important to coho diet in autumn (49%) and winter (76%) (Fig. 13b). Terrestrial contribution to total coho diet peaked in May (78%) and October (56%) and was lowest in January, February, and July (all 0%). At a seasonal resolution, terrestrial resources were important to coho diet in summer (19%) and spring (21%) (Fig. 13b). Aquatic contribution to total coho diet was high all months of the year, except for September (32%) and December (7%) when salmon eggs were available and in May (22%) when terrestrial invertebrates dominated the diet (Fig. 12b). The months of January, February, and July were supported solely by aquatic prey resources (100%). At a seasonal resolution, aquatic resources were important to coho diet in all seasons, but to varying degrees: summer (81%), autumn (39%), winter (20%), and spring (79%) (Fig. 13b). Similar patterns in broad energy contribution (marine, terrestrial, aquatic) were seen in steelhead diet proportion by month. Marine contribution to total steelhead diet showed up in September (69%) and November (96%), corresponding with spawning times for Chinook salmon (September and chum or coho salmon (November) (Fig. 12e). At a seasonal resolution, marine resources were important to steelhead diet in autumn (68%) (Fig. 13e). Terrestrial contribution to total steelhead diet peaked in May (75%) and was lowest in November, December, January, February, March, and June (all 0%). At a seasonal resolution, terrestrial resources were important to steelhead diet in spring (56%), summer (19%), and autumn (16%) (Fig. 13e). Aquatic contribution to total steelhead diet was high all months of the year, except for September (15%) and November (4%) when salmon eggs were available and May (25%) and October (44%) when terrestrial invertebrates dominated the diet (Fig. 12e). At a seasonal resolution, aquatic resources were important to steelhead diet in all seasons, but to varying degrees different from that seen in coho: summer (81%), autumn (15%), winter (100%), and spring (44%) (Fig. 13e).

Diet composition. Monthly and seasonal diet contents of juvenile steelhead and coho demonstrated the importance of a variety of invertebrate prey resources at different points in the year. No single prey resource uniformly dominated diet biomass throughout the year at a monthly or seasonal resolution for either coho (Fig. 12a, Fig. 13a) or steelhead (Fig. 12d, Fig. 13d). The annual portfolio contributing to coho diet consisted of 13 orders of prey resources and 42 unique prey resources. The annual portfolio contributing to steelhead diet consisted of 12 orders of prey resources and 43 unique prey resources. For coho, Ephemeroptera (41%) and Hymenoptera (16%) dominated summer diets, salmon eggs (49%) and Diptera (21% dominated autumn diets, salmon eggs (76%) dominated winter diets, and Plecoptera (43%) combined with Coleoptera (27%) dominated spring diets (Fig. 13a). For steelhead, Ephemeroptera (53%) and Hymenoptera (19%) dominated summer diets, salmon eggs (68%) dominated autumn diets, Trichoptera (95%) dominated winter diets, and Coleoptera (32%) combined with Hymenoptera (28%) dominated spring diets (Fig. 13d).

Dominant prey resources. The top two specific prey resources that contributed to fish diet also varied by month. Some prey items only showed up as a top contributor to coho diet during one month of the year (Table 1) (e.g. rove beetles). Other prey resources showed up as a top contributor across multiple months for coho (e.g. predaceous diving beetles). Steelhead diets also revealed varied prey resources that contributed the bulk of their diet each month (Table 2). Mayfly nymphs (spiny crawler, small minnow, and flathead) were the largest contributors to steelhead diets in June, July, and August; however, ephemeral prey resources became the dominant prey items when available (e.g. salmon eggs).

Fish size. The size frequency distribution (Fig. 12c) and mean size of coho sampled showed a growth progression starting in June at 65.96 mm fork length (FL) (SD=5.04, n=50) and finishing the following May at 97.45 mm FL (SD=7.55, n=20). The size frequency distribution (Fig. 12f) and mean size of steelhead sampled showed two age classes of juveniles residing in the river system. Age 0 fish (<100 mm FL) showed a growth progression starting in August at 71.7 mm fork length (FL) (SD=6.82, n=33) and finishing the following May at 94 mm FL (SD=5.66, n=2). The mean size of fish larger than 100 mm FL fluctuated throughout the year with sizes averaging between 122 mm FL and 145 mm FL throughout the year.

Feeding selectivity

The prey items that provided the largest proportion of fish diets were often positively selected for from the environment during that timeframe for both juvenile coho (Table 1) and steelhead (Table 2).

Benthic. Coho benthic selectivity showed clear patterns of preference and avoidance of invertebrate prey items available in the benthic environment (Table 3). Coho avoided flathead mayfly nymphs during all months (E= -0.63 to -1.00) except for August when river flow was at an annual low (E=0.79). Rolled wing stonefly nymphs were preferred by coho in all months except for July (E= -1) and October (E= -0.17). Some prey items were available most months of the year but avoided by coho during all months: common stonefly nymphs, crane fly larva, northern case maker caddis nymphs, and spiny crawler mayfly nymphs. Small minnow mayfly nymphs were preferred by coho in June, August, October, December, February, March, April but avoided in July, September, November, and May. Likewise, steelhead displayed distinct patterns of preference and avoidance of benthically available invertebrate prey items (Table 4). Steelhead avoided northern case maker caddis nymphs, riffle beetle larva, crane fly larva, and common stonefly nymphs year-round. Spiny crawler mayfly nymphs were preferred by steelhead in June but avoided during all other months. Stripetail stonefly nymphs were preferred by steelhead in April but avoided all other months. Steelhead preferred flathead mayfly nymphs in July and August but avoided them the rest of the year. Steelhead preferred small minnow mayfly nymphs July through October but avoided these prey items the rest of the year.

Drift. Coho drift selectivity showed patterns of preference and avoidance of invertebrate prey items available in the benthic environment (Table 5). Coho avoided northern case maker caddis nymphs year-round. Rolled wing stonefly nymphs were preferred by coho most of the year except for June (E= -0.24) and July (E= -1.00). Small minnow mayfly nymphs were preferred by coho in November through March but avoided the rest of the year. Coho preferred non-biting midge larva at all points in time that this prey resource occurred in the drift. Adult mayflies were preferred by coho in April and May. steelhead displayed distinct patterns of preference and avoidance of invertebrate prey items available in the drift (Table 6). Steelhead avoided northern case maker caddis nymphs and riffle beetle larva year-round. Steelhead preferred flathead mayfly nymphs in July but avoided them the rest of the year. Steelhead preferred non-biting midge larva July through October, rolled wing stonefly nymphs June through September, and small minnow mayfly nymphs June through July, but avoided these prey items the rest of the year.

Terrestrial. Coho terrestrial selectivity showed clear patterns of preference and avoidance of invertebrate prey items available in the terrestrial environment (Table 7). In general, coho avoided most terrestrially available invertebrates with two exceptions: adult rolled wing stoneflies were preferred October through January and adult non-biting midges were preferred November through January. While these two invertebrates were considered aquatic due to their larval origin, they were found in the terrestrial environment in their adult stage. Steelhead displayed distinct patterns of preference and avoidance of invertebrate prey items available in the terrestrial environment (Table 8). steelhead preferred ants during May, July, and August and preferred flying ants in September and October. Adult rolled wing stoneflies were preferred by steelhead in October. Caterpillars, adult crane flies, adult dance flies, leaf hoppers, spiders, and wasps were avoided year-round by steelhead. Ground beetles were preferred by steelhead in May and October but avoided all other months of the year.

Discussion

This study quantified the portfolio of prey resources available to juvenile salmonids throughout the annual cycle, and how fish integrated this trophic diversity through their foraging behavior. Our results suggest that stream-rearing juvenile steelhead trout and coho salmon exploit complementary prey resources throughout the year, showing temporally distinct preference and avoidance of stable and ephemeral prey items. Indeed, our data revealed greater complexity in the seasonal dynamics of prey resources than previously documented. For example, instead of a single temporal peak of terrestrial inputs, taxon diversity drove multiple distinct peaks of terrestrial inputs to fish diets. Moreover, contrary to predictions of functional extinction of salmon at low abundances, we found that marine subsidies from ESA-listed populations generated the highest ration size of the annual cycle for both steelhead and coho.

Asynchronous prey resource portfolio

Sampling prey abundances through the annual cycle revealed how different prey resources stabilize the aggregate portfolio of prey resources available in the environment. While there are large bodies of work on how physical aspects of rivers vary in space (Vannote et al. 1980; Tockner et al. 2000) and time (Poff et al. 1997), our understanding of heterogeneity in biotic aspects, such as food webs, is comparatively lacking (Naiman et al. 2012). We found evidence of a portfolio effect in the biomass of invertebrates sampled across time from benthic, drift, and terrestrial environmental samples. This derived from strong asynchrony in peaks in the biomass produced in each type of environment. We found that prey asynchrony was fractal, in the sense that it was similarly expressed at multiple levels of analysis. For example, at higher resolution, focusing on each environmental source of prey as the aggregate portfolio, we observed similar asynchrony. However, the invertebrate taxa within each component stock exhibited variance-dampening (Figge 2004) where the temporal variation prolonged broad resource pulses, thus minimizing periods of low prey abundance in the environment. For example, while there was some synchrony observed as invertebrate abundances declined during autumn and winter, the four sources reached their annual low during different months, thus off-setting periods of prey scarcity for consumers.

Timing of environmental availability of prey resources

Phenological shifts in the structure and size of the prey resource portfolio coincided with shifts in environmental phenology (e.g. flow, temperature) and shifts in fish life-history phenology. Benthic invertebrate biomass in riffles peaked in April and May, coinciding with higher flows from spring snowmelt and juvenile salmon outmigration to saltwater. Benthic invertebrate biomass in pools peaked in August, coinciding with the potential stressors of high temperature (and thus elevated metabolic costs), low drift biomass, and post-emergence growth of young-of-year salmonids. Drift invertebrate biomass peaked in April, coinciding with spring snowmelt, low invertebrate biomass available in pools, and juvenile salmon outmigration. Terrestrial invertebrate biomass peaked in September, coinciding with low flow, low drift biomass, low benthic pool biomass, declining benthic riffle biomass, and the timeframe when juvenile salmonids likely began storing lipids in preparation for overwinter survival (Berg and Bremset 1998). Sampling prey resources in the environment revealed asynchronous dynamics of prey abundance, but abundance may correlate poorly with patterns of predator consumption if many prey items are invulnerable (Kauffman et al. 2007) or if predators are highly selective (Stephens and Krebs 1986). Indeed, we found that the composition of prey resources in fish stomachs was often dissimilar to that in the environment, demonstrating that data on foraging ecology is needed to understand the functional significance of prey resource portfolios.

Fish preference and avoidance of prey resources

Fish diets exhibited temporally variable levels of selectivity and avoidance of specific invertebrate prey resources. For example, while flathead mayfly nymphs provided the greatest source of mass to steelhead diets in August and were positively selected for during that month (E= 0.81 in benthic samples, not found in drift samples), they were avoided almost every other month of the year (E= -1.00) except for July when they were also positively selected for (E= 0.37). As August and September are generally the points of lowest flow in Washington rivers, we found that the availability of drifting prey items is often also at its lowest during this time while benthic invertebrate production is high (Fig. 7). While aquatic resources may have been available and preferred during summer and winter, ephemeral terrestrial and marine subsidies that offer higher energy density (Cummins and Wuycheck 1971; Hendry and Berg 1999) and were preferred when available. For example, while small quantities of rove beetles were seen in multiple months, the largest pulse was observed in May when they were positively selected for by coho (E= 0.85 in terrestrial samples) and contributed 66% of coho diet. Rove beetles were largely avoided during the rest of the year (E= -1.00 to -0.71) except in November when they were again preferred (E= 0.42) but did not provide a substantial contribution to diet biomass. Preference of terrestrial invertebrates was not surprising due to two main factors: terrestrial invertebrates tend to be more active in daytime than aquatic invertebrates and their larger size makes them more visible in the drift and therefore more susceptible to fish predation (Nakano et al. 1999a; Edwards and Huryn 1996). However, diet samples from juvenile salmonids may differ in the proportion of aquatic and terrestrial invertebrates based on whether the fish defend foraging stations by hierarchy or float freely (Nielsen 1992). Like terrestrial invertebrates, salmon eggs were highly visible, preferred prey resources that provided the bulk of fish diet during their short-lived availability. Some ephemeral prey items, like salmon eggs, occurred in fish diet samples but did not occur in concurrent environmental samples. This was possibly due to the timing of fish feeding or a high level of selectivity where these prey items were removed from the drift so quickly that environmental samples failed to capture their true abundance. While environmental factors such as high flows certainly affect the ability of fish to forage, these data support a pattern of preferential feeding year-round with top contributing diet items virtually always being positively selected for against their relative availability in the environment.

Subsidies to fish diets

External subsidies were largely exploited by juvenile steelhead and coho during transitional periods (e.g. spring smoltification, autumn shift from somatic growth to lipid storage) while *in situ* prey resources were a major source of energy during periods with extreme metabolic differences (e.g. summer growth and winter survival). Increased rations were observed in fish in late spring-early summer and again in autumn, corresponding with ephemeral resource pulses of terrestrial and marine subsidies, respectively. However, the autumn pulse of marine subsidies was considerably larger than the spring pulse of terrestrial subsidies: steelhead rations in September were 2 orders of magnitude greater than the mass of March rations (the lowest annual rations observed) while rations in May were only 1 order of magnitude greater than the mass of March rations. Moore et al. (2007) argued that the role of salmon within freshwater ecosystems could become functionally extinct at low spawning densities because superimposition of redds is required to release large quantities of eggs into the stream drift where they would be available to consumers. This may be particularly true for species that are less competitive at preying on eggs (Bentley et al. 2012). While juvenile coho salmon are known to rely heavily on eggs where salmon are still superabundant (Rinella et al. 2012), they are less benthically-oriented than trout species (Bisson et al. 1988) and, therefore, it is likely they are less effective at exploiting eggs that are not readily available in the drift. Thus, we did not expect marine subsidies to provide substantial foraging in an area where salmon runs are severely depressed. However, we found that the pulse of eggs in September that provided the greatest ration of the year for both steelhead and coho came from a small spawning population of ESA-listed Chinook salmon. Two possible explanations are that 1) juvenile fish in this system don’t require redd superimposition to access substantial quantities of eggs or 2) even at low spawner densities, adult salmon are patchily distributed (Einum and Nislow 2005) and superimpose redds.

Marine resource contribution to the year-round energy portfolio

Diverging patterns in fish diet at seasonal and monthly resolutions emphasized the importance of temporally continuous sampling. At a seasonal resolution, marine contributions to coho diet appear to occur twice (autumn and winter) while contributions to steelhead diet appear to only occur once (autumn). However, at a monthly resolution, we found that each focal species benefitted from two pulses of egg subsidies, with the timing of the second pulse differing. At a monthly resolution, marine resources were most abundant in September and December for coho and September and November for steelhead. This corresponds with Chinook salmon spawning in September and coho and chum spawning in November through December. The earlier onset of chum/coho eggs in steelhead diets may be because steelhead are better adapted to holding in riffles where salmon spawn (Bisson et al. 1988). Phenological diversity among salmon taxa has been shown to benefit consumers by prolonging pulses of eggs. For stream-dwelling fishes this has been shown in rainbow trout that move among tributaries to exploit intraspecific variation in sockeye salmon spawning (Ruff et al. 2011). We found that coho and steelhead juveniles benefitted from species-level variation in spawn-timing, which allowed them to consume eggs for a longer portion of autumn into early winter. This inter-specific level diversity has been shown to also correlate with higher levels of salmon consumption in black bears (Service et al. 2019). While age-0 salmonids in northern populations are often unable to exploit egg subsidies because they have a shorter (and more thermally constrained) period over which to grow large enough to swallow eggs, we found that fish in this system were able to consume eggs during their first year. Diet samples from coho as small as 78mm fork length showing eggs from both pulses of spawning. Armstrong et al. (2010) found that fish as small as 43mm could consume soft fresh eggs but needed to be at least 67mm to consume water hardened eggs. This suggests that the coho salmon in this study were also feeding on water-hardened eggs, supporting the notion that the eggs were derived from redd superimposition or scouring during high flows, rather than spillage during spawning (which would provide fresh eggs).

Terrestrial resource contribution to the year-round energy portfolio

Terrestrial subsidies also revealed different patterns between seasonal and monthly resolutions. Based on other studies such as Nakano and Murakami (2001), we predicted that terrestrial invertebrates would provide a unimodal peak of energy during summer. What we found was a more complex pattern. At a seasonal resolution, terrestrial invertebrates did not appear to be a major source of energy for coho, comprising 3-21% of seasonal diet biomass. However, at a monthly resolution, the component taxa within the aggregate terrestrial subsidy produced multiple peaks of substantial energy contribution. For example, 78% of coho diet came from terrestrial invertebrates in May, 39% in October, and 31% in June. The peak in May terrestrial invertebrate biomass in coho diet was predominantly from ephemerally available rove beetles. The June terrestrial biomass peak for coho was driven by ants and October by spiders. Steelhead, on the other hand, revealed terrestrial invertebrates as the dominant energy source at both seasonal and monthly resolutions. In spring, steelhead ate terrestrial invertebrates at a rate of 1.27 times the mass of aquatic invertebrates. At a monthly resolution, peaks in May and October terrestrial invertebrate biomass in steelhead diet were both predominantly from ground beetles. Thus, we found that the contribution of terrestrial invertebrates was not as simple as a seasonal pulse, but instead reflected monthly pulses from different taxa that were differentially consumed by our two focal species. Baxter et al. (2005) suggested that low contribution of terrestrial prey may limit fish growth; our results suggest that phonological diversity in terrestrial inputs is likely important as well.

Aquatic resource contribution to the year-round energy portfolio

Aquatic invertebrates provided a stable prey resource year-round for both steelhead and coho. Aquatic invertebrates were particularly important in winter when prey consumption can slow the depletion of lipid stores. At a seasonal resolution, the highest proportions of aquatic invertebrates were found in diets in summer and spring for coho and summer and winter for steelhead. However, the importance of aquatic invertebrates at a monthly resolution revealed almost year-round dominance: over 50% of diet biomass consisted of aquatic resources in 9 out of 12 months for coho and 7 out of 11 months for steelhead (sample size from one month was low and consisted of empty stomachs). Additionally, the prey items that appeared repeatedly (e.g. rolled wing stonefly nymphs, adult predaceous diving beetles, small minnow mayfly nymphs) in fish diets present the possibility of a baseline of stable *in situ* food resources available throughout a large portion of the year. However, ephemeral prey resources (e.g. salmon eggs, rove beetles, ants, pupa stage of non-biting midges) were generally highly preferred when available and provided the bulk of diet mass during those times, even when stable aquatic invertebrates were more abundant. Therefore, the contributions of marine, terrestrial, and aquatic prey resources complement each other with aquatic resources providing a relatively consistent level of *in situ* energy between the pulses of marine and terrestrial subsidies. Resources with low relative abundance may still be functionally critical when their phenology is unique within the resource portfolio (Armstrong et al. 2020).

Linking trophic resources and phases of juvenile salmonid freshwater rearing

By overlapping seasonal fish foraging with the physiological processes that fish experience as they complete the full annual cycle of freshwater rearing, several patterns emerged. How fish allocate energy for competing demands (e.g. somatic growth and lipid storage) can drastically impact juvenile fish survival (Post and Parkinson 2001). Fish may allocate energy toward somatic growth until a size threshold is reached, after which energy is allocated toward lipid storage (Biro et al. 2005). Our results suggested that the prey resources that contributed substantially to juvenile coho and steelhead diets shifted at each phase of rearing. For example, in the summer when environmental conditions (e.g. physiologically optimal temperatures, long daylight hours, low stream flow) were likely more favorable for foraging and growth, the most important prey items for coho and steelhead were aquatically-derived, with Ephemeroptera providing the bulk of diet mass, specifically flathead and small minnow mayfly nymphs. In autumn, when energy was likely allocated towards lipid storage (Biro et al. 2005; Berg and Bremset 1998), marine-derived nutrients were most important for coho and steelhead, with salmon eggs providing the bulk of diet mass. In winter, when depletion of fat stores could be offset by prey consumption, aquatic invertebrates were most important for steelhead, particularly Trichoptera. Consumption of eggs from later runs of salmon spawning provided coho with most of their winter foraging biomass. Then in spring, when fish would be undergoing stressful physiological changes as part of the parr-smolt transformation, or “smoltification” process, readies them to migrate to saltwater, terrestrial invertebrates became most important for steelhead, particularly Coleoptera (i.e. ground beetles) and Hymenoptera (i.e. bees, ants), while aquatic invertebrates and terrestrial invertebrates were important for coho with Plecoptera (i.e.stripetail stonefly nymphs and rolled wing stonefly nymphs) and Coleoptera (i.e.

rove beetles) providing the bulk of diet mass. Growth of stream-rearing salmonids is often food-limited (Quinn 2005). Decreased availability of prey resources (Boss and Richardson 2002; Wipfli and Baxter 2010) and unfavorable temperature (Brett and Groves 1979; Elliott 1982) can result in reduced growth. Furthermore, the interaction between food and temperature can impact fish growth. Lower levels of food can reduce the optimum temperature of water for juvenile salmonid growth, exacerbating the stress of warming (Brett et al. 1982). The complementary prey resources that support fish during different phases of their life cycle during freshwater rearing (e.g. summer somatic growth, autumn lipid storage, over-wintering, smoltification) may provide additional data that could be incorporated into life-cycle modeling and restoration plans. As temperatures rise in freshwater systems during summer, knowing the specific resources that support fish at that time could be particularly useful for guiding restoration. By considering the links between fish foraging and intrinsic physiological processes, habitat restoration efforts could be strategically targeted to support fish at different points in their development (Pikitch et al. 2004).

Considerations

While our data are temporally continuous on a monthly scale and represent several days of sampling during each month, they are not temporally continuous on a daily scale as year-round daily sampling was not feasible. Therefore, we acknowledge that it is possible that very short-lived ephemeral prey pulses were not fully accounted for in the diet or environmental data. Our diet data were paired with stable isotope samples to provide a broader view of trophic pathways; however, these samples were not processed in time for inclusion in this thesis.

Conclusion

We found that juvenile salmon foraging behavior integrated a portfolio of prey resources and that temporal variation in these resources overlapped with the phenology of key rearing phases. At a seasonal resolution, patterns in prey resource dominance in our focal system were stronger, but also failed to capture the full impact of ephemeral prey resources. We found three key pulses of ephemeral prey resources that dominated fish diets at critical times of development: terrestrial invertebrates in May during the stressful smoltification process, Chinook salmon eggs in September at the nexus of somatic growth and lipid storage, and chum and coho salmon eggs in November/December at the onset of winter. Marine-derived nutrients in Pacific Northwest rivers are estimated to be only 6-7% of their historic values due to the collapse anadromous Pacific salmon (Gresh et al. 2000). While the ESA-listed population of spawning adult Chinook salmon in the Skokomish river is very small, during their September spawning run, eggs were found to be a significant portion of both coho and steelhead diet, supporting the largest prey ration sizes per fish found in the year. As winter mortality is possibly constraining to freshwater rearing of salmonids, the increased ration size observed in autumn due to multiple pulses of salmon eggs could offer greater understanding of how fish allocate energy in preparation for overwintering and thereby potentially increase over-winter survival (Hurst and Conover 2003). The aggregate energy portfolio supporting juvenile salmonids throughout freshwater residence exhibited monthly and seasonal variation with year-round foraging opportunities maximized by asynchronous pulses from individual prey taxa. The timing of ephemeral energy resources often coincided with periods of stress as fish underwent physiological changes. The synergy of ephemeral and stable prey resources supporting juvenile coho salmon and steelhead trout throughout the year may have important implications for fish fitness, survival, and conservation efforts.

References

Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60:309-320.

Allen, K. R. 1951. The Horokiwi stream: a study of a trout population. Bullet of New Zealand Department of Fishery 10:1-231.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445-1454.

Armstrong, J. B., D. E. Schindler, C. J. Cunningham, W. Deacy, and P. Walsh. 2020. Watershed complexity increases the capacity for salmon-wildlife interactions in coastal ecosystems. Conservation Letters 13(2):e12689.

Armstrong, J. B., G. T. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099-1122.

Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences 43(1):160-168.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Beauchamp, D. A., D. H. Wahl, and B. M. Johnson. 2007. Predator-Prey Interactions. Pages 765-842 in C. S. Guy and M. L. Brown, editors. 2007. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23(1):189-207.

Benke, A. C., A. D. Huryn, L. A. Smock, and B. J. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):1-17.

Berejikian, B. A., L. A. Campbell, and M. E. Moore. 2013. Large scale freshwater habitat features influence the degree of anadromy in eight Hood Canal *Oncorhynchus mykiss* populations. Canadian Journal of Fisheries and Aquatic Sciences 70:756-765.

Berejikian, B. A., M. E. Moore, and S. J. Jeffries. 2016. Predator-prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. Marine Ecology Progress Series 543:21-35.

Berg, O. K., and G. Bremset. 1998. Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout. Journal of Fish Biology 52(6):1272-1288.

Bilby, R. E., B. R. Franse, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 55:1909-1918.

Biro, P. A., J. R. Post, and M. V. Abrahams. 2005. Ontogeny of energy allocation reveals selective pressure promoting risk-taking behavior in young fish cohorts. Proceedings Biological Sciences 272(1571):1443-1448.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262-273.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242-2252.

Boss, S. M., and J. S. Richardson. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1044-1053.

Brady, M. E., J. B. Armstrong, and A. Chione. In draft. Beyond summer: review of the temporal aspects of juvenile salmon and riverscape studies reveals the need for year-round research.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pp 279-352 in Fish Physiology, vol 8. W.S. Hoar, D.J. Randall, and J.R. Brett, eds. New York: Academic Press.

Brett, J. R., W. C. Clarke, and J. E. Shelburn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile Chinook salmon *Oncorhynchus tshawytscha*. Canadian Technical Report of Fisheries and Aquatic Sciences No 1127.

Brett, M. T., G. W. Holtgrieve, and D. E. Schindler. 2018. An assessment of assumptions and uncertainty in deuterium-based estimates of terrestrial subsidies to aquatic consumers. Ecology 99(5):1073-1088.

Brown, A. V., and P. P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. Hydrobiologia 220:99-108.

Bull, C. D., N. B. Metcalfe, and M. Mangel. 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. Proc. R. Soc. Lond. B 263:13-18.

Cleary, J. S., M. J. Bradford, and D. M. Janz. 2012. Seasonal and spatial variation in lipid and triacylglycerol levels in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from the Bridge River, British Columbia. Limnologica 42(2):144-150.

Cloe, W. W., and G. C. Garman. 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36:106-114.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric Equivalents for Investigations in Ecological Energetics, SIL Communications, 1953-1996, 18(1):1-158.

Cunjak, R. A., A. Curry, and G. Power. 1987. Seasonal energy budget of brook trout in streams: implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116(6):817-828.

Deacy, W. W., J. B. Armstrong, W. B. Leacock, C. T. Robbins, D. D. Gustine, E. J. Ward, J. A. Erlenbach, and J. A. Stanford. 2017. Resource synchronization disrupts predation. Proceedings of the National Academy of Sciences 114(39):10432-10437.

Dineen, G., S. S. C. Harrison, and P. S. Giller. 2007. Seasonal analysis of aquatic and terrestrial invertebrate supply to streams with grassland and deciduous riparian vegetation. Biology and Environment: Proceedings of the Royal Irish Academy 107B(3):167-182.

Dockray, J. J., S. D. Reid, and C. M. Wood. 1996. Effects of elevated summer temperatures and reduced pH on metabolism and growth of juvenile rainbow trout (*Oncorhynchus mykiss*) on unlimited ration. Canadian Journal of Fisheries and Aquatic Sciences 53:2752-2763.

Doctor-Shelby, K., and B. Berejikian. In Draft. Trophic dynamics and temperature interact to determine growth and age-at-smoltification in Hood Canal steelhead, *Oncorhynchus mykiss.*

Edwards, E. D., and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. Hydrobiologia 337:151-159.

Einum, S., and K. H. Nislow. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143:203-210.

Elliott, J. M. 1982. The effects of temperature and ration size on the growth and energetics of salmonids in captivity. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry 73(1):81-91.

Figge, F. 2004. Bio-folio: applying portfolio theory to biodiversity. Biodiversity and Conservation 13:827-849.

Giles, N. 1980. A stomach sampler for use on live fish. Journal of Fish Biology 16:253-261.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in freshwater systems of the Pacific Northwest. Fisheries 25(1):15-21.

Groot, C., L. Margolis, and W. C. Clarke, editors. 1995. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Hafs, A. W., J. M. Niles, and K. J. Hartman. 2011. Efficiency of gastric lavage on age-0 brook trout and the influence on growth and survival. North American Journal of Fisheries Management 31:530–534.

Hendry, A. P. and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology 77:1663-1675.

Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181-2194.

Hatchery Scientific Review Group (HSRG). March 2004. Hatchery Reform Recommendations for the Puget Sound and Coastal Washington Hatchery Reform Project: Hood Canal. 62 p. Long Live the Kings, 1305 Fourth Avenue, Suite 810, Seattle, WA 98101 (available from www.hatcheryreform.org)

Hurst, T. P., and D. O. Conover. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84:3360-3369.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, 555 pp.

Jaecks, T., and T. P. Quinn. 2014. Ontogenetic shift to dependence on salmon-derived nutrients in Dolly Varden char from the Iliamna River, Alaska. Environmental Biology of Fishes 97:1323-1333.

Johansen, M., E. B. Thorstad, A. H. Rikardsen, J. I. Koksvik, O. Ugedal, A. J. Jensen, L. Saksgård, and T. F. Næsje. 2010. Prey availability and juvenile Atlantic salmon feeding during winter in a regulated subarctic river subject to loss of ice cover. Hydrobiologia 644:217-229.

Johnson, J. H., J. E. McKenna, and K. A. Douglass. 2013. Movement and feeding ecology of recently emerged steelhead in Lake Ontario tributaries. Journal of Applied Ichthyology 29: 221-225.

Jones, W., W. S. C. Gurney, D. C. Speirs, P. J. Bacon, and A. F. Youngson. 2002. Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. Journal of Animal Ecology 71:916-924.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters 10:690-700.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46(3):303-316.

Li, J. L., W. J. Gerth, R. P. Van Driesche, D. S. Bateman, and A. T. Herlihy. 2016. Seasonal and spatial fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 73:1642-1649.

Light, R. W., P. H. Alder, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81–85.

Limm, M. P., and M. P. Marchetti. 2009. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Environmental Biology of Fishes 85:141-151.

Mason, C. F., and S. M. MacDonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology 12:305-311.

McCarthy, S. G., J. J. Duda, J. M. Emlen, G. R. Hodgson, and D. A. Beauchamp. 2009. Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River watershed, California. Transactions of the American Fisheries Society 138:506-521.

McCormick, S. D., and R. L. Saunders. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Society Symposium 1:211-229.

McMeans, B. C., K. S. McCann, T. D. Tunney, A. T. Fisk, A. M. Muir, N. Lester, B. Shuter, and N. Rooney. 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecological Monographs 86(1):4-19.

Meehan, W. R., and R. A. Miller. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. Journal of the Fisheries Research Board of Canada 35:1359-1363.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America, 4th edn. Kendall Hunt, Dubuque, IA.

Moore, J. W., D. E. Schindler, and C. P. Ruff. 2008. Habitat saturation drives thresholds in stream subsidies. Ecology 89(2):306-312.

Naiman R. J., and R. E. Bilby, eds. 1998. River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. New York: Springer-Verlag.

Naiman, R. J., and H. De'camps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences 109(52):21201-21207.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. PNAS 98(1):166-170.

Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara. 1999a. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecological Research 14:351-360.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999b. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441.

Nielsen, J. L. 1992. Macrohabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Point No Point Treaty Council (PNPTC). 2015. Hood Canal steelhead management plan: 2014-2015. 19p.

Poff, N. L., D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47(11):769-784.

Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82(4):1040-1051.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press: Seattle, Washington.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz, and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in steam-dwelling salmonids increase with salmon spawner density. Canadian Journal of Fisheries and Aquatic Sciences 69:73-84.

Roni, P. and A. Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. North American Journal of Fisheries Management 20:683-692.

Roni, P. 2000. Responses of fishes and salamanders to instream restoration efforts in western Oregon and Washington. Doctoral dissertation. University of Washington, Seattle.

Rosenfeld, J. S., and E. Raeburn. 2009. Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity. Ecology of Freshwater Fish 18:572-584.

Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology 92(11):2073-2084.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336-343.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52:1944-1956.

Schindler, D. E., R. Hillborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609-612.

Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13(5):257-263.

Service, C. N., A. W. Bateman, M. S. Adams, K. A. Artelle, T. E. Reimchen, P. C. Paquet, and C. T. Darimont. 2019. Salmonid species diversity predicts salmon consumption by terrestrial wildlife. Journal of Animal Ecology 88:392-404.

Skokomish Indian Tribe and Washington Department of Fish and Wildlife (SIT and WDFW). 2017. Recovery Plan for Skokomish River Chinook 2017 update. Skokomish Indian Tribe, Skokomish, WA; Washington Department of Fish and Wildlife, Olympia, WA.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press: Princeton, New Jersey.

Thompson, J. N., and D. A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. Transactions of the American Fisheries Society 143:910-925.

Thornton, E. J., J. J. Duda, and T. P. Quinn. 2017. Influence of species, size and relative abundance on the outcomes of competitive interactions between brook trout and juvenile coho salmon. Ethology Ecology & Evolution 29(2):157-169.

Tockner, K., Malard, F., and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14:2861-2883.

Twomey, H. G., and P. S. Giller. 1990. Stomach flushing and individual Panjet tattooing of salmonids: an evaluation of the long-term effects on two wild populations. Aquaculture and Fisheries Management 21:137-142.

Uno, H., and S. Pneh. 2020. Effect of source habitat spatial heterogeneity and species diversity on the temporal stability of aquatic-to-terrestrial subsidy by emerging aquatic insects. Ecological Research 35(3):474-481.

U.S. Fish and Wildlife Service (USFWS). 2011. Biological Sampling in the Skokomish River Basin, Washington: Army Corps of Engineers General Investigation. Fisheries Division, Washington Fish and Wildlife Office, Lacey, Washington.

Vanderploeg, H. A., and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecological Modelling 7:135–149.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

Washington State Conservation Commission (WCC). 2003. Salmon and Steelhead Habitat Limiting Factors: Water Resource Inventory Area 16: Dosewallips-Skokomish Basin. Olympia, WA.

Washington Department of Natural Resources (WDNR). 1997. Washington State salmonid stock inventory: bull trout/Dolly Vardon. Olympia, WA.

Weber, N., N. Bouwes, and C. E. Jordan. 2014. Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. Canadian Journal of Fisheries and Aquatic Sciences 71(8):1158-1170.

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-NWFSC-24. Seattle, Washington.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:1259-1269.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35(8):373-387.

Wipfli, M. S. and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957-969.

Wipfli, M. S., J. P. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Woo, I., M. J. Davis, C. S. Ellings, S. Hodgson, J. Y. Takekawa, G. Nakai, and S. E. W. De La Cruz. 2019. A mosaic of estuarine habitat types with prey resources from multiple environmental strata supports a diversified foraging portfolio for juvenile Chinook salmon. Estuaries and Coasts 42:1938-1954.

Wright, L. A. 2010. Winter feeding ecology of coho salmon (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*) in the Skokomish River, Washington. (Published master's thesis). The Evergreen State College, Olympia, Washington.

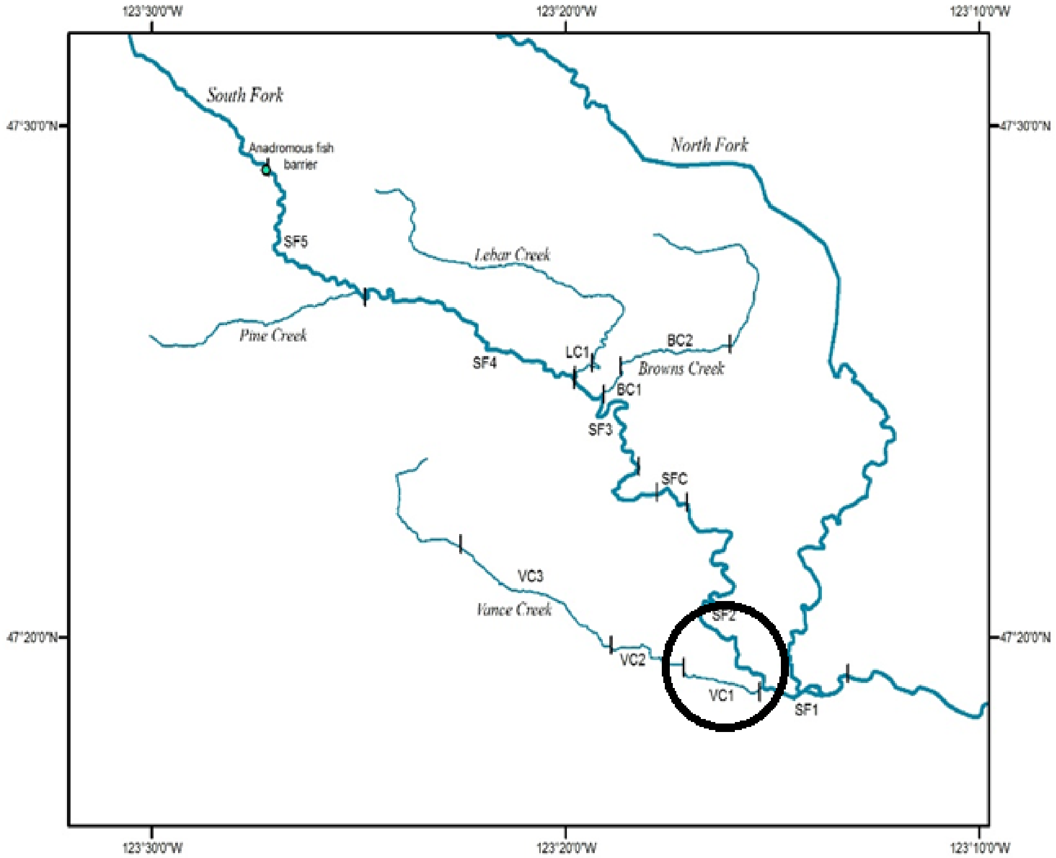


Figure 6. Study system map
South Fork Skokomish River with tributaries, anadromy barrier, and survey reaches.

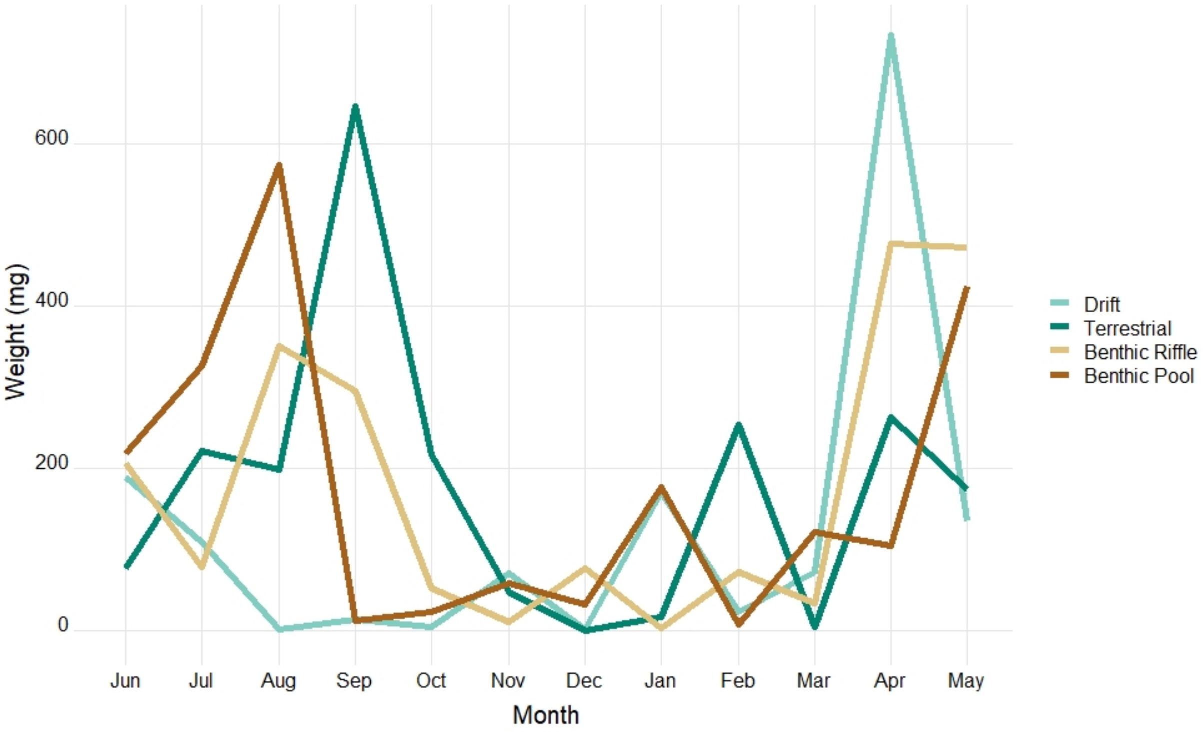


Figure 7. Monthly total environmental productivity
Monthly mass (mg) of invertebrates found in environmental samples. Drift samples n=6 per month. Terrestrial samples n=10 per tree species per month. Benthic samples n=5 pool and n=5 riffle per month.

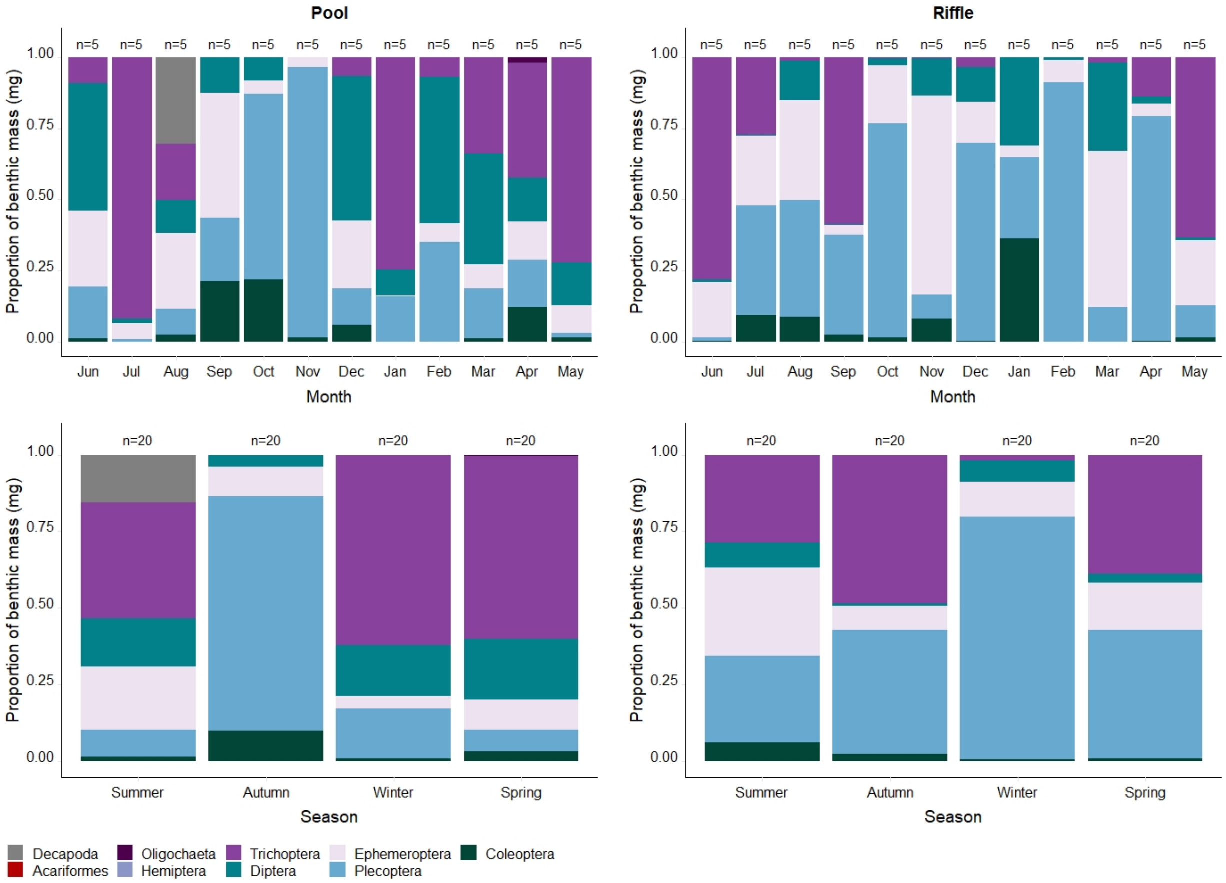


Figure 8. Benthic invertebrate composition

Monthly and seasonal resolution of invertebrates found in the benthic environment with proportion by order found in pools (A, C) and riffles (B, D). Seasons defined as Summer (June, July, August), Autumn (September, October, November), Winter (December, January, February), and Spring (March, April, May).

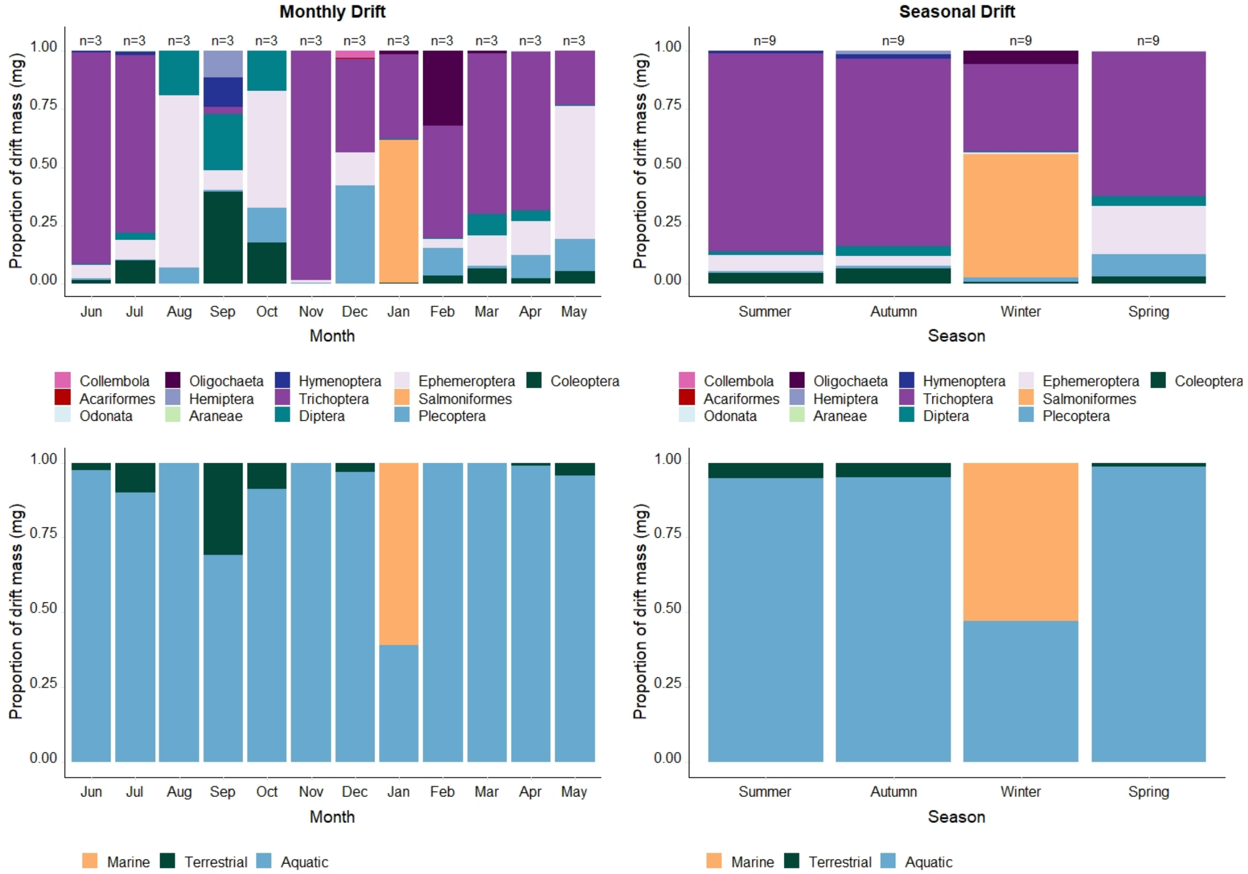


Figure 9. Drift invertebrate composition
Monthly and seasonal resolution of invertebrates found in the drift environment: A) monthly drift invertebrate proportions by order, B) seasonal drift proportions by order, C) monthly proportional contribution of marine, aquatic, and terrestrial energy pathways available in the drift, D) seasonal proportional contribution of marine, aquatic, and terrestrial energy pathways available in the drift. Seasons defined as Summer (June, July, August), Autumn (September, October, November), Winter (December, January, February), and Spring (March, April, May).

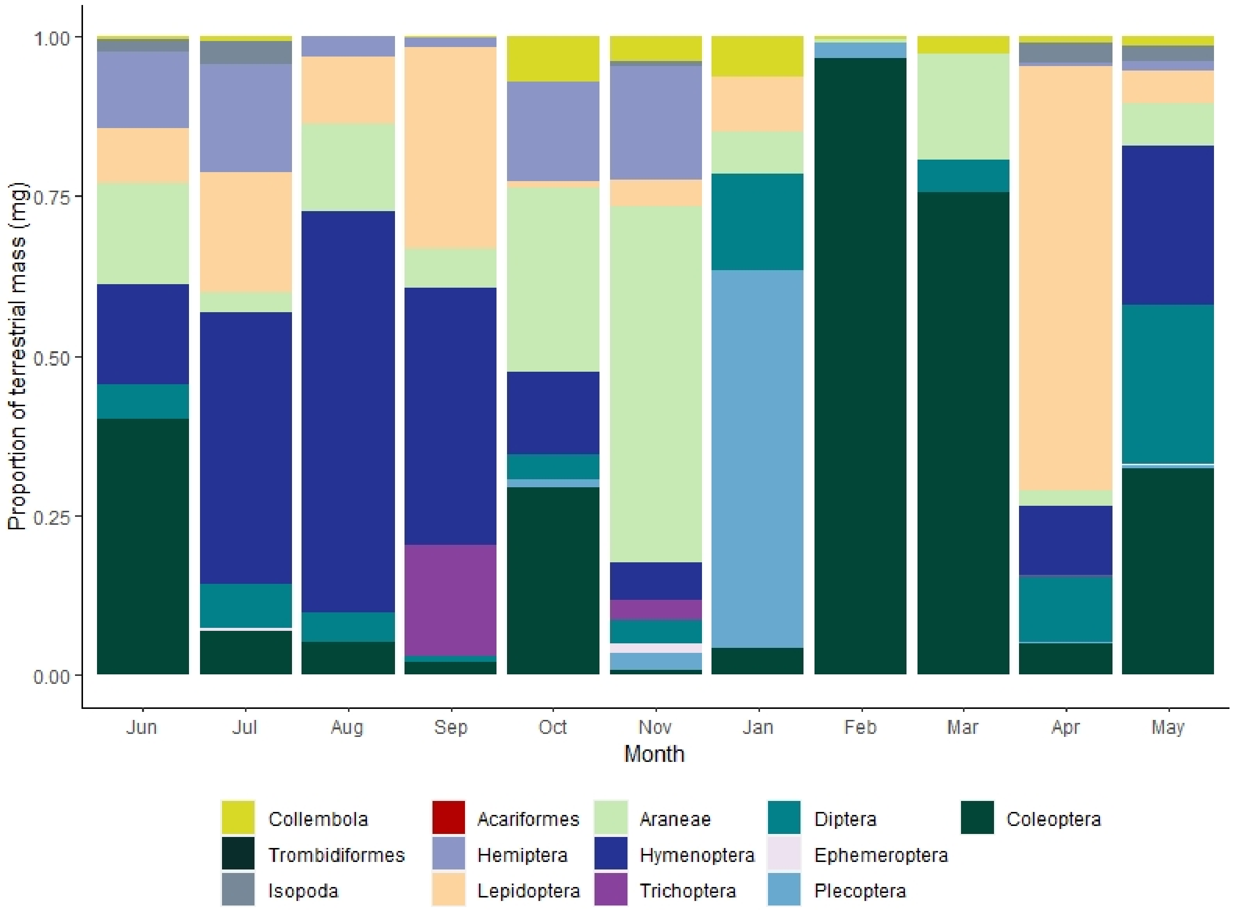


Figure 10. Terrestrial invertebrate composition
Monthly proportion of invertebrates by order found in the terrestrial environment associated with six common riparian vegetation species: Bigleaf Maple, Red Alder, Sitka Willow, Vine Maple, Knotweed, and Blackberry.

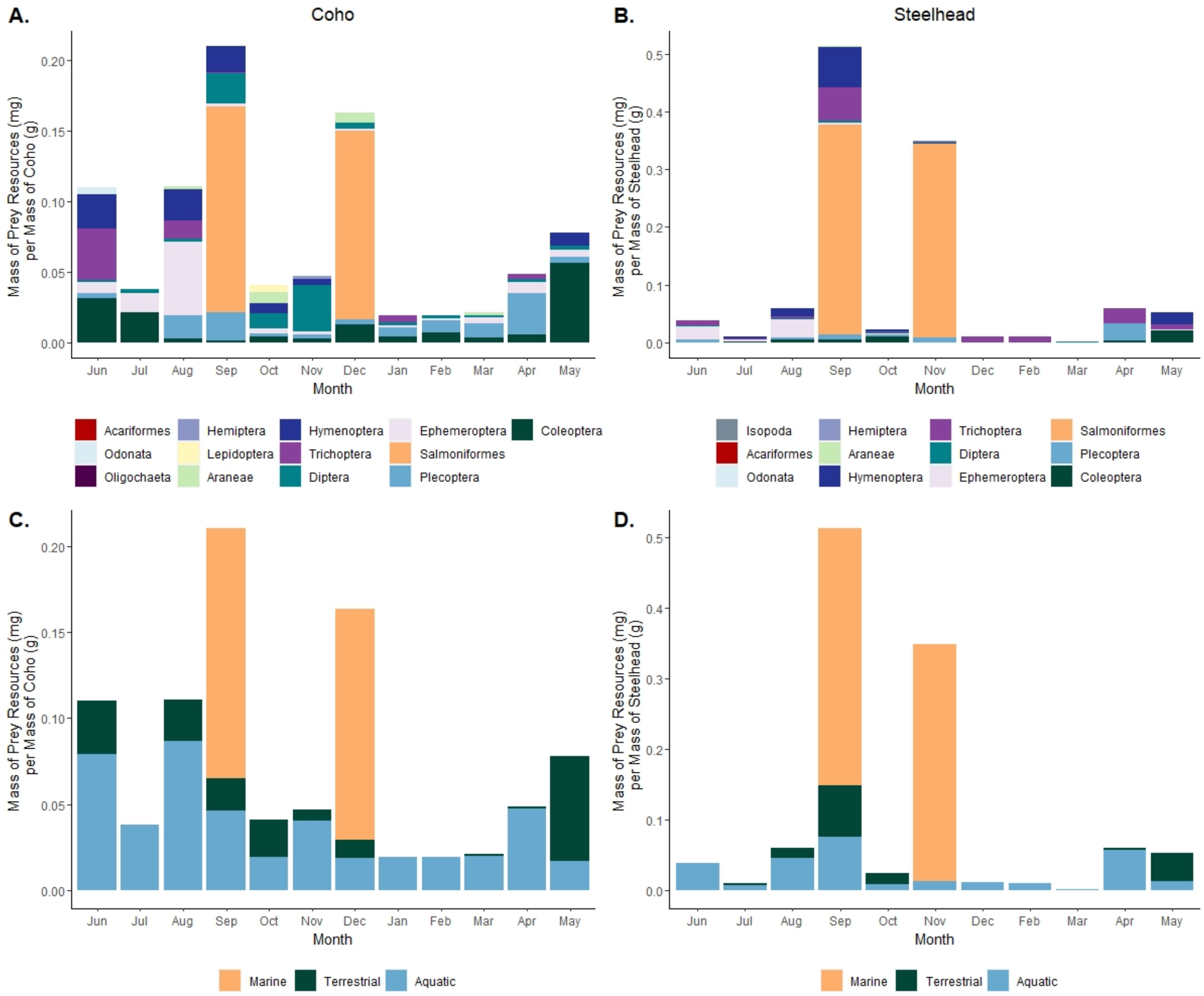


Figure 11. Fish rations

Monthly average ration of prey resources (mg) per mass (g) of fish by prey order for coho (A) and steelhead (B); Monthly average ration of prey resources (mg) per mass (g) of fish by trophic pathway (i.e. marine, terrestrial, aquatic) for coho (C) and steelhead (D).

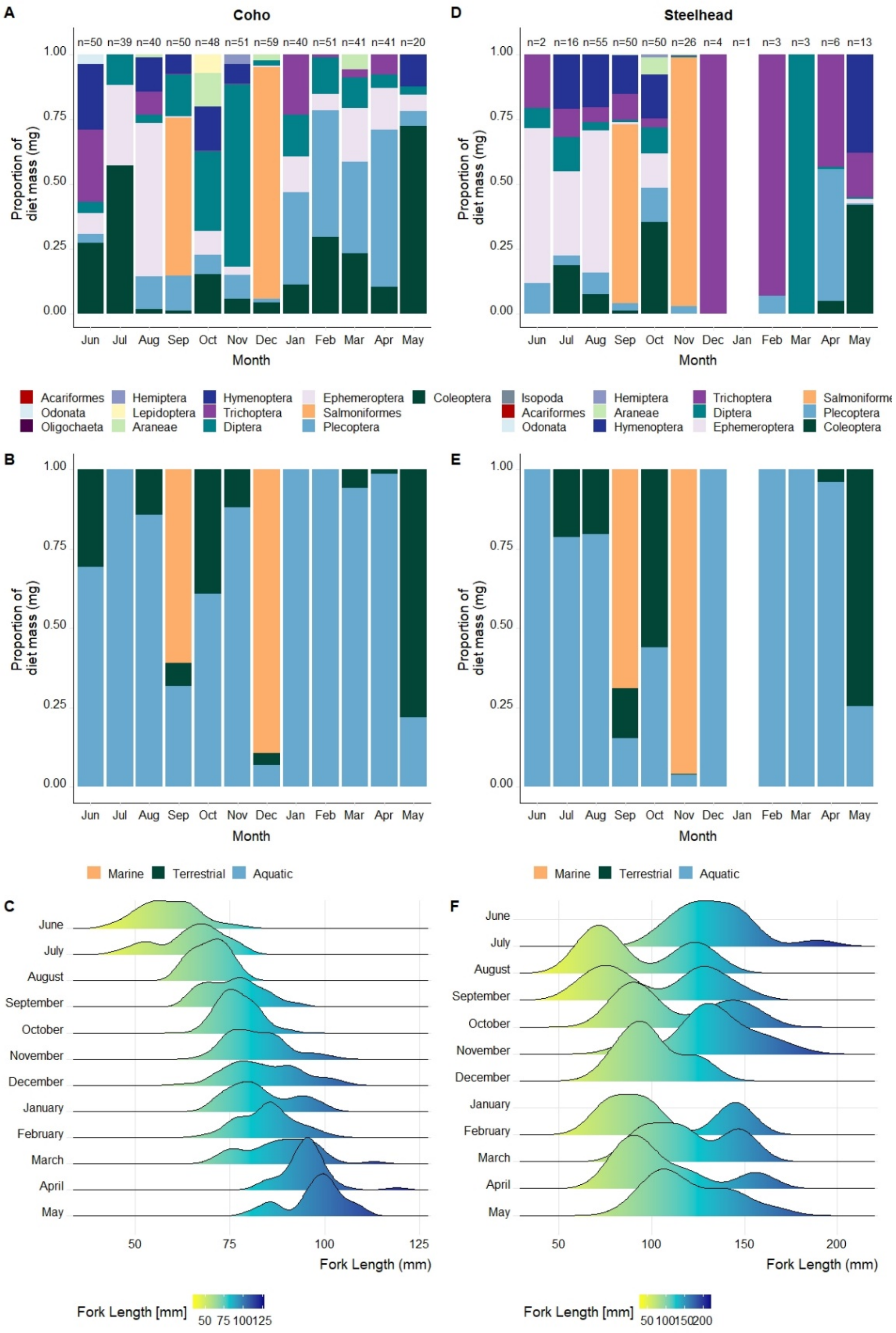


Figure 12. Fish diet composition and size by month

Monthly resolution of diet, energy pathways, and size distributions for juvenile coho and steelhead: 1) proportion of invertebrates found in the diets (A, D), 2) proportional contribution of marine, aquatic, and terrestrial energy pathways (B,E), and 3) cohort fork length size frequencies (C, F).

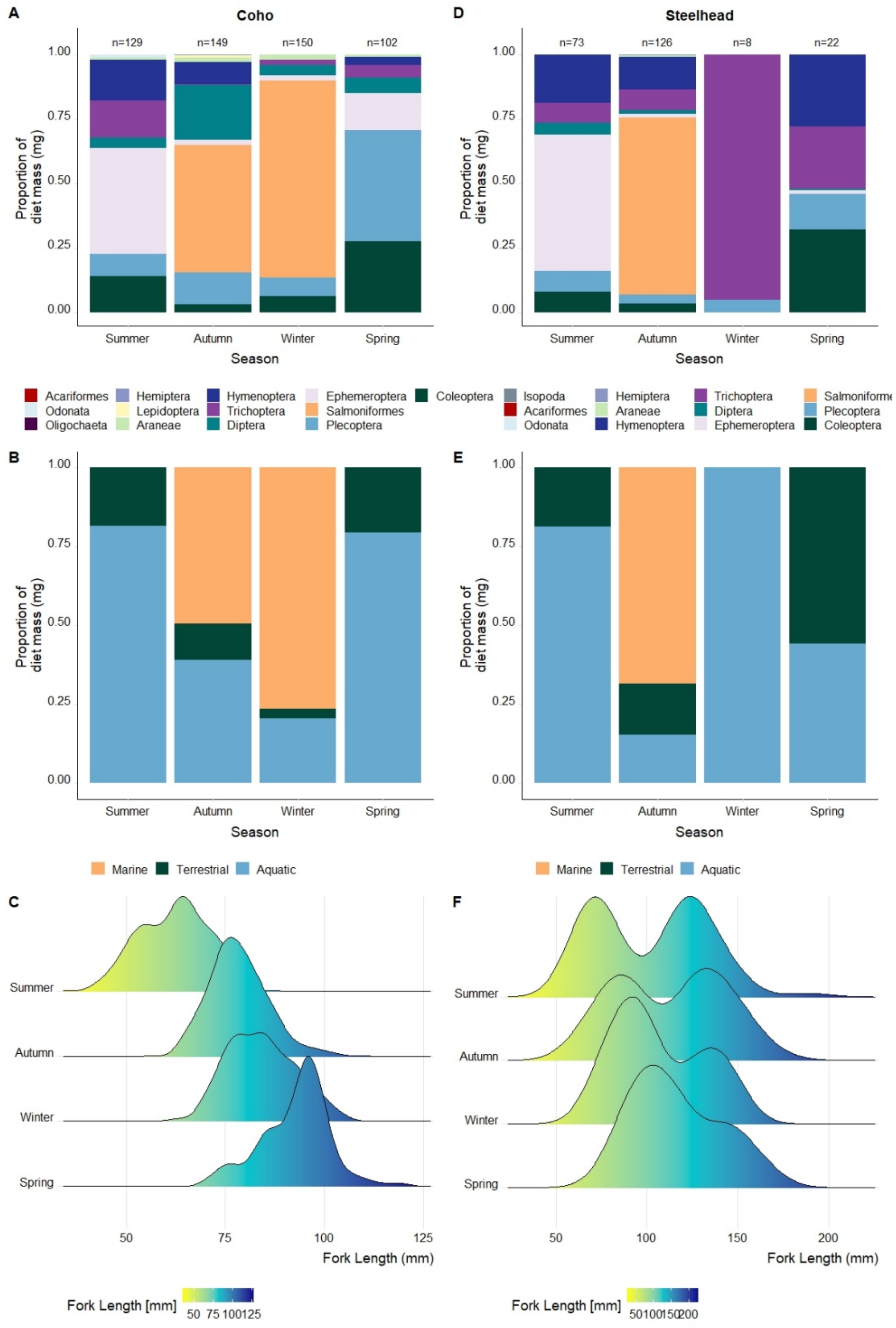
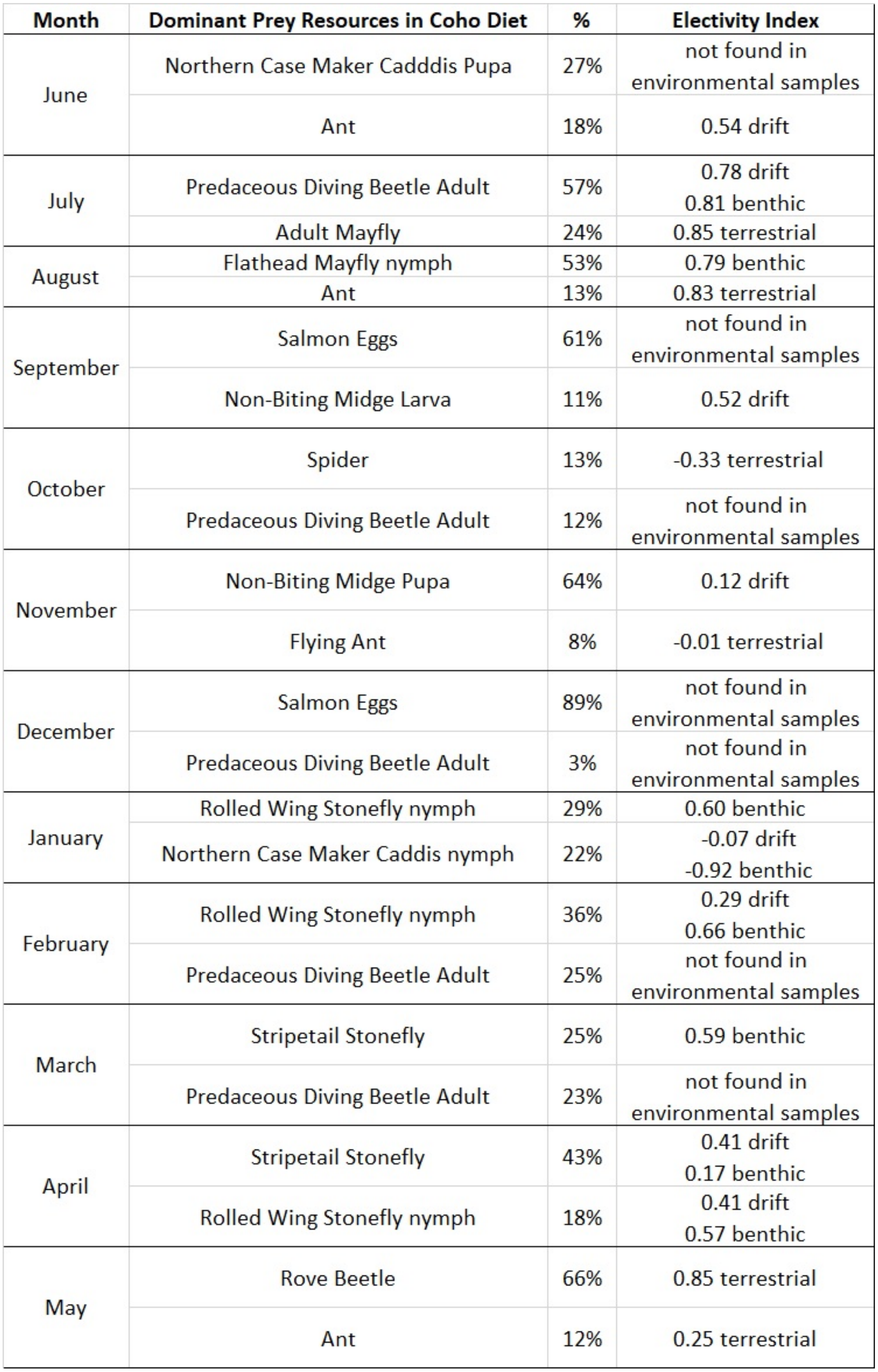


Figure 13. Fish diet composition and size by season

Seasonal resolution of diet, energy pathways, and size distributions for juvenile coho and steelhead: 1) proportion of invertebrates found in the diets (A, D), 2) proportional contribution of marine, aquatic, and terrestrial energy pathways (B, E), and 3) cohort fork length size frequencies (C, F). Seasons defined as Summer (June, July, August), Autumn (September, October, November), Winter (December, January, February), and Spring (March, April, May).

Table 1. Top prey resources for coho

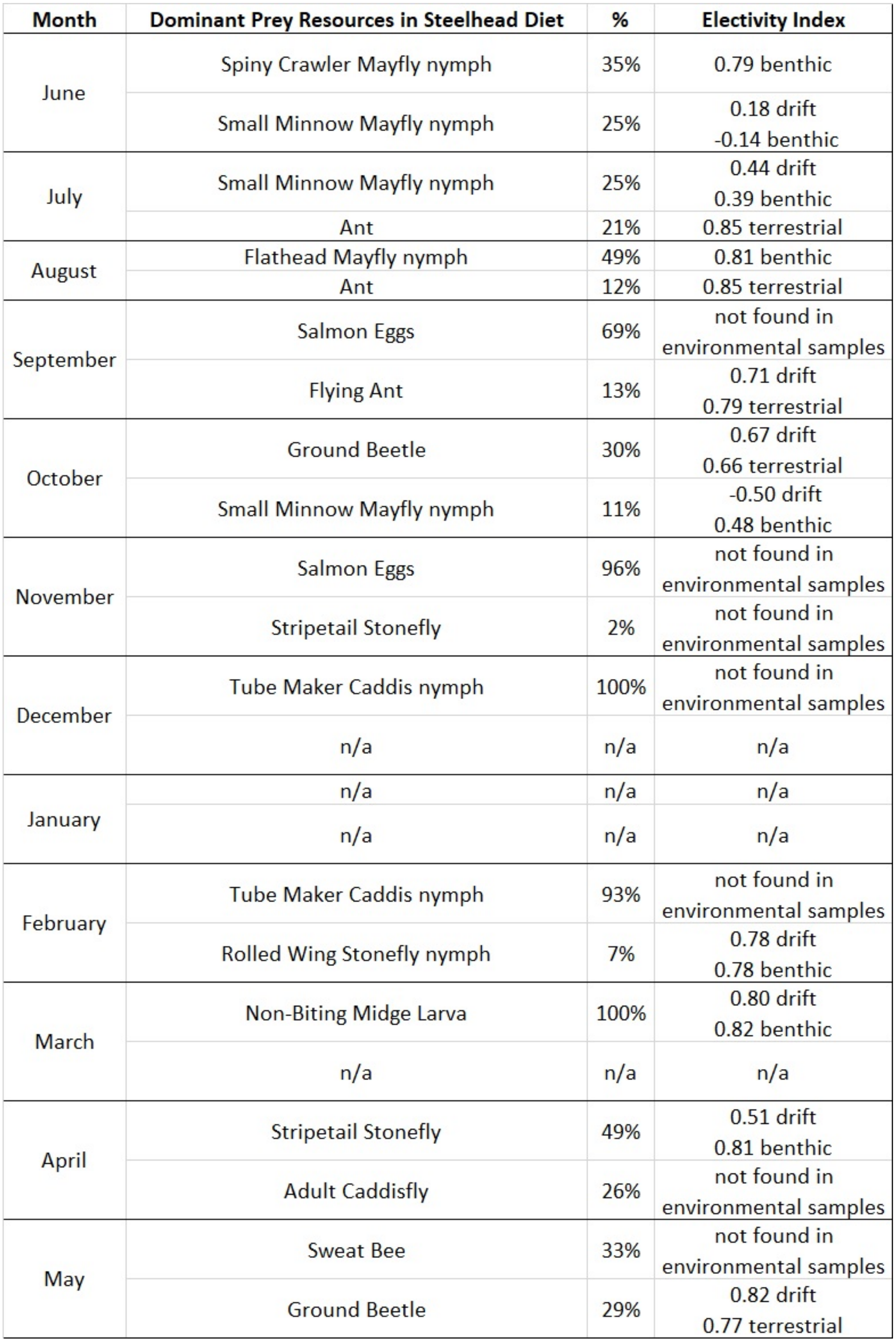
Monthly dominant prey resources in juvenile coho diet by month with Vanderploeg and Scavia Electivity Index of preference or avoidance.



Month	Dominant Prey Resources in Coho Diet	%	Electivity Index
June	Northern Case Maker Cadddis Pupa	27%	not found in environmental samples
	Ant	18%	0.54 drift
July	Predaceous Diving Beetle Adult	57%	0.78 drift 0.81 benthic
	Adult Mayfly	24%	0.85 terrestrial
August	Flathead Mayfly nymph	53%	0.79 benthic
	Ant	13%	0.83 terrestrial
September	Salmon Eggs	61%	not found in environmental samples
	Non-Biting Midge Larva	11%	0.52 drift
October	Spider	13%	-0.33 terrestrial
	Predaceous Diving Beetle Adult	12%	not found in environmental samples
November	Non-Biting Midge Pupa	64%	0.12 drift
	Flying Ant	8%	-0.01 terrestrial
December	Salmon Eggs	89%	not found in environmental samples
	Predaceous Diving Beetle Adult	3%	not found in environmental samples
January	Rolled Wing Stonefly nymph	29%	0.60 benthic
	Northern Case Maker Caddis nymph	22%	-0.07 drift -0.92 benthic
February	Rolled Wing Stonefly nymph	36%	0.29 drift 0.66 benthic
	Predaceous Diving Beetle Adult	25%	not found in environmental samples
March	Stripetail Stonefly	25%	0.59 benthic
	Predaceous Diving Beetle Adult	23%	not found in environmental samples
April	Stripetail Stonefly	43%	0.41 drift 0.17 benthic
	Rolled Wing Stonefly nymph	18%	0.41 drift 0.57 benthic
May	Rove Beetle	66%	0.85 terrestrial
	Ant	12%	0.25 terrestrial

Table 2. Top prey resources for steelhead

Monthly dominant prey resources in juvenile steelhead diet by month with Vanderploeg and Scavia Electivity Index of preference or avoidance.



Month	Dominant Prey Resources in Steelhead Diet	%	Electivity Index
June	Spiny Crawler Mayfly nymph	35%	0.79 benthic
	Small Minnow Mayfly nymph	25%	0.18 drift -0.14 benthic
July	Small Minnow Mayfly nymph	25%	0.44 drift 0.39 benthic
	Ant	21%	0.85 terrestrial
August	Flathead Mayfly nymph	49%	0.81 benthic
	Ant	12%	0.85 terrestrial
September	Salmon Eggs	69%	not found in environmental samples
	Flying Ant	13%	0.71 drift 0.79 terrestrial
October	Ground Beetle	30%	0.67 drift 0.66 terrestrial
	Small Minnow Mayfly nymph	11%	-0.50 drift 0.48 benthic
November	Salmon Eggs	96%	not found in environmental samples
	Stripetail Stonefly	2%	not found in environmental samples
December	Tube Maker Caddis nymph	100%	not found in environmental samples
	n/a	n/a	n/a
January	n/a	n/a	n/a
	n/a	n/a	n/a
February	Tube Maker Caddis nymph	93%	not found in environmental samples
	Rolled Wing Stonefly nymph	7%	0.78 drift 0.78 benthic
March	Non-Biting Midge Larva	100%	0.80 drift 0.82 benthic
	n/a	n/a	n/a
April	Stripetail Stonefly	49%	0.51 drift 0.81 benthic
	Adult Caddisfly	26%	not found in environmental samples
May	Sweat Bee	33%	not found in environmental samples
	Ground Beetle	29%	0.82 drift 0.77 terrestrial

Table 3. Prey selectivity: coho vs. benthic

coho prey selectivity of monthly diet contents compared to benthic invertebrate availability using Vanderploeg and Scavia's electivity index, where values <0 indicate avoidance and values >0 indicate preference (Vanderploeg and Scavia 1979).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Aquatic Invertebrates, Larval												
Burrower Mayfly nymph	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Common Stonefly nymph	NA	-1.00	-1.00	-1.00	NA	-1.00	-1.00	NA	-1.00	-1.00	-1.00	-1.00
Crane Fly larva	-1.00	-1.00	-1.00	NA	-1.00	NA	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Crayfishes	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Dance Fly Larva	NA	NA	-0.79	NA	NA	NA	NA	NA	-1.00	NA	-1.00	NA
Flathead Mayfly nymph	-0.75	-1.00	0.79	-0.72	-0.63	-0.70	-1.00	NA	-1.00	-1.00	-1.00	-1.00
Free Living Caddis nymph	-1.00	NA	NA	NA	NA	NA	-1.00	NA	NA	NA	NA	NA
Non-Biting Midge Larva	-0.20	NA	-0.42	NA	0.59	0.26	0.66	NA	NA	-0.65	0.27	-1.00
Northern Case Maker Caddis nymph	-1.00	-1.00	-0.09	-0.98	NA	NA	-1.00	-0.92	-1.00	-0.94	-0.93	-1.00
Riffle Beetle Larva	0.73	-1.00	-0.60	-0.03	-0.67	NA	0.36	NA	NA	-1.00	-0.80	-1.00
Rolled Wing Stonefly nymph	0.44	-1.00	0.02	0.67	-0.17	0.35	0.00	0.60	0.66	0.55	0.57	0.51
Saddle Case Maker Caddis	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Small Minnow Mayfly nymph	0.14	-0.50	0.07	-0.33	0.34	-0.79	0.34	NA	0.12	0.13	0.28	-0.23
Spiny Crawler Mayfly nymph	-1.00	-1.00	-1.00	NA	NA	NA	-1.00	NA	NA	NA	-1.00	-1.00
Stripetail Stonefly	-1.00	-1.00	-0.08	0.39	-1.00	NA	NA	-1.00	0.28	0.59	0.17	-1.00
Tube Maker Caddis nymph	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.07	NA	NA
Aquatic Invertebrates, Adult												
Adult Caddisfly	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Predaceous Diving Beetle Adult	NA	0.81	-0.05	-1.00	NA	0.32	NA	NA	NA	NA	0.53	0.76
Terrestrial Invertebrates, Non-Flying												
none												
Terrestrial Invertebrates, Flying												
none												
Marine Nutrients												
none												

Table 4. Prey selectivity: steelhead vs. benthic

steelhead prey selectivity of monthly diet contents compared to benthic invertebrate availability using Vanderploeg and Scavia's electivity index, where values <0 indicate avoidance and values >0 indicate preference (Vanderploeg and Scavia 1979).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Aquatic Invertebrates, Larval												
Burrower Mayfly nymph	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Common Stonefly nymph	NA	-1.00	-1.00	-0.78	NA	-1.00	NA	NA	-1.00	-1.00	-1.00	-1.00
Crane Fly larva	-1.00	-1.00	-1.00	NA	-1.00	NA	NA	NA	-1.00	-1.00	-1.00	-1.00
Crayfishes	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Dance Fly Larva	NA	NA	-1.00	NA	NA	NA	NA	NA	-1.00	NA	-1.00	NA
Flathead Mayfly nymph	-1.00	0.37	0.81	-1.00	-0.59	-1.00	NA	NA	-1.00	-1.00	-1.00	-1.00
Free Living Caddis nymph	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Non-Biting Midge Larva	-0.74	NA	-0.26	NA	0.50	-1.00	NA	NA	NA	0.82	-1.00	-1.00
Northern Case Maker Caddis nymph	-0.77	-0.93	-0.27	-1.00	NA	NA	NA	NA	-1.00	-1.00	-1.00	-0.90
Riffle Beetle Larva	-1.00	-0.57	-1.00	-1.00	-0.72	NA	NA	NA	NA	-1.00	-1.00	-1.00
Rolled Wing Stonefly nymph	0.19	-0.29	0.07	-0.07	-0.21	0.71	NA	NA	0.78	-1.00	0.40	-0.09
Saddle Case Maker Caddis	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Small Minnow Mayfly nymph	-0.14	0.39	0.16	0.13	0.48	-1.00	NA	NA	-1.00	-1.00	-1.00	0.26
Spiny Crawler Mayfly nymph	0.79	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00
Stripetail Stonefly	-1.00	-1.00	-0.24	-0.59	-0.96	NA	NA	NA	-1.00	-1.00	0.81	-1.00
Tube Maker Caddis nymph	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	NA	NA
Aquatic Invertebrates, Adult												
Adult Caddisfly	NA	NA	NA	0.73	NA	NA	NA	NA	NA	NA	NA	NA
Predaceous Diving Beetle Adult	NA	0.65	-1.00	-1.00	NA	-1.00	NA	NA	NA	NA	-1.00	0.79
Terrestrial Invertebrates, Non-Flying												
none												
Terrestrial Invertebrates, Flying												
none												
Marine Nutrients												
none												

Table 5. Prey selectivity: coho vs. drift
coho prey selectivity of monthly diet contents compared to drift invertebrate availability using Vanderploeg and Scavia's electivity index, where values <0 indicate avoidance and values >0 indicate preference (Vanderploeg and Scavia 1979).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Aquatic Invertebrates, Larval												
Aquatic Earthworm	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00	-1.00	NA	NA
Crane Fly larva	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00	NA
Flathead Mayfly nymph	NA	-1.00	NA	NA	NA	NA	NA	NA	-1.00	-1.00	-1.00	-1.00
horse fly larva	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	NA
Non-Biting Midge Larva	NA	0.38	0.18	0.52	0.51	NA	NA	NA	0.64	0.01	NA	NA
Non-Biting Midge Pupa	NA	NA	-0.86	-0.32	0.12	NA	NA	NA	NA	NA	NA	NA
Northern Case Maker Caddis nymph	-1.00	-1.00	NA	-0.82	NA	-1.00	-1.00	-0.07	-1.00	-0.99	-0.98	-1.00
Riffle Beetle Larva	NA	NA	NA	-0.87	-0.45	NA	NA	0.52	-0.27	-1.00	-0.80	-1.00
Rolled Wing Stonefly nymph	-0.24	-1.00	0.39	0.78	0.10	NA	0.08	NA	0.29	0.46	0.41	0.38
Small Minnow Mayfly nymph	-0.59	-0.28	-0.62	-0.87	-0.39	0.33	0.48	NA	0.02	0.68	-0.06	-0.43
Spiny Crawler Mayfly nymph	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00	-1.00
Stripetail Stonefly	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.41	-1.00
Tube Maker Caddis nymph	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.41	NA
Aquatic Invertebrates, Adult												
Adult Mayfly	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.47	0.76
Adult Stonefly	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	NA	NA	NA
Dance Fly Adult	NA	-1.00	NA	-1.00	-0.19	NA	NA	NA	NA	NA	NA	NA
Non-Biting Midge Adult	NA	NA	NA	-1.00	-0.13	NA	NA	NA	NA	NA	NA	NA
Predaceous Diving Beetle Adult	NA	0.78	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Terrestrial Invertebrates, Non-Flying												
Ant	0.54	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Golden Snow Flea	NA	NA	NA	NA	NA	NA	-1.00	NA	NA	NA	NA	NA
Ground Beetle	-0.15	-1.00	NA	-1.00	-0.76	NA	NA	NA	NA	NA	NA	-1.00
Leafhopper	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Terrestrial Invertebrates, Flying												
Flying Ant	NA	-1.00	NA	-0.11	NA	NA	NA	NA	NA	NA	NA	NA
Lady Beetle	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Leaf Beetle	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00
Rove Beetle	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Marine Nutrients												
Salmon Eggs	NA	NA	NA	NA	NA	NA	NA	-1.00	NA	NA	NA	NA

Table 6. Prey selectivity: steelhead vs. drift

steelhead prey selectivity of monthly diet contents compared to drift invertebrate availability using Vanderploeg and Scavia’s electivity index, where values <0 indicate avoidance and values >0 indicate preference (Vanderploeg and Scavia 1979).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Aquatic Invertebrates, Larval												
Aquatic Earthworm	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00	NA	NA
Crane Fly larva	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00	NA
Flathead Mayfly nymph	NA	0.42	NA	NA	NA	NA	NA	NA	-1.00	-1.00	-1.00	-1.00
horse fly larva	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	NA
Non-Biting Midge Larva	NA	0.36	0.26	0.04	0.14	NA	NA	NA	-1.00	0.80	NA	NA
Non-Biting Midge Pupa	NA	NA	-1.00	-1.00	-0.33	NA	NA	NA	NA	NA	NA	NA
Northern Case Maker Caddis nymph	-0.87	-0.92	NA	-1.00	NA	NA	NA	NA	-1.00	-1.00	-1.00	-0.94
Riffle Beetle Larva	NA	NA	NA	-1.00	-0.71	NA	NA	NA	-1.00	-1.00	-1.00	-1.00
Rolled Wing Stonefly nymph	0.55	0.10	0.34	0.69	-0.24	NA	NA	NA	0.78	-1.00	-0.54	-0.91
Small Minnow Mayfly nymph	0.18	0.44	-0.62	-0.19	-0.50	NA	NA	NA	-1.00	-1.00	-1.00	-0.84
Spiny Crawler Mayfly nymph	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00	-1.00
Stripetail Stonefly	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.51	-1.00
Tube Maker Caddis nymph	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.77	NA
Aquatic Invertebrates, Adult												
Adult Mayfly	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00
Adult Stonefly	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	NA	NA	NA
Dance Fly Adult	NA	-1.00	NA	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA
Non-Biting Midge Adult	NA	NA	NA	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA
Predaceous Diving Beetle Adult	NA	0.44	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Terrestrial Invertebrates, Non-Flying												
Ant	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Golden Snow Flea	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ground Beetle	-1.00	-1.00	NA	-1.00	0.67	NA	NA	NA	NA	NA	NA	0.82
Leafhopper	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Terrestrial Invertebrates, Flying												
Flying Ant	NA	-1.00	NA	0.71	NA	NA	NA	NA	NA	NA	NA	NA
Lady Beetle	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Leaf Beetle	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00
Rove Beetle	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Marine Nutrients												
Salmon Eggs	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table 7. Prey selectivity: coho vs. terrestrial

coho prey selectivity of monthly diet contents compared to terrestrial invertebrate availability using Vanderploeg and Scavia's electivity index, where values <0 indicate avoidance and values >0 indicate preference (Vanderploeg and Scavia 1979).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Aquatic Invertebrates, Larval												
none												
Aquatic Invertebrates, Adult												
Adult Caddisfly	NA	NA	NA	-1.00	NA	-1.00	NA	NA	NA	NA	NA	NA
Adult Mayfly	NA	0.85	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA
Adult Stonefly	NA	NA	NA	NA	0.13	0.59	NA	0.58	NA	NA	NA	NA
Black Fly Adult	NA	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	-1.00
Crane Fly Adult	-1.00	-1.00	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	-1.00
Dance Fly Adult	-1.00	NA	-1.00	NA	0.14	0.06	NA	-1.00	NA	-1.00	NA	-1.00
Non-Biting Midge Adult	-1.00	NA	NA	NA	-0.25	0.65	NA	0.62	NA	NA	NA	-0.19
Terrestrial Invertebrates, Non-Flying												
Ant	NA	-1.00	0.83	-0.69	NA	-1.00	NA	NA	NA	NA	NA	0.25
caterpillar	-1.00	-1.00	-1.00	-1.00	0.78	-1.00	NA	-1.00	NA	NA	NA	-1.00
click beetle	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Globular Springtail	NA	NA	NA	NA	-1.00	-1.00	NA	-1.00	NA	-1.00	NA	-1.00
Golden Snow Flea	NA	NA	NA	NA	-1.00	-1.00	NA	-1.00	NA	-1.00	NA	-1.00
Ground Beetle	NA	-1.00	-1.00	-1.00	-0.96	NA	NA	NA	NA	NA	NA	-1.00
Isopod	-1.00	-1.00	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	-1.00
Leafhopper	-1.00	-1.00	-1.00	-1.00	-1.00	-0.06	NA	NA	NA	NA	NA	-1.00
plant bug	-1.00	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Spider	-1.00	-1.00	-0.01	-1.00	-0.33	-1.00	NA	-1.00	NA	0.67	NA	-1.00
Terrestrial Invertebrates, Flying												
Flying Ant	0.74	NA	-1.00	0.80	-0.01	NA	NA	NA	NA	NA	NA	-1.00
Lady Beetle	0.73	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Leaf Beetle	-1.00	-1.00	-1.00	NA	-1.00	NA	NA	NA	NA	NA	NA	NA
Rove Beetle	-1.00	NA	-1.00	NA	-0.71	0.42	NA	-1.00	NA	-1.00	NA	0.85
sweat bee	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA
Wasp	-1.00	-1.00	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA	-1.00
Marine Nutrients												
none												

Table 8. Prey selectivity: steelhead vs. terrestrial

steelhead prey selectivity of monthly diet contents compared to terrestrial invertebrate availability using Vanderploeg and Scavia's electivity index, where values <0 indicate avoidance and values >0 indicate preference (Vanderploeg and Scavia 1979).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Aquatic Invertebrates, Larval												
none												
Aquatic Invertebrates, Adult												
Adult Caddisfly	NA	NA	NA	-0.45	NA	NA	NA	NA	NA	NA	NA	NA
Adult Mayfly	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Adult Stonefly	NA	NA	NA	NA	0.57	NA	NA	NA	NA	NA	NA	NA
Black Fly Adult	NA	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00
Crane Fly Adult	NA	-1.00	NA	NA	-1.00	NA	NA	NA	NA	NA	-1.00	-1.00
Dance Fly Adult	NA	NA	-1.00	NA	-1.00	NA	NA	NA	NA	NA	-1.00	-1.00
Non-Biting Midge Adult	NA	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	0.86	-1.00
Terrestrial Invertebrates, Non-Flying												
Ant	NA	0.85	0.85	-0.69	NA	NA	NA	NA	NA	NA	-1.00	0.42
caterpillar	NA	-1.00	-1.00	-1.00	-1.00	NA	NA	NA	NA	NA	-1.00	-1.00
click beetle	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	NA
Globular Springtail	NA	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	-1.00	-1.00
Golden Snow Flea	NA	NA	NA	NA	-1.00	NA	NA	NA	NA	NA	NA	-1.00
Ground Beetle	NA	-1.00	-1.00	-1.00	0.66	NA	NA	NA	NA	NA	NA	0.77
Isopod	NA	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	-1.00	-1.00
Leafhopper	NA	-1.00	-1.00	-1.00	-0.63	NA	NA	NA	NA	NA	-1.00	-1.00
plant bug	NA	-1.00	-1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA
Spider	NA	-1.00	-1.00	-1.00	-0.14	NA	NA	NA	NA	NA	-1.00	-1.00
Terrestrial Invertebrates, Flying												
Flying Ant	NA	NA	-1.00	0.79	0.43	NA	NA	NA	NA	NA	-1.00	-1.00
Lady Beetle	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Leaf Beetle	NA	-1.00	-1.00	NA	-1.00	NA	NA	NA	NA	NA	NA	NA
Rove Beetle	NA	NA	-1.00	NA	-0.05	NA	NA	NA	NA	NA	NA	0.66
sweat bee	NA	NA	NA	-0.96	NA	NA	NA	NA	NA	NA	NA	NA
Wasp	NA	-1.00	-1.00	-1.00	NA	NA	NA	NA	NA	NA	-1.00	-1.00
Marine Nutrients												
none												

CHAPTER 4. GENERAL CONCLUSIONS

Through my thesis, I explored temporal variation in juvenile salmonid trophic ecology during freshwater rearing with the aim of informing salmon recovery, conservation, and habitat restoration. First, I quantified existing temporal biases within the past 30 years of research to identify knowledge gaps (Chapter 2). I looked at the distribution of study timing throughout the year and the extent, or duration, of each study. Then, I evaluated the prey resources available to and utilized by juvenile salmonids throughout a full annual cycle (Chapter 3). I collected stomach contents from juvenile coho salmon and steelhead trout and compared these on a monthly basis to prey items found in the environment using benthic, drift, and terrestrial sampling. The results from this work indicate that 1) field studies focusing on juvenile *Oncorhynchus* spp. during freshwater rearing over the past 30 years have been biased toward summer and against winter and 2) juvenile coho salmon and steelhead trout utilize temporally variable ephemeral and stable prey resources derived from aquatic, terrestrial, and marine origins.

In Chapter 2, I found that winter studies were underrepresented (13% occurred in December-February) and summer studies overrepresented (40% occurred in June-August). Over four times as many studies occurred in June than those that occurred in December. Most studies collected data from a single season (57%) and rarely did a study collect data from more than 4 months out of the year (27%). I found that these biases were generally true in riverscape studies, all juvenile ecological studies, and within the ecological sub-topics of fish-habitat interactions, trophic ecology, and spatial distribution. There is some evidence to suggest that winter survival is a constraining factor to freshwater productivity in salmon (Bustard and Narver 1975). Winter fish habitat has, therefore, been a major focus of restoration efforts (Cederholm et al. 1997). This makes the lack of winter studies is concerning as we base restoration efforts off potentially incomplete data.

In Chapter 3, I found that the energy portfolio consisted of complementary prey resources with no one prey resource providing the bulk of fish diet every month of the year. Most importantly, in critical months, the bulk of rations came from ephemeral and relatively scarce prey items. I found that in May as fish were undergoing smoltification, 66% of coho diet came from terrestrial rove beetles which were virtually only found during May. Then, in September as fish were transitioning from summer growth to fall lipid storage in preparation for winter, eggs from a very small run of ESA-listed Chinook provided 61% and 69% of total fish ration for coho and steelhead, respectively. Juvenile salmonids benefited from inter-species variation among spawning adult salmon as well with eggs found in juvenile coho diets in December and steelhead diets in November, corresponding with the overlapping spawning of chum and coho salmon. The months where salmon eggs were available as a prey resource were also the months with the highest average ration weight found per fish stomach for both coho and steelhead. In winter, when depletion of lipid stores is offset by consumption of prey resources, aquatic invertebrates were the primary contributors to fish diet. Aquatic invertebrates again became important to fish diet in summer, but with much greater diversity than seen in winter.

The extraordinary circumstances created by the COVID-19 pandemic have hindered completion of two additional components of this research that are still ongoing as we wait for laboratory results: 1) stable isotopes to identify trophic pathways over weeks instead of just days as seen in diet samples and 2) the impact of riparian plants on the prey resource portfolio utilized by juvenile salmonids. These data will greatly enhance future results.

Pacific salmon are of enormous importance culturally, economically, and ecologically. Their continued decline despite huge investments in habitat restoration is of increasing concern. As of 2005, there were almost 40,000 river restoration projects in the United States totaling an estimated $14-$15 billion (Bernhardt et al. 2005). These numbers have likely climbed significantly higher in the past 15 years. There is some troubling evidence that current restoration approaches are ineffective in restoring biological diversity to stream ecosystems (Stranko et al. 2012). I make the argument that managing for critical prey resources at critical points in time during freshwater rearing may be beneficial to recovering dwindling salmon populations. This research project advances knowledge necessary to improving salmon recovery and focus on the importance of seasonal food web interactions across ecosystems by investigating links between plants, aquatic invertebrates, terrestrial invertebrates, ephemeral marine resources, and juvenile salmonids.

References

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308(5722):636–637.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32(5):667-680.

Cederholm, C. J., R. E. Bilby, P. A. Bisson, T. W. Bumstead, B. R. Fransen, W. J. Scarlett, and J. W. Ward. 1997. Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. North American Journal of Fisheries Management 17:947-963.

Stranko, S. A., R. H. Hilderbrand, and M. A. Palmer. 2012. Comparing the fish and benthic macroinvertebrate diversity of restored urban streams to reference streams. Restoration Ecology 20(6):747-755.

GENERAL BIBLIOGRAPHY

Allan, J. D. 1978. Trout predation and the size-composition of stream drift. Limnology and Oceanography 23:1231-1237.

Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:183-192.

Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60:309-320.

Allen, K. R. 1951. The Horokiwi stream: a study of a trout population. Bullet of New Zealand Department of Fishery 10:1-231.

Anderson, W. B., Wait, D.A., and Stapp, P. 2008. Resources from another place and time: Responses to pulses in a spatially subsidized system. Ecology 89(3):660-670.

Angermeier, P. L., and R. A. Smogor. 1994. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. Canadian Journal of Fisheries and Aquatic Sciences 52:936-949.

Angradi, T. R., and J. S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 47:199-209.

Armstrong, J. B., and D. E. Schindler. 2013. Going with the flow: spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. Ecosystems 16:1429-1441.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91(5):1445-1454.

Armstrong, J. B., G. T. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099-1122.

Armstrong, J. B., D. E. Schindler, C. J. Cunningham, W. Deacy, and P. Walsh. 2020. Watershed complexity increases the capacity for salmon-wildlife interactions in coastal ecosystems. Conservation Letters 13(2):e12689.

Arrington, D. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes "run on empty"? Ecology 83:2145-2151.

Baldwin, C. M., D. A. Beauchamp, and C. P. Gubala. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. Transactions of the American Fisheries Society 131:143-158.

Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences 43(1):160-168.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Nonnative stream fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656-2663.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2007. Invading rainbow trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. Oecologia 153:461-470.

Beauchamp, D. A. 2009. Bioenergetic Ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. American Fisheries Society Symposium 70, 2009.

Beauchamp, D. A., D. H. Wahl, and B. M. Johnson. 2007. Predator-Prey Interactions. Pages 765-842 in C. S. Guy and M. L. Brown, editors. 2007. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitats in northwestern Washington streams. Transactions of the American Fisheries Society 126:217-229.

Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23(1):189-207.

Benfield, E. F. 1996. Leaf breakdown in stream ecosystems. Methods in Stream Ecology, 27:579-589.

Benke, A. C., A. D. Huryn, L. A. Smock, and B. J. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):1-17.

Berejikian, B. A., L. A. Campbell, and M. E. Moore. 2013. Large scale freshwater habitat features influence the degree of anadromy in eight Hood Canal *Oncorhynchus mykiss* populations. Canadian Journal of Fisheries and Aquatic Sciences 70:756-765.

Berejikian, B. A., M. E. Moore, and S. J. Jeffries. 2016. Predator-prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. Marine Ecology Progress Series 543:21-35.

Berg, O. K., and G. Bremset. 1998. Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout. Journal of Fish Biology 52(6):1272-1288.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308(5722):636–637.

Bilby, R. E., B. R. Franse, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 55:1909-1918.

Bilby, R. E., T. Bennett, and P. Roni. 2002. Utilization of nitrogen from spawning salmon by juvenile Chinook salmon and steelhead in two tributaries of the Columbia River. Report prepared for Bonneville Power Administration. BPA Contract #99-041-00. Pp 1-40.

Biro, P. A., J. R. Post, and M. V. Abrahams. 2005. Ontogeny of energy allocation reveals selective pressure promoting risk-taking behavior in young fish cohorts. Proceedings Biological Sciences 272(1571):1443-1448.

Bisson, P. A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. Journal of the Fisheries Research Board of Canada 35:971-975.

Bisson, P. A., J. L. Nielsen, R. A. Palmason., and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 in N. B. Armantrout (Ed.) Acquisition and Utilization of Aquatic Inventory Information. Symposium proceedings, October 28-30, 1981, Portland, Oregon. The Hague Publishing, Billings, MT.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262-273.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242-2252.

Boss, S. M., and J. S. Richardson. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1044-1053.

Brady, M. E., J. B. Armstrong, and A. Chione. In draft. Beyond summer: review of the temporal aspects of juvenile salmon and riverscape studies reveals the need for year-round research.

Bramblett, R. G., M. D. Bryant, B. E. Wright, and R. G. White. 2002. Seasonal use of small tributary and main-stem habitats by juvenile steelhead, coho salmon, and dolly varden in a southeastern Alaska drainage basin. Transactions of the American Fisheries Society 131:498-506.

Brenkman, S. J., J. J. Duda, C. E. Torgersen, E. Welty, G. R. Pess, R. Peters, and M. L. McHenry. 2012. A riverscape perspective of Pacific salmonids and aquatic habitats prior to large-scale dam removal in the Elwha River, Washington, USA. Fisheries Management and Ecology 19(1):36-53.

Brennan, S. R., D. E. Schindler, T. J. Cline, T. E. Walsworth, G. Buck, and D. P. Fernandez. 2019. Shifting habitat mosaics and fish production across river basins. Science 364(6442):783-786.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pp 279-352 in Fish Physiology, vol 8. W. S. Hoar, D. J. Randall, and J. R. Brett, eds. New York: Academic Press.

Brett, J. R., W. C. Clarke, and J. E. Shelburn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile Chinook salmon *Oncorhynchus tshawytscha*. Canadian Technical Report of Fisheries and Aquatic Sciences No 1127.

Brett, M. T., G. W. Holtgrieve, and D. E. Schindler. 2018. An assessment of assumptions and uncertainty in deuterium-based estimates of terrestrial subsidies to aquatic consumers. Ecology 99(5):1073-1088.

Bridcut, E. E. 2000. A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. Hydrobiologia 427:83-100.

Brown, A. V., and P. P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. Hydrobiologia 220:99-108.

Brown, R. S., W. A. Hubert, and S. F. Daly. 2011. A primer on winter, ice, and fish: what fisheries biologists should know about winter ice processes and stream-dwelling fish. Fisheries 36(1):8-26.

Bull, C. D., N. B. Metcalfe, and M. Mangel. 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. Proc. R. Soc. Lond. B 263:13-18.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32(5):667-680.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389-1406.

Canning, D. J., J. L. Randlette, and W. A. Haskins. 1988. Skokomish River comprehensive flood control management plan. Washington Department of Ecology, Report 87-24, Olympia, Washington.

Cederholm, C. J., R. E. Bilby, P. A. Bisson, T. W. Bumstead, B. R. Fransen, W. J. Scarlett, and J. W. Ward. 1997. Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. North American Journal of Fisheries Management 17:947-963.

Claeson, S. M., C. J. LeRoy, J. R. Barry, and K. A. Kuehn. 2014. Impacts of invasive riparian knotweed to litter decomposition, aquatic fungi, and macroinvertebrates. Biological Invasions 16(7):1531-1544.

Cleary, J. S., M. J. Bradford, and D. M. Janz. 2012. Seasonal and spatial variation in lipid and triacylglycerol levels in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from the Bridge River, British Columbia. Limnologica 42(2):144-150.

Cloe, W. W., and G. C. Garman. 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36:106-114.

Collins, S. F., C. V. Baxter, A. M. Marcarelli, and M. S. Wipfli. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. Ecosphere 7(3):e01248.

Connolly, P. J., and J. H. Petersen. 2003. Bigger is not always better for overwintering young-of-year steelhead. Transactions of the American Fisheries Society 132:262-274.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric Equivalents for Investigations in Ecological Energetics, SIL Communications, 1953-1996, 18(1):1-158.

Cummins, K. W., C. E. Cushing, and G. W. Minshall. 1995. Introduction: an overview of stream ecosystems. In: River and Stream Ecosystems (eds C. E. Cushing, K. W. Cummins, and G. W. Minshall) pp 1-8. Elsevier, New York.

Cunjak, R. A., A. Curry, and G. Power. 1987. Seasonal energy budget of brook trout in streams: implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116(6):817-828.

Deacy, W. W., J. B. Armstrong, W. B. Leacock, C. T. Robbins, D. D. Gustine, E. J. Ward, J. A. Erlenbach, and J. A. Stanford. 2017. Resource synchronization disrupts predation. Proceedings of the National Academy of Sciences 114(39):10432-10437.

Denton, K. P., H. B. Rich Jr., J. W. Moore, and T. P. Quinn. 2010. The utilization of a Pacific salmon *Oncorhynchus nerka* by three populations of charr *Salvelinus* spp. Journal of Fish Biology 77:1006-1023.

Dineen, G., S. S. C. Harrison, and P. S. Giller. 2007. Seasonal analysis of aquatic and terrestrial invertebrate supply to streams with grassland and deciduous riparian vegetation. Biology and Environment: Proceedings of the Royal Irish Academy 107B(3):167-182.

Dockray, J. J., S. D. Reid, and C. M. Wood. 1996. Effects of elevated summer temperatures and reduced pH on metabolism and growth of juvenile rainbow trout (*Oncorhynchus mykiss*) on unlimited ration. Canadian Journal of Fisheries and Aquatic Sciences 53:2752-2763.

Doctor-Shelby, K., and B. Berejikian. In Draft. Trophic dynamics and temperature interact to determine growth and age-at-smoltification in Hood Canal steelhead, *Oncorhynchus mykiss.*

Dunham, J. B., M. E. Rahn, R. E. Schroeter, and S. W. Breck. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. Western North American Naturalist 60:304-310.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.

Edwards, E. D., and A. D. Huryn, 1995. Annual contribution of terrestrial invertebrates to a New Zealand stream New Zealand Journal of Marine and Freshwater Research 29:467-477.

Edwards, E. D., and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. Hydrobiologia 337:151-159.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503-523.

Einum, S., and K. H. Nislow. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143:203-210.

Elliott, J. M. 1982. The effects of temperature and ration size on the growth and energetics of salmonids in captivity. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry 73(1):81-91.

Erős, T., P. Gustafsson, and L. A. Greenberg. 2012. Forest-stream linkages: effects of terrestrial invertebrate input and light on diet and growth of Brown Trout (*Salmo trutta*) in a boreal forest stream. PLoS ONE 7(5): e36462.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6): 483-498.

Favrot, S. D., B. C. Jonasson, and J. T. Peterson. 2018. Fall and winter microhabitat use and suitability for spring Chinook salmon parr in a U.S. Pacific Northwest river. Transactions of the American Fisheries Society 147(1): 151-170.

Fierro, P., L. Quilodrán, C. Bertrán, I. Arismendi, J. Tapia, F. Peña-Cortés, E. Hauenstein, R. Arriagada, E. Fernández, and L. Vargas-Chacoff. 2016. Rainbow trout diets and macroinvertebrates assemblages responses from watersheds dominated by native and exotic plantations. Ecological Indicators 60:655-667.

Figge, F. 2004. Bio-folio: applying portfolio theory to biodiversity. Biodiversity and Conservation 13:827-849.

Flitcroft, R., K. Burnett, J. Snyder, G. Reeves, and L. Ganio. 2014. Riverscape patterns among years of juvenile coho salmon in midcoastal Oregon: implications for conservation. Transactions of the American Fisheries Society 143:26-38.

Foote, C. J., and G. S. Brown. 1998. Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 55:1524-1533.

Forrester, G. E., J. G. Chase, and W. McCarthy. 1994. Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. Environmental Biology of Fishes 39:301-311.

Fraser, N. H. C., and N. B. Metcalfe. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. Functional Ecology 11:385-391.

Garman, G. C. 1991. Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. Environmental Biology of Fishes 30:325-331.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems: Pacific salmon subsidize freshwater and terrestrial ecosystems through several pathways, which generates unique management and conservation issues but also provides valuable research opportunities. Bioscience 52:917-928

Giannico, G. R., and S. G. Hinch. 2007. Juvenile coho salmon (*Oncorhychus kisutch*) responses to salmon carcasses and in-stream wood manipulations during winter and spring. Canadian Journal of Fisheries and Aquatic Sciences 64:324-335.

Giles, N. 1980. A stomach sampler for use on live fish. Journal of Fish Biology 16:253-261.

Graca, M. A. S. 2001. The role of invertebrates in leaf litter decomposition in streams--a review. International Review of Hydrobiology 86:383-393.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in freshwater systems of the Pacific Northwest. Fisheries 25(1):15-21.

Groot, C., L. Margolis, and W. C. Clarke, editors. 1995. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8(9): 993-1009.

Hafs, A. W., J. M. Niles, and K. J. Hartman. 2011. Efficiency of gastric lavage on age-0 brook trout and the influence on growth and survival. North American Journal of Fisheries Management 31:530–534.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80(1):4-18.

Hatchery Scientific Review Group (HSRG). March 2004. Hatchery Reform Recommendations for the Puget Sound and Coastal Washington Hatchery Reform Project: Hood Canal. 62 p. Long Live the Kings, 1305 Fourth Avenue, Suite 810, Seattle, WA 98101 (available from www.hatcheryreform.org)

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63(6):1840-1856.

Heim, K. C., T. E. McMahon, L. Calle, M. S. Wipfli, and J. A. Falke. 2019. A general model of temporary aquatic habitat use: water phenology as a life history filter. Fish and Fisheries 20:802-816.

Hendry, A. P. and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology 77:1663-1675.

Hicks, B. J., M. S. Wipfli, and D. W. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oecologia 144:558-569.

Hladyz, S., K. Abjornsson, P. S. Giller, and G. Woodward. 2011. Impacts of an aggressive riparian invader on community structure and ecosystem functioning in stream food webs. Journal of Applied Ecology 48(2):443-452.

Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609-1612.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181-2194.

Huet, M. 1959. Profiles and biology of western European streams as related to fish management. Transactions of the American Fisheries Society 88:155-163.

Hunt, R. L. 1975. Use of terrestrial invertebrates as food by salmonids. In: Coupling of Land and Water Systems (ed. A. D. Hasler) pp. 137-152. Springer-Verlag, New York.

Hurst, T. P., and D. O. Conover. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology 84:3360-3369.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnological Oceanography 41:243-252.

Huusko, A., L. Greenberg, M. Stickler, T. Linnansaari, M. Nykänen, T. Vehanen, S. Koljonen, P. Louhi, and K. Alfredsen. 2007. Life in the ice lane: the winter ecology of stream salmonids. River Research and Applications 23:469-491.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, 555 pp.

Irvine, J. R., and B. R. Ward. 1989. Patterns of timing and size of wild coho salmon (*Oncorhynchus kisutch*) smolts migrating from the Keogh River watershed on northern Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences 46:1086-1094.

Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biology 21:2540-2553.

Jaecks, T., and T. P. Quinn. 2014. Ontogenetic shift to dependence on salmon-derived nutrients in Dolly Varden char from the Iliamna River, Alaska. Environmental Biology of Fishes 97:1323-1333.

Johansen, M., E. B. Thorstad, A. H. Rikardsen, J. I. Koksvik, O. Ugedal, A. J. Jensen, L. Saksgård, and T. F. Næsje. 2010. Prey availability and juvenile Atlantic salmon feeding during winter in a regulated subarctic river subject to loss of ice cover. Hydrobiologia 644:217-229.

Johnson, J. H., and N. H. Ringler. 1980. Diets of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) relative to prey availability. Canadian Journal of Zoology 58(4):553-558.

Johnson, J. H., J. E. McKenna, and K. A. Douglass. 2013. Movement and feeding ecology of recently emerged steelhead in Lake Ontario tributaries. Journal of Applied Ichthyology 29: 221-225.

Johnson, J. M., and D. M. Post. 1996. Morphological constraints on intracohort cannibalism in age-0 largemouth bass. Transactions of the American Fisheries Society 125:809-812.

Jones, W., W. S. C. Gurney, D. C. Speirs, P. J. Bacon, and A. F. Youngson. 2002. Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. Journal of Animal Ecology 71:916-924.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters 10:690-700.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46(3):303-316.

Kaylor, M. J., and D. R. Warren. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. Ecosphere 8(6):e01845. 10.1002/ecs2.1845.

Kennedy, B. P., K. H. Nislow, and C. L. Folt. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. Ecology 89:2529–2541.

Kennedy, T. A., and S. A. Hobbie. 2004. Saltcedar (*Tamarix remosissima*) invasion alters organic matter dynamics in a desert stream. Freshwater Biology 49:65-76.

Kline, T. C., J. J. Goering, and R. J. Piorkowski. 1997. The effect of salmon carcasses on Alaskan freshwaters. Pages 179–204 in A. M. Milner, and M. W. Oswood, editors. Freshwaters of Alaska: ecological syntheses. Springer-Verlag, New York.

Kominoski, J. S., L. B. Marczak, and J. S. Richardson. 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. Ecology 92(1):151-159.

LeRoy, C. J., and J. C. Marks. 2006. Litter quality, stream characteristics, and litter diversity influence decomposition rates and macroinvertebrates. Freshwater Biology 51(4):605-617.

LeRoy, C. J., D. G. Fischer, W. M. Andrews, L. Belleveau, C. H. Barlow, J. A. Schweitzer, J. K. Bailey, J. C. Marks, and J. C. Kallestad. 2016. Salmon carcasses influence genetic linkages between forests and streams. Canadian Journal of Fisheries and Aquatic Sciences 73(6):910-920.

Li, J. L., W. J. Gerth, R. P. Van Driesche, D. S. Bateman, and A. T. Herlihy. 2016. Seasonal and spatial fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 73:1642-1649.

Lichatowich, J. A. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, District of Columbia, USA

Light, R. W., P. H. Alder, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81–85.

Limm, M. P., and M. P. Marchetti. 2009. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Environmental Biology of Fishes 85:141-151.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. A. Hoffman, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. Austral Ecology 37:757-757.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Mason, C. F., and S. M. MacDonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology 12:305-311.

McCabe, G. J., M. P. Clark, and L. E. Hay. 2007. Rain-on-snow events in the western United States. Bulletin of the American Meteorological Society 88(3):319-328.

McCarthy, S. G., J. J. Duda, J. M. Emlen, G. R. Hodgson, and D. A. Beauchamp. 2009. Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River watershed, California. Transactions of the American Fisheries Society 138:506-521.

McCormick, S. D., and R. L. Saunders. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Society Symposium 1:211-229

McMeans, B. C., K. S. McCann, M. M. Guzzo, T. J. Bartley, C. Bieg, P. Blanchfield, T. Fernandes, H. Giacomini, T. Middel, M. Rennie, M. Ridgway, and B. Shuter. 2020 (preprint). Winter in water: differential responses and the maintenance of biodiversity. bioRxiV doi: https://doi.org/10.1101/849109.

McMeans, B. C., K. S. McCann, T. D. Tunney, A. T. Fisk, A. M. Muir, N. Lester, B. Shuter, and N. Rooney. 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecological Monographs 86(1):4-19.

Meehan, W. R., and R. A. Miller. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. Journal of the Fisheries Research Board of Canada 35:1359-1363.

Mejia, F. H., A. K. Fremier, J. R. Benjamin, J. R. Bellmore, A. Z. Grimm, G. A. Watson, and M. Newsom. 2019. Stream metabolism increases with drainage area and peaks asynchronously across a stream network. Aquatic Sciences 81:9.

Mellon, C. D., M. S. Wipfli, and J. L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. Freshwater Biology 53:2331-2343.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America, 4th edn. Kendall Hunt, Dubuque, IA.

Moore, J. W., D. E. Schindler, and C. P. Ruff. 2008. Habitat saturation drives thresholds in stream subsidies. Ecology 89(2):306-312.

Moore, J. W., D. E. Schindler, J. L. Carter, J. Fox, J. Griffiths, and G. W. Holtgrieve. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. Ecology 88:1278-1291.

Moore, M. E., B. A. Berejikian., and E. P. Tezak. 2010. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. Transactions of the American Fisheries Society 139:49-61.

Mouton, A. M., M. Buysse, M. Stevens, T. Van Den Neucker, and J. Coeck. 2012. Evaluation of riparian habitat restoration in a lowland river. River Research and Applications 28:845-857.

Myrvold, K. M., and B. P. Kennedy. 2019. Seasonal variation in growth, consumption and growth efficiency in overwintering juvenile steelhead. Ecology of Freshwater Fish 00:1-15. https://doi.org/10.1111/eff.12526

Naiman R. J., and R. E. Bilby, eds. 1998. River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. New York: Springer-Verlag.

Naiman, R. J., and H. De'camps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences 109(52):21201-21207.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399-417.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98(1):155-170.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999b. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441.

Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara. 1999a. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecological Research 14:351-360.

Näslund, J., D. Aldvén, and L. Závorka. 2015. Eggs from anadromous adults provide marine-derived nutrients to Atlantic salmon and brown trout parr in late autumn – observations from a Swedish coastal stream. Environmental Biology of Fishes DOI 10.1007/s10641-015-0436-y

Nelson, M. C., and J. D. Reynolds. 2015. Effects of subsidies from spawning chum and pink salmon on juvenile coho salmon body size and migration timing. Ecosphere 6(10):209.

Neverman, D., and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. Oecologia 98:247-256.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49(4):783-789.

Nielsen, J. L. 1992. Macrohabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Nowlin, W. H., M. J. Vanni, and L. H. Yang. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. Ecology 89(3):647-659.

Persson, A., and C. Bronmark. 2002. Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. Oikos 97:272-281.

Peterson, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:343-368.

Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. Science 305:346–347.

Poff, N. L., D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47(11):769-784.

Point No Point Treaty Council (PNPTC). 2015. Hood Canal steelhead management plan: 2014-2015. 19p.

Polis, G. A., and K. O. Winemiller. 1996. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27(6):787-802.

Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82(4):1040-1051.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press: Seattle, Washington.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Aquatic and Fisheries Sciences 53:1555-1564.

Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54:1211-1234.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz, and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Aquatic and Fisheries Sciences 69:73-84.

Roni, P. 2000. Responses of fishes and salamanders to instream restoration efforts in western Oregon and Washington. Doctoral dissertation. University of Washington, Seattle.

Roni, P. and A. Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. North American Journal of Fisheries Management 20:683-692.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess, 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1-20.

Roon, D. A., M. S. Wipfli, T. L. Wurtz, and A. L. Blanchard. 2016. Invasive European bird cherry (*Prunus padus*) reduces terrestrial prey subsidies to urban Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 73:1-12.

Rosenfeld, J. S. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953-968.

Rosenfeld, J. S., and E. Raeburn. 2009. Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity. Ecology of Freshwater Fish 18:572-584.

Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pool and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58(3):585-593.

Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology 92(11):2073-2084.

Sabo, J. L., and M. E. Power. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860-1869.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336-343.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Sato, T., K. Watanabe, M. Kanaiwa, Y. Niizuma, Y. Harada, and K. D. Lafferty. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology 92(1):201-207.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52:1944-1956.

Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13(5):257-263.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1(1):31-37.

Schindler, D. E., R. Hillborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609-612.

Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71-81.

Service, C. N., A. W. Bateman, M. S. Adams, K. A. Artelle, T. E. Reimchen, P. C. Paquet, and C. T. Darimont. 2019. Salmonid species diversity predicts salmon consumption by terrestrial wildlife. Journal of Animal Ecology 88:392-404.

Skokomish Indian Tribe and Washington Department of Fish and Wildlife (SIT and WDFW). 2017. Recovery Plan for Skokomish River Chinook 2017 update. Skokomish Indian Tribe, Skokomish, WA; Washington Department of Fish and Wildlife, Olympia, WA.

Smeraldo, S., M. D. Febbraro, L. Bosso, C. Flaquer, D. Guixé, F. Lisón, A. Meschede, J. Juste, J. Prüger, X. Puig-Montserrat, and D. Russo. 2018. Ignoring seasonal changes in the ecological niche of non-migratory species may lead to biases in potential distribution models: lessons from bats. Biodiversity and Conservation 27:2425-2441.

Smits, A. P., D. E. Schindler, J. B. Armstrong, M. T. Brett, J. L. Carter, and B. S. Santos. 2016. Thermal constraints on stream consumer responses to a marine resource subsidy. Canadian Journal of Fisheries and Aquatic Sciences 73:1661-1671.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129–1157.

Steingrimsson, S. O., and G. M. Gislason. 2002. Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxa, North-East Iceland. Environmental Biology of Fishes 63:417-426.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press: Princeton, New Jersey.

Stranko, S. A., R. H. Hilderbrand, and M. A. Palmer. 2012. Comparing the fish and benthic macroinvertebrate diversity of restored urban streams to reference streams. Restoration Ecology 20(6):747-755.

Tattam, I. A., H. W. Li, G. R. Giannico, and J. R. Ruzycki. 2017. Seasonal changes in spatial patterns of *Oncorhynchus mykiss* growth require year-round monitoring. Ecology of Freshwater Fish 26(3):434-443.

Thompson, J. N., and D. A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. Transactions of the American Fisheries Society 143:910-925.

Thornton, E. J., J. J. Duda, and T. P. Quinn. 2017. Influence of species, size and relative abundance on the outcomes of competitive interactions between brook trout and juvenile coho salmon. Ethology Ecology & Evolution 29(2):157-169.

Tockner, K., Malard, F., and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14:2861-2883.

Twomey, H. G., and P. S. Giller. 1990. Stomach flushing and individual Panjet tattooing of salmonids: an evaluation of the long-term effects on two wild populations. Aquaculture and Fisheries Management 21:137-142.

U.S. Fish and Wildlife Service (USFWS). 2011. Biological Sampling in the Skokomish River Basin, Washington: Army Corps of Engineers General Investigation. Fisheries Division, Washington Fish and Wildlife Office, Lacey, Washington.

Uehlinger, U. 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. Freshwater Biology 51(5):938-950.

Uno, H., and S. Pneh. 2020. Effect of source habitat spatial heterogeneity and species diversity on the temporal stability of aquatic-to-terrestrial subsidy by emerging aquatic insects. Ecological Research 35(3):474-481.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in Lake Tahoe (California–Nevada) Basin. Ecosystems 6:274–288.

Vanderploeg, H. A., and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecological Modelling 7:135–149.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of North American Benthological Society 8(1):2-8.

Washington Department of Natural Resources (WDNR). 1997. Washington State salmonid stock inventory: bull trout/Dolly Vardon. Olympia, WA.

Washington State Conservation Commission (WCC). 2003. Salmon and steelhead Habitat Limiting Factors: Water Resource Inventory Area 16: Dosewallips-Skokomish Basin. Olympia, WA.

Weber, N., N. Bouwes, and C. E. Jordan. 2014. Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. Canadian Journal of Fisheries and Aquatic Sciences 71(8):1158-1170.

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-NWFSC-24. Seattle, Washington.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393-425.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393-425.

Whited, D. C., M. S. Lornag, M. J. Harner, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2007. Climate, hydrologic disturbance, and succession: drivers of floodplain pattern. Ecology 88(4):940-953.

Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47(4):501-515.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:1259-1269.

Wipfli, M. S. and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957-969.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35(8):373-387.

Wipfli, M. S., and J. Musslewhite. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia 520:153-163.

Wipfli, M. S., J. P. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: Salmon carcasses increase growth rates of steam-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Woo, I., M. J. Davis, C. S. Ellings, S. Hodgson, J. Y. Takekawa, G. Nakai, and S. E. W. De La Cruz. 2019. A mosaic of estuarine habitat types with prey resources from multiple environmental strata supports a diversified foraging portfolio for juvenile Chinook salmon. Estuaries and Coasts 42:1938-1954.

Woodward, G., and A. G. Hildrew. 2002. Food web structure in riverine landscapes. Freshwater Biology 47:777-798.

Wright, L. A. 2010. Winter feeding ecology of coho salmon (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*) in the Skokomish River, Washington. (Published master's thesis). The Evergreen State College, Olympia, Washington.

Wurtsbaugh, W. A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333:846-848.

Young, M. K., R. B. Rader, and T. A. Belish. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. Transactions of the American Fisheries Society, 126:428-437.

APPENDIX A. INFLUENCE OF NATIVE AND INVASIVE TERRESTRIAL PLANTS ON MACROINVERTEBRATE PREY RESOURCES SUPPORTING JUVENILE SALMONIDS

Megan E. Brady and Jonathan B. Armstrong

Abstract

Riparian vegetation contributes allochthonous energy into adjacent aquatic ecosystems directly through falling terrestrial invertebrates and indirectly through aquatic invertebrate utilization of abscised leaves. Terrestrial invertebrates are known to fuel a substantial portion of fish diet. However, less is known about how this resource subsidy varies between native and non-native vegetation. We examined aquatic-terrestrial linkages between juvenile steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) and native and non-native vegetation in the South Fork Skokomish River, Washington, USA. First, we compared aquatic invertebrate colonization of abscised leaves in autumn from four native vegetation species (bigleaf maple, red alder, vine maple, and Sitka willow) and two non-native vegetation species (Himalayan blackberry, and Bohemian knotweed). Then, we evaluated biomass and community composition of terrestrial invertebrates falling into an adjacent river from our six species of vegetation. Finally, we examined links between juvenile salmonid foraging and terrestrial associations of invertebrate prey resources. We found that community composition and biomass were dissimilar between invertebrates found colonizing submerged, abscised leaves. Surprisingly, one of the key contributors to coho diet in autumn (Diptera) were found predominantly associated with submerged Himalayan blackberry leaves and not with those of native vegetation. Furthermore, we found that the terrestrial prey and terrestrial adult forms of aquatic prey foraged by juvenile salmonids were very often associated with specific riparian vegetation. For example, in October,

ground beetles contributed 30% of steelhead diet and 96% of ground beetles found in terrestrial samples were associated with red alder. At times, the non-native plants had a greater biomass of terrestrial invertebrates associated with them; however, this biomass was not utilized by juvenile salmonids. Despite a lower quantity of invertebrates, native plants were associated with more of the specific prey resources that were utilized or preferred by juvenile salmonids. Greater understanding of the effects of specific native and non-native plants on salmonid foraging could help inform targeted habitat restoration and salmon recovery.

Introduction

Allochthonous inputs from riparian zones often subsidize adjacent stream food webs, providing energy-rich prey resources and bridging seasonal energy deficits (Allen 1951; Hynes 1970; Allan et al. 2003; Nakano et al. 1999b; Wipfli and Baxter 2010; Edwards and Huryn 1995; Benfield 1996; Peterson and Cummins 1974; Wallace et al. 1997). These allochthonous inputs to streams take two forms: primary, direct inputs of terrestrial invertebrates that fall into the water as high energy prey available to predatory fishes, such as juvenile salmonids, and secondary production from aquatic invertebrate shredders (Quinn 2005; Wipfli 1997; Baxter et al. 2005), thus providing a vital pathway of energy flow within food webs by breaking down leaves from coarse to fine particulate organic matter (CPOM to FPOM) (Polis and Winemiller 1996; Naiman and De'camps 1997; Cummins et al. 1995). A significant portion of stream salmonid diet is comprised of terrestrial invertebrates, particularly in summer and autumn when terrestrial subsidies have been known to contribute over 50% of fish diet (Cloe and Garman 1996; Kawaguchi and Nakano 2001; Wipfli 1997; Mason and MacDonald 1982).

Changes in riparian habitat can have cascading effects across ecosystem boundaries. Riparian composition determines the type of terrestrial prey subsidies provided to streams (Naiman and De'camps 1997; Mason and MacDonald 1982; Edwards and Huryn 1996). Inter- and intraspecific variation in leaf nutrients has been shown to alter decomposition rates as well as the abundance and diversity of invertebrate colonization (Graca 2001; Kominoski et al. 2011; LeRoy et al. 2016; Hladyz et al. 2011; LeRoy and Marks 2006). As deciduous plant litter is preferred by aquatic invertebrates, changes in riparian composition may alter the prey resources available to fish throughout the year (Iversen 1974; Hieber and Gessner 2002). The effects of fire, deforestation, canopy composition and openness, anthropogenic habitat degradation (waves from large boats, dredging, land development, and pollution) and biological invasions have been shown to affect stream ecosystems by altering primary productivity, invertebrate composition and abundance, stream food web dynamics and prey available to predatory fish, temperature, flow, and the quantity and quality of fish spawning and rearing habitats (Mellon et al. 2008; Erős et al. 2012; Hladyz et al. 2009; Graca 2001; Arrington et al. 2002; Kaylor and Warren 2017; Mouton et al. 2012; Fierro et al. 2016; Hawkins et al. 1982). Invasive plant species impact riparian zones by altering biodiversity, light availability, bank stability, terrestrial invertebrate composition and biomass, ecosystem processes like carbon cycling, and food web structure (Claeson et al. 2014; Ehrenfeld 2003; Caitling 2005). However, changes in aquatic ecosystem processes and invertebrate assemblages in detritus-based food webs due to the presence of terrestrial invasive plant species in riparian communities are poorly understood (Claeson et al. 2014; Hladyz et al. 2011; Naiman and De'camps 1997; Kennedy and Hobbie 2004).

The impact of invasive terrestrial plants on fish is largely unknown due to the unique characteristics of each invasive species (but see Fierro et al. 2016; Roon et al. 2016). Himalayan blackberry, *Rubus armeniacus*, is a widespread invasive plant species in the Pacific Northwest. Little is known about how the presence of this perennial plant alters the flow of organic matter in aquatic food webs through allochthonous inputs of direct and indirect prey subsidies to streams. Bohemian knotweed, *Polygonum bohemicum*, is an aggressive and highly prevalent species native to Asia that is now found throughout the Pacific Northwest. It has intrinsically different leaf properties compared to native plants that may impact terrestrial and aquatic food webs (Claeson et al. 2014).

Riparian management directly and indirectly influences fish productivity by altering the food supply available through aquatic and terrestrial food webs (Allan et al. 2003). Knowledge of terrestrial-aquatic food web linkages is essential to effective habitat restoration. We examined the seasonal colonization of abscised riparian vegetation by aquatic invertebrates and monthly contributions of terrestrial invertebrate prey resources associated with six species of riparian vegetation to juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) diets. The purpose of our work is to understand how direct terrestrial inputs and influence the energy portfolio available to juvenile salmonids. Our study in western Washington did the following: 1) compared aquatic invertebrate colonization of abscised leaves from four native (bigleaf maple, red alder, vine maple, Sitka willow) and two invasive (Bohemian knotweed, Himalayan blackberry) riparian plant species, 2) evaluated monthly contribution of terrestrial invertebrate prey resources into an adjacent river, and 3) examined preferential foraging of juvenile salmonids and identified major terrestrial sources of preferred prey resources.

Methods

Study System

The Hood Canal is an 80-km fjord that comprises one of the four sub-basins of Puget Sound, Washington, USA. Puget Sound steelhead have been listed as threatened under the Endangered Species Act (ESA) since 2007 and populations continue to decline despite greatly reduced fishing mortality associated with commercial, recreational, and tribal fisheries (Moore et al. 2010).

This study examines the South Fork Skokomish River (Fig. 14), a 44.2 km long (37.0 km anadromy limit) river originating in the Olympic Mountains and flowing into the southwest side of Hood Canal, and its largest tributary, Vance Creek. It is a rain-dominant stream with an elevation of 1646 m, mean annual water temperature of 8.1°C, and mean annual flow of 20.95 m3s-1 (Berejikian et al. 2013). Tidal influence extends up the mainstem Skokomish River to the confluence of the South Fork and North Fork (Canning et al. 1988). A rotary screw trap operated by NOAA is located at river mile 1.8, one mile upstream from the confluence of the South Fork Skokomish and Vance Creek.

Anadromous populations of steelhead, coho, and chum (*O. keta*) reside in the study river. Chinook (*O. tshawytscha*) are present in low numbers in the South Fork Skokomish and are largely regarded as hatchery strays and not a viable population. The South Fork Skokomish historically supported pink salmon, spring Chinook, and early run summer chum; however, these populations have been extirpated (WDNR 1997).

The invasive terrestrial plants Himalayan blackberry and Bohemian knotweed are present throughout Hood Canal in varying degrees of understory dominance. There is a higher prevalence of non-native plants in the lowest reaches of the South Fork Skokomish River.

Invertebrate collection was conducted under a Washington State Department of Fish and Wildlife Scientific Collection Permit.

Data Collection

Sampling for terrestrial invertebrates was conducted monthly. Leaf litter pack deployment, however, only occurred during the fall season due to the use of abscised leaves.

Leaf litter aquatic invertebrate colonization

Stream macroinvertebrates were surveyed in riffles and pools with leaf litter bags with 6.44mm mesh size to allow in larger shredder invertebrates (LeRoy and Marks 2006). Abscised leaves were collected in autumn from several trees along the river to account for genetic diversity (LeRoy et al. 2007). Each bag was filled with 5 g of air-dried leaves (LeRoy et al. 2016; Hladyz et al. 2011). Treatments consisted of 6 species in isolation: Himalayan blackberry *(Rubus armeniacus)*, Bohemian knotweed (*Polygonum bohemicum)*, bigleaf maple (*Acer macrophylum)*, red alder (*Alnus rubra)*, vine maple (*Acer circinatum)*, and Sitka willow (*Salix sitchensis*). Five replicates of each of the 6 treatment types were placed at 5 pool and 5 riffle locations and secured to the river-bank (n=60). The leaf packs were collected on 9 December 2018 after 28 days in the river. Entire bags were transported to the lab in polyethylene zip-top bags and processed within 12 hours. Invertebrates were collected by rinsing the leaves over a sieve (500 µm). All samples were preserved in 70% ethanol. Preserved invertebrates were counted, measured, and identified to order and genus (Merritt et al. 2008) when possible with life stage (larvae, pupae, adult) noted. Intact invertebrates were measured to the nearest millimeter to calculate dry mass based on published length-mass regressions (Sabo et al. 2002; Sample et al. 1993; Benke et al. 1999).

Terrestrial invertebrate subsidies to river system

Fallout traps were deployed for 24 hours monthly to quantify the input of terrestrial invertebrates into the river system from specific terrestrial plant species. Traps were placed on the stream bank, underneath the same six species of plants used in the leaf litter colonization sampling (bigleaf maple, red alder, Sitka willow, vine maple, Bohemian knotweed, and Himalayan blackberry) to collect falling terrestrial invertebrates. Knotweed plants die back in the winter and, therefore, were not sampled during the months of December-May when the traps would only collect invertebrates from nearby vegetation of other species. Ten replicate traps were deployed for each of the plant species. Each trap was filled with approximately 1 liter of water and a small amount of dish detergent to break surface-water tension. Invertebrates were preserved and identified as described for leaf litter samples.

Data analysis

Leaf litter aquatic invertebrate colonization

Proportion and mass were calculated for each prey item (by order and species) found in terrestrial samples for each of the six riparian plant species examined.

Diversity of invertebrates was recorded as counts based on taxonomic composition found associated with each tree species in the submerged autumn leaf samples. We calculated Shannon’s diversity index (H’) using the ‘vegan’ R package based on the following equation:

$$H' = -\sum p_i \ln p_i$$

measured where pi is the proportional abundance of the ith species

$$p_i = n_i/N$$

Additionally, we used the ‘vegan’ R package to calculate species richness and evenness.

Macroinvertebrate assemblages among treatments were compared with non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis distance (dissimilarity).

Terrestrial invertebrate subsidies to river system

Monthly proportions and mass were calculated for each of the prey items (by order and species) found in terrestrial samples for each of the six riparian plant species examined.

Monthly diversity of invertebrates was recorded as counts based on taxonomic composition found associated with each plant species sampled for terrestrial invertebrates. We calculated Shannon's diversity index (H') using the 'vegan' R package based on the following equation:

$$H' = -\sum p_i \ln p_i$$

measured where pi is the proportional abundance of the ith species

$$p_i = n_i/N$$

Additionally, we used the 'vegan' R package to calculate species richness and evenness.

Results

Leaf litter aquatic invertebrate colonization

Aquatic invertebrate colonization of submerged leaf litter packs revealed unique order proportions according to leaf species (Fig. 15). Alder leaf litter was dominated by Plecoptera (63%) and Trichoptera (30%). Blackberry leaf litter was dominated by Diptera (60%) and Plecoptera (27%). Knotweed leaf litter was dominated by Plecoptera (63%) and Trichoptera (36%). Bigleaf maple leaf litter was dominated by Plecoptera (65%) and Trichoptera (32%).

Vine maple leaf litter was dominated by Coleoptera (72%) and Plecoptera (19%). Sitka willow leaf litter was dominated by Trichoptera (58%) and Plecoptera (40%).

Aquatic invertebrate species were rarely found on all leaf species (Fig. 16). Flathead mayfly nymphs only found associated with the knotweed leaf litter. Common stonefly nymphs were most abundant associated with knotweed and bigleaf maple leaf litter. Crane fly larva was only found with bigleaf maple leaf litter. Dance fly larva were most abundant associated with blackberry leaf litter. Free living caddis fly larva were most abundant with knotweed and willow leaf litter. Non-biting midge larva were not highly abundant but were found in small amounts associated with alder, blackberry, and willow leaf litter. Casemaker caddis fly larva were most abundant with bigleaf maple. Predaceous diving beetle larva were only found with vine maple leaf litter. Riffle beetle larva were found primarily on alder leaf litter. Rolled wing stonefly nymphs were most associated with alder and knotweed. Small minnow mayfly nymphs were found in small amounts on all vegetation types. Stripetail stonefly nymphs were most abundant with alder and vine maple leaf litter. Tube maker caddis fly larva were found in small amounts on blackberry and bigleaf maple leaf litter. Invertebrate species community assemblages on plant species did not closely resemble each other, except for alder and knotweed, which were more similar than dissimilar (Fig. 17).

Shannon’s diversity index ranked willow (H=2.04) leaf litter to host the most diverse assemblage of aquatic invertebrate species, while vine maple (H=1.72) hosted the least diverse invertebrate assemblage (Table 9). Invertebrate species richness was greatest among willow and blackberry (S=11) and lowest among vine maple (S=8) (Table 10). Pielou’s ranking of species evenness was highest for bigleaf maple (J=0.87) and lowest for blackberry (J=0.81) (Table 11).

Terrestrial invertebrate subsidies to river system

The proportion of terrestrial invertebrates associated with the six plant species included in this study varied greatly between plants species and month (Fig. 18). Across the full year, the greatest proportion of invertebrates associated with alder were ground beetles (31%), caterpillars (19%), and spiders (12%). The greatest proportion of invertebrates associated with blackberry were caterpillars (69%), spiders (8%), ants (5%), and leafhoppers (5%). The greatest proportion of invertebrates associated with knotweed were caterpillars (36%), ants (21%), and spiders (14%). The greatest proportion of invertebrates associated with bigleaf maple were caterpillars (28%), ground beetles (14%), leafhoppers (9%), and wasps (9%). The greatest proportion of invertebrates associated with vine maple were ground beetles (56%), spiders (20%), and caterpillars (4%). The greatest proportion of invertebrates associated with willows were sweat bees (30%), adult caddisflies (17%), and wasps (12%).

Terrestrial invertebrate biomass peaked at different points in the year for each of the plant species examined (Fig. 19). The highest biomass in January came from alder (8.97mg) consisting primarily of adult Plecoptera (82%). The highest biomass in February came from vine maple (178.13mg) consisting primarily of Coleoptera (98%). The highest biomass in March came from vine maple (2.16mg) consisting primarily of Coleoptera (99%). The highest biomass in April came from blackberry (184.49mg) consisting primarily of Lepidoptera (93%). The highest biomass in May came from willow (70.47mg) consisting primarily of Hymenoptera (57%) and Diptera (21%). The highest biomass in June came from willow (55.62mg) consisting primarily of Coleoptera (48%) and Araneae (20%). The highest biomass in July came from knotweed (137.95mg) consisting primarily of Hymenoptera (59%) and Hemiptera (17%). The highest biomass in August came from knotweed (84.18mg) consisting primarily of Hymenoptera (54%).

The highest biomass in September came from willow (337.74mg) consisting primarily of Hymenoptera (65%) and adult Trichoptera (34%). The highest biomass in October came from alder (92.59mg) consisting primarily of Coleoptera (49%) and Hemiptera (20%). The highest biomass in November came from knotweed (25.98mg) consisting primarily of Araneae (88%).

Shannon's diversity index showed variation within terrestrial invertebrates grouped by both plant species and month (Table 12). The average annual diversity index for plant species was as follows: alder H=1.28 (sd=0.53), blackberry H=1.27 (sd=0.51), knotweed H=0.88 (sd=0.85), bigleaf maple H=1.28 (sd=0.53), vine maple H=1.00 (sd=0.51), and willow H=1.29 (sd=0.43). Aside from December when no invertebrates were collected due to ice and snow, March had the overall lowest average diversity among all plant types (H=0.42, sd=0.43). July had the overall highest average diversity among all plant types (H=1.78, sd=0.30). Species richness was again variable by both plant species and month (Table 13). Average annual terrestrial invertebrate species richness was lowest in knotweed (S=4.09, sd=4.38) and highest for blackberry (S=6.55, sd=2.84) and willow (S=6.55, sd=3.09). March had the overall lowest average species richness among all plant types (S=1.5, sd=1.26), while July (S=8.5, sd=2.57) and September (S=8.5, sd=1.89) had the greatest species richness. Pielou's species evenness index also showed differences between plant species and month (Table 14). Average annual terrestrial invertebrate evenness was lowest in knotweed (J=0.46, sd=0.41) and highest in willow (J=0.74, sd=0.12). October had the overall lowest average species evenness among all plant types (J=0.43, sd=0.23) while June had the greatest species evenness (J=0.87, sd=0.10).

The dominant terrestrial invertebrate prey items found in juvenile coho and steelhead diets each month (Table 1 and Table 2 from Brady and Armstrong *In Draft)* were found associated with specific vegetation (Table 15). Ants made up 12-21% of fish diet with 88-100%

of terrestrial ant samples found associated with willows in August and May, but 98% of terrestrial ants associated with knotweed in July. Adult mayflies provided 24% of coho diet in July and were associated exclusively with willows (100%). Ground beetles comprised 30% of steelhead diet in October and were primarily associated terrestrially with alders (96%); but in May when they comprised 29% of steelhead diet, they were primarily associated with bigleaf maples (55%) and alders (43%). Spiders contributed 13% of coho diet in October and were most associated with vine maple (57%), alder (24%), and blackberry (13%) during that same time period. The rove beetles that provided 66% of May coho diet were found primarily associated with willows (67%) and bigleaf maples (30%) in the terrestrial environment that month.

As we chose to focus resources on temporal sampling, we acknowledge that these data likely hold spatial biases.

Discussion

The influences of riparian plants, both native and invasive, on stream ecosystems are complex. Although other studies have addressed the influence of invasive terrestrial plants on native plants (Stinson et al. 2006; Vila and Weiner 2004) and some have addressed the differences in ecosystem processes such as decomposition (Claeson et al. 2014; Gordon 1998), this study highlights patterns in invertebrate interactions with terrestrial vegetation within the terrestrial ecosystem and across ecosystem boundaries in an aquatic ecosystem throughout a full year. Our results suggest that direct and indirect prey resource availability for stream fishes may be influenced by riparian composition.

It is well-established that the leaves from riparian plants are colonized by different aquatic invertebrate communities once they fall into the river in autumn (Kawaguchi and Nakano

2001; Wipfli 1997; Nakano et al. 1999a; Dineen et al. 2007; Allan et al. 2003; Mason and MacDonald 1982; Nakano and Murakami 2001; Dunham et al. 2000; Garman 1991; Edwards and Huryn 1996; Hunt 1975; Li et al. 2016). Our study found links between invertebrate prey resources supporting juvenile salmonids and the seasonally submerged leaves supporting those invertebrate prey resources. We found that aquatic invertebrate colonization of submerged leaf litter in late autumn-early winter varied in diversity, richness, and evenness for each of the leaf species examined. The leaf litter from the native plants Bigleaf Maple, Red Alder, and Sitka Willow along with the invasive plant Bohemian knotweed all were colonized dominantly by Plecoptera and Trichoptera nymphs. The native plant Vine Maple was dominantly colonized by Coleoptera while the invasive plant species Himalayan Blackberry was dominantly colonized by Diptera. The invasive plants were never the top contributor of invertebrate biomass for prey items that our previous work revealed to be preferred or important to juvenile steelhead and coho diets (Brady and Armstrong *In Draft*). For example, while the greatest biomass of Plecoptera was found on Knotweed leaves, most of this was from common stoneflies, which were never a major prey resource for juvenile salmonids during the year in our study system. The other two species of stonefly nymphs found on leaves (stripetail stonefly and rolled wing stonefly) were preferred prey resources for juvenile salmonids. These two species were found in greater abundance on native Alder leaves than any other leaf. We believe this indirect relationship between leaves and fish warrants further exploration.

Direct inputs of terrestrial invertebrates into stream systems provide an energy-rich prey resource for stream fishes (Cummins and Wuycheck 1971). Both native and invasive terrestrial plants can impact the food web of juvenile salmonids through varying type and abundance of inputs of terrestrial prey into the aquatic system. Consistent with other research (Wipfli 1997;

Nakano et al. 1999a; Kawaguchi and Nakano 2001; Dineen et al. 2007; Allan et al. 2003; Mason and MacDonald 1982; Nakano and Murakami 2001; Dunham et al. 2000; Garman 1991; Edwards and Huryn 1996; Hunt 1975; Li et al. 2016), we found that terrestrial invertebrates contributed a substantial portion of the energy portfolio supporting stream-dwelling fishes; however, the year-round study of this subsidy revealed differences in the temporal variation of this importance not previously captured. Furthermore, we found that the terrestrial invertebrates that were important to juvenile salmonid diet were found associated with specific riparian plant species; additionally, 9 of these important terrestrial prey resources were principally associated with native vegetation while only 1 prey resource was principally associated with an invasive plant species. For example, ants were provided 12%-13% of juvenile salmonid diet in August in our study river (Brady and Armstrong *In Draft*) with 88% of all terrestrially collected ants coming from the fallout traps beneath Sitka Willows. September provided insights into aspects of quantity versus quality. Knotweed pan traps collected 224.53mg of invertebrate biomass while Bigleaf Maple traps collected only 41.07mg. However, the invertebrates associated with Knotweed were not consumed by either juvenile steelhead or coho, but the invertebrates associated with Bigleaf Maple were. Flying ants were entirely associated with Bigleaf Maple and provided 13% of juvenile steelhead diet in September, only to be exceeded in biomass by ephemeral salmon eggs. Ground beetles in October provided 30% of total steelhead diet biomass with 96% of terrestrially collected beetles associated with Red Alder trees. Rove beetles in May proved to be an important ephemeral terrestrial resource for juvenile coho salmon, comprising 66% of total diet that month as they underwent smoltification and began the migration from freshwater to saltwater. Rove beetles were primarily found associated in the terrestrial environment with Willows (67%) and Bigleaf Maples (30%). Just as diverse prey resources are important at different times of the year, our data suggest that riparian plants host different terrestrial prey items preferred by juvenile salmonids that complete a complementary energy portfolio.

While our previous research has shown that adult rolled wing stoneflies did not appear in fish diets in January (Brady and Armstrong *In Draft*), they were abundant in the terrestrial fallout trap samples for January. The majority of adult stonefly biomass in January was associated with alder trees (72%) with minor associations with bigleaf maple (12%), vine maple (8%), and Sitka willow (8%). However, the aquatic nymph form of this prey resource was an important diet component at several points throughout the year for both juvenile coho and steelhead. Though poorly studied, riparian impacts on the adult reproductive phase of aquatic invertebrates has the potential to impact larval stages that are more frequently utilized as prey resources by juvenile salmonids (Briers and Gee 2004). There is some research to suggest that adult stonefly reproduction requires feeding (Hynes 1942; De Figueroa and Sanchez-Ortega 2000). As such, stonefly association with specific riparian plants may be related to food resources. Similarly, adult mayflies were found to be an important food source for juvenile coho in the month of July, providing 24% of fish diet that month. The terrestrial adult form of this aquatic invertebrate was found exclusively associated with willow plants (100%) during the same time frame. However, there is no evidence that mayflies require food to reproduce in their adult phase, so association with a specific riparian plant may have more to do with microclimate factors such as air temperature, wind speed, or humidity (Briers and Gee 2004). Therefore, terrestrial habitat utilization of the adult form may be important to consider as an indirect influence on juvenile salmonid food resource availability, but further research is needed.

Habitat restoration typically removes invasive plants to benefit native plants as invasive plants often outcompete native plants for space and resources (Alpert et al. 2000). It is also thought that invasive plant displacement of native plants degrades wildlife habitat (Masters and Sheley 2001; Richardson et al. 2007). However, invasive plant removal may not actually improve wildlife habitat (Cohen et al. 2012) and the impact across ecosystem boundaries to stream-dwelling fish has not been largely explored. This research provides evidence that diverse riparian vegetation provides direct inputs of terrestrial invertebrates available to the juvenile salmonid energy portfolio as well as inputs of leaf litter that indirectly affects fish food diversity through the benefit to larval forms of aquatic invertebrates. We believe that riparian habitat restoration would benefit from considering cross-ecosystem relationships between plants, invertebrates, and fish.

References

Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60:309-320.

Allen, K. R. 1951. The Horokiwi stream: A study of a trout population. Bullet of New Zealand Department of Fishery 10:1-231.

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility, and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution, and Systematics 3(1):52-66.

Arrington, D. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes “run on empty”? Ecology 83:2145-2151.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Benfield, E. F. 1996. Leaf breakdown in stream ecosystems. Methods in Stream Ecology, 27:579-589.

Benke, A. C., A. D. Huryn, L. A. Smock, and B. J. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Berejikian, B. A., L. A. Campbell, and M. E. Moore. 2013. Large scale freshwater habitat features influence the degree of anadromy in eight Hood Canal *Oncorhynchus mykiss* populations. Canadian Journal of Fisheries and Aquatic Sciences 70:756-765.

Brady, M. E., J. B. Armstrong, and A. Chione. In draft. Beyond summer: review of the temporal aspects of juvenile salmon and riverscape studies reveals the need for year-round research.

Briers, R. A., and J. H. R. Gee. 2004. Riparian forestry management and adult stream insects. Hydrology and Earth System Sciences Discussions, European Geosciences Union 8(3):545-549.

Canning, D. J., J. L. Randlette, and W. A. Haskins. 1988. Skokomish River comprehensive flood control management plan. Washington Department of Ecology, Report 87-24, Olympia, Washington.

Claeson, S. M., C. J. LeRoy, J. R. Barry, and K. A. Kuehn. 2014. Impacts of invasive riparian knotweed to litter decomposition, aquatic fungi, and macroinvertebrates. Biological Invasions 16(7):1531-1544.

Cloe, W. W., and G. C. Garman. 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36:106-114.

Cohen, J. S., J. C. Maerz, and B. Blossey. 2012. Traits, not origin, explain impacts of plants on larval amphibians. Ecological Adaptations 22(1):218-228.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric Equivalents for Investigations in Ecological Energetics, SIL Communications, 1953-1996, 18(1):1-158.

Cummins, K. W., C. E. Cushing, and G. W. Minshall. 1995. Introduction: an overview of stream ecosystems. In: River and Stream Ecosystems (eds C. E. Cushing, K. W. Cummins, and G. W. Minshall) pp 1-8. Elsevier, New York.

De Figueroa, J. M. T., and A. Sanchez-Ortega. 2000. Imaginal feeding of twelve nemouroidean stonefly species (Insecta, Plecoptera). Annals of the Entomological Society of America 93(2):251-253.

Dineen, G., S. S. C. Harrison, and P. S. Giller. 2007. Seasonal analysis of aquatic and terrestrial invertebrate supply to streams with grassland and deciduous riparian vegetation. Biology and Environment: Proceedings of the Royal Irish Academy 107B(3):167-182.

Dunham, J.B., Rahn, M.E., Schroeter, R.E., and Breck, S.W. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. Western North American Naturalist 60:304-310.

Edwards, E. D., and A. D. Huryn, 1995. Annual contribution of terrestrial invertebrates to a New Zealand stream New Zealand Journal of Marine and Freshwater Research 29:467-477.

Edwards, E. D., and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. Hydrobiologia 337:151-159.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503-523.

Erős, T., P. Gustafsson, and L. A. Greenberg. 2012. Forest-stream linkages: effects of terrestrial invertebrate input and light on diet and growth of Brown Trout (*Salmo trutta*) in a boreal forest stream. PLoS ONE 7(5): e36462.

Fierro, P., L. Quilodrán, C. Bertrán, I. Arismendi, J. Tapia, F. Peña-Cortés, E. Hauenstein, R. Arriagada, E. Fernández, and L. Vargas-Chacoff. 2016. Rainbow trout diets and macroinvertebrates assemblages responses from watersheds dominated by native and exotic plantations. Ecological Indicators 60:655-667.

Garman, G. C. 1991. Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. Environmental Biology of Fishes 30:325-331.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8(4):975-989.

Graca, M.A.S. 2001. The role of invertebrates in leaf litter decomposition in streams--a review. International Review of Hydrobiology 86:383-393.

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63(6):1840-1856.

Hieber Ruiz, M., and M. Gessner. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026-1038.

Hladyz, S., K. Abjornsson, P. S. Giller, and G. Woodward. 2011. Impacts of an aggressive riparian invader on community structure and ecosystem functioning in stream food webs. Journal of Applied Ecology 48(2):443-452.

Hladyz, S., M. O. Gessner, P. S. Giller, J. Pozo, and G. Woodward. 2009. Resource quality and stoichiometric constraints on stream ecosystem functioning. Freshwater Biology 54:957-970.

Hunt, R.L. 1975. Use of terrestrial invertebrates as food by salmonids. In: Coupling of Land and Water Systems (ed. A.D. Hasler) pp. 137-152. Springer-Verlag, New York.

Hunt, R. L. 1975. Use of terrestrial invertebrates as food by salmonids. In: Coupling of Land and Water Systems (ed. A.D. Hasler) pp. 137-152. Springer-Verlag, New York.

Hynes, H. B. N. 1942. A study on the feeding of adult stoneflies (Plecoptera). Proceedings of the Royal Entomological Society of London. Series A, General Entomology 17:81-82.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, 555 pp.

Iversen, T. M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. Oikos 25:278-282.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46(3):303-316.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46(3):303-316.

Kaylor, M. J., and D. R. Warren. 2017. Linking riparian shade and the legacies of forest management to fish and vertebrate biomass in forested streams. Ecosphere 8(6):e01845. 10.1002/ecs2.1845.

Kennedy, T. A., and S. A. Hobbie. 2004. Saltcedar (*Tamarix remosissima*) invasion alters organic matter dynamics in a desert stream. Freshwater Biology 49:65-76.

Kominoski, J. S., L. B. Marczak, and J. S. Richardson. 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. Ecology 92(1):151-159.

LeRoy, C. J., T. G. Whitman, S. C. Wooley, and J. C. Marks. 2007. Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. Journal of the North American Benthological Society 26(3):426-438.

LeRoy, C. J., and J. C. Marks. 2006. Litter quality, stream characteristics, and litter diversity influence decomposition rates and macroinvertebrates. Freshwater Biology 51(4):605-617.

LeRoy, C. J., D. G. Fischer, W. M. Andrews, L. Belleveau, C. H. Barlow, J. A. Schweitzer, J. K. Bailey, J. C. Marks, and J. C. Kallestad. 2016. Salmon carcasses influence genetic linkages between forests and streams. Canadian Journal of Fisheries and Aquatic Sciences 73(6):910-920.

Li, J. L., W. J. Gerth, R. P. Van Driesche, D. S. Bateman, and A. T. Herlihy. 2016. Seasonal and spatial fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 73:1642-1649.

Mason, C. F., and S. M. MacDonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology 12:305-311.

Masters, R. A., and R. L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. Journal of Rangeland Management 54:502-517.

Mellon, C. D., M. S. Wipfli, and J. L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. Freshwater Biology 53:2331-2343.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America, 4th edn. Kendall Hunt, Dubuque, IA.

Moore, M. E., B. A. Berejikian., and E. P. Tezak. 2010. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. Transactions of the American Fisheries Society 139:49-61.

Mouton, A. M., M. Buysse, M. Stevens, T. Van Den Neucker, and J. Coeck. 2012. Evaluation of riparian habitat restoration in a lowland river. River Research and Applications 28:845-857.

Naiman, R. J., and H. De'camps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98(1):155-170.

Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara. 1999a. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecological Research 14:351-360.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999b. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441.

Peterson, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:343-368.

Polis, G. A., and K. O. Winemiller. 1996. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press: Seattle, Washington.

Richardson, D. M., P. M. Holmes, K. J. Esler, S. M. Galatowitsch, J. C. Stromberg, S. P. Kirkman, P. Pysek, and R. J. Hobbs. 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Diversity and Distributions 13:126-139.

Roon, D. A., M. S. Wipfli, T. L. Wurtz, and A. L. Blanchard. 2016. Invasive European bird cherry (*Prunus padus*) reduces terrestrial prey subsidies to urban Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 73:1-12.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336-343.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, S. G. Hallett, D. Prati, and J. N. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biology 4(5):e140

Vila, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. Oikos 105:229-238.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Washington Department of Natural Resources (WDNR). 1997. Washington State salmonid stock inventory: bull trout/Dolly Vardon. Olympia, WA.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:1259-1269.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. Fisheries 35(8):373-387.

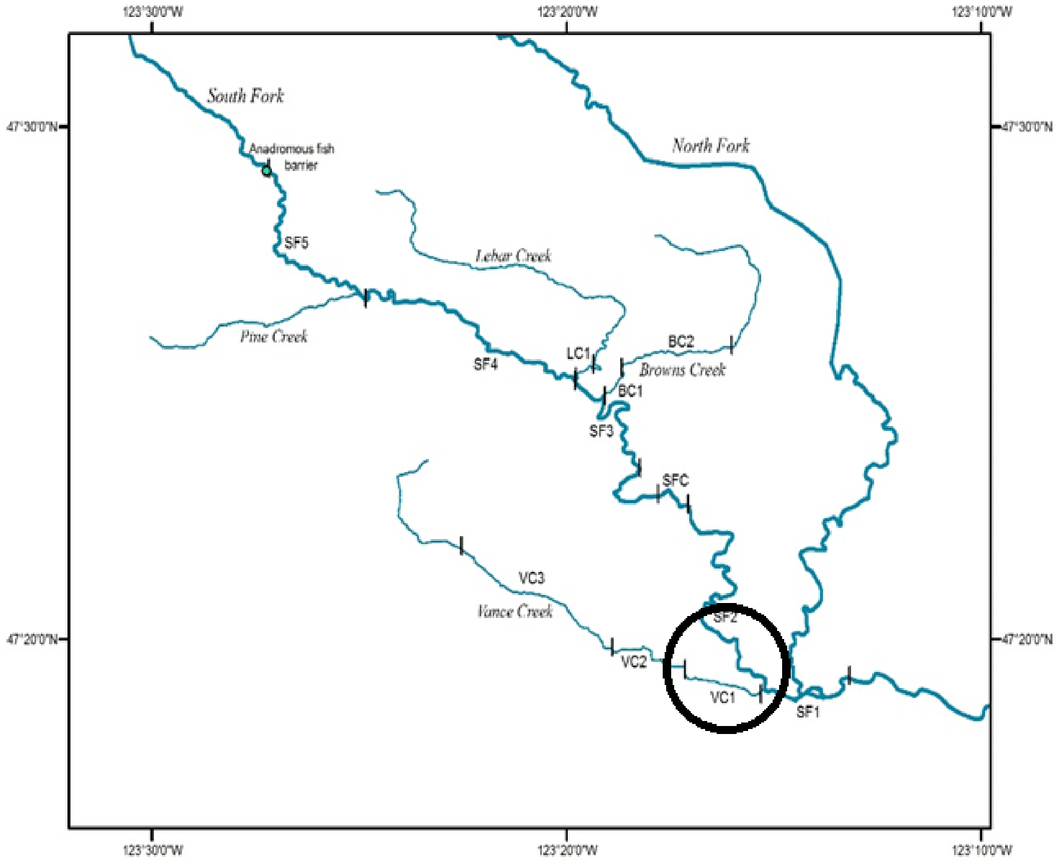


Figure 14. Study system map

South Fork Skokomish River with tributaries, anadromy barrier, and survey reaches.

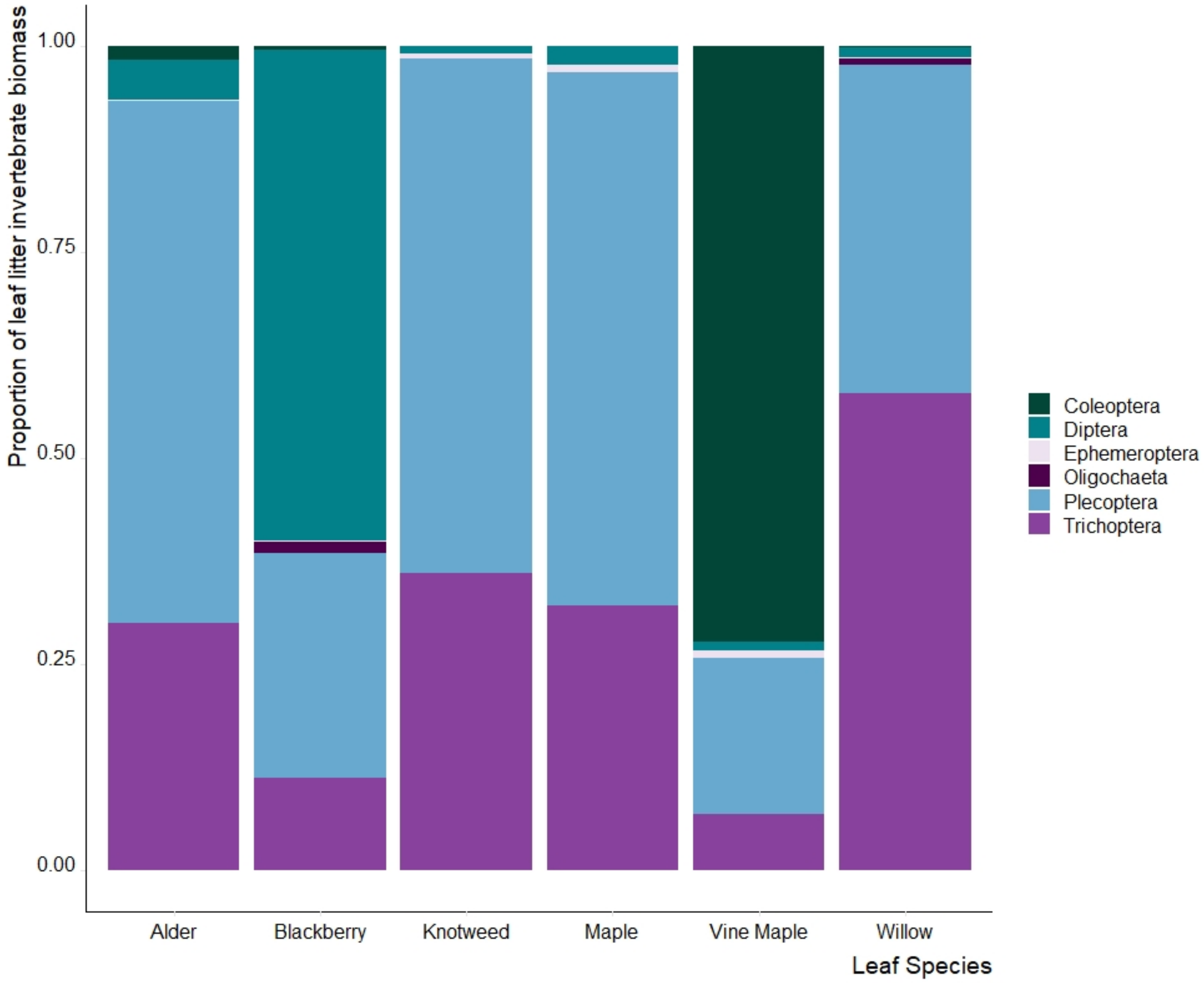


Figure 15. Leaf colonization by aquatic invertebrates
Proportion of total aquatic invertebrate colonization of leaf litter packs by invertebrate order, grouped by leaf species. All treatments n=10, retrieved from river after 28 days.

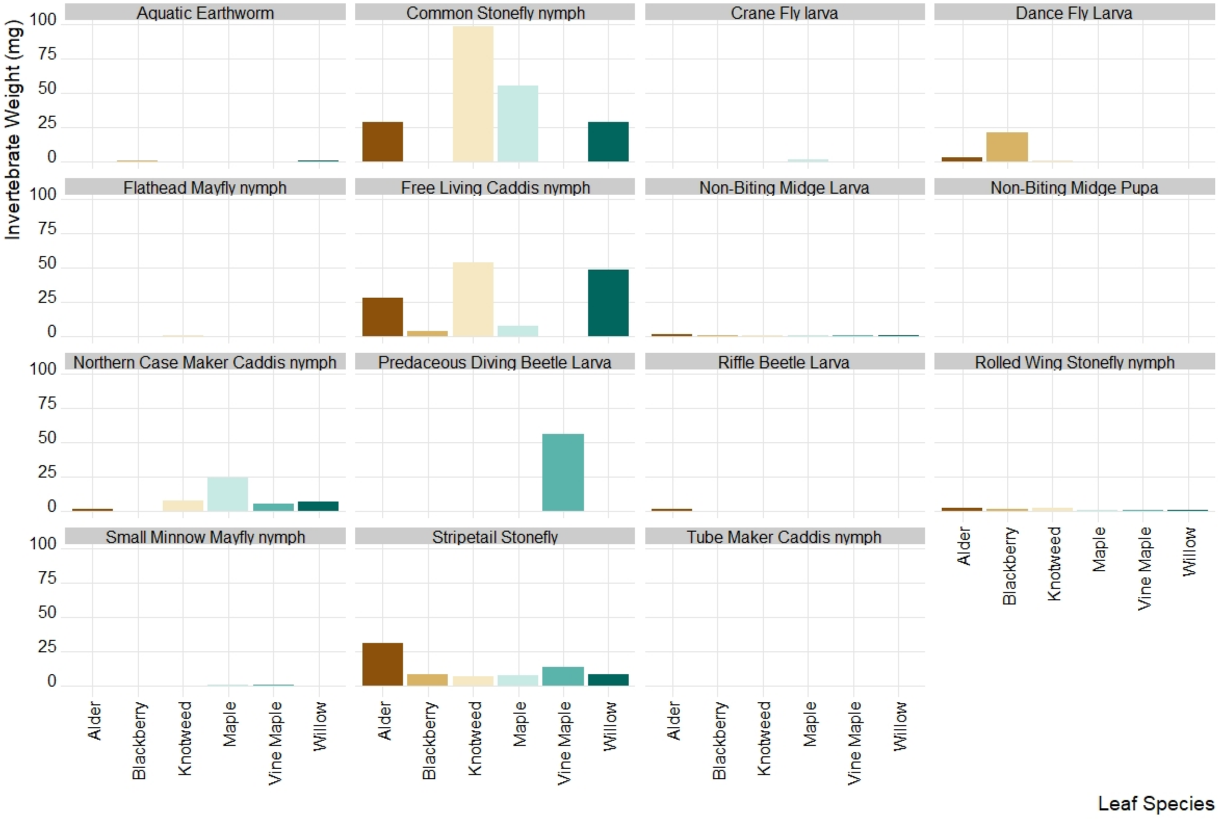


Figure 16. Aquatic invertebrate biomass on submerged leaves
Weight of aquatic invertebrate colonization of leaf litter packs by invertebrate species, grouped by leaf species. All treatments n=10, retrieved from river after 28 days.

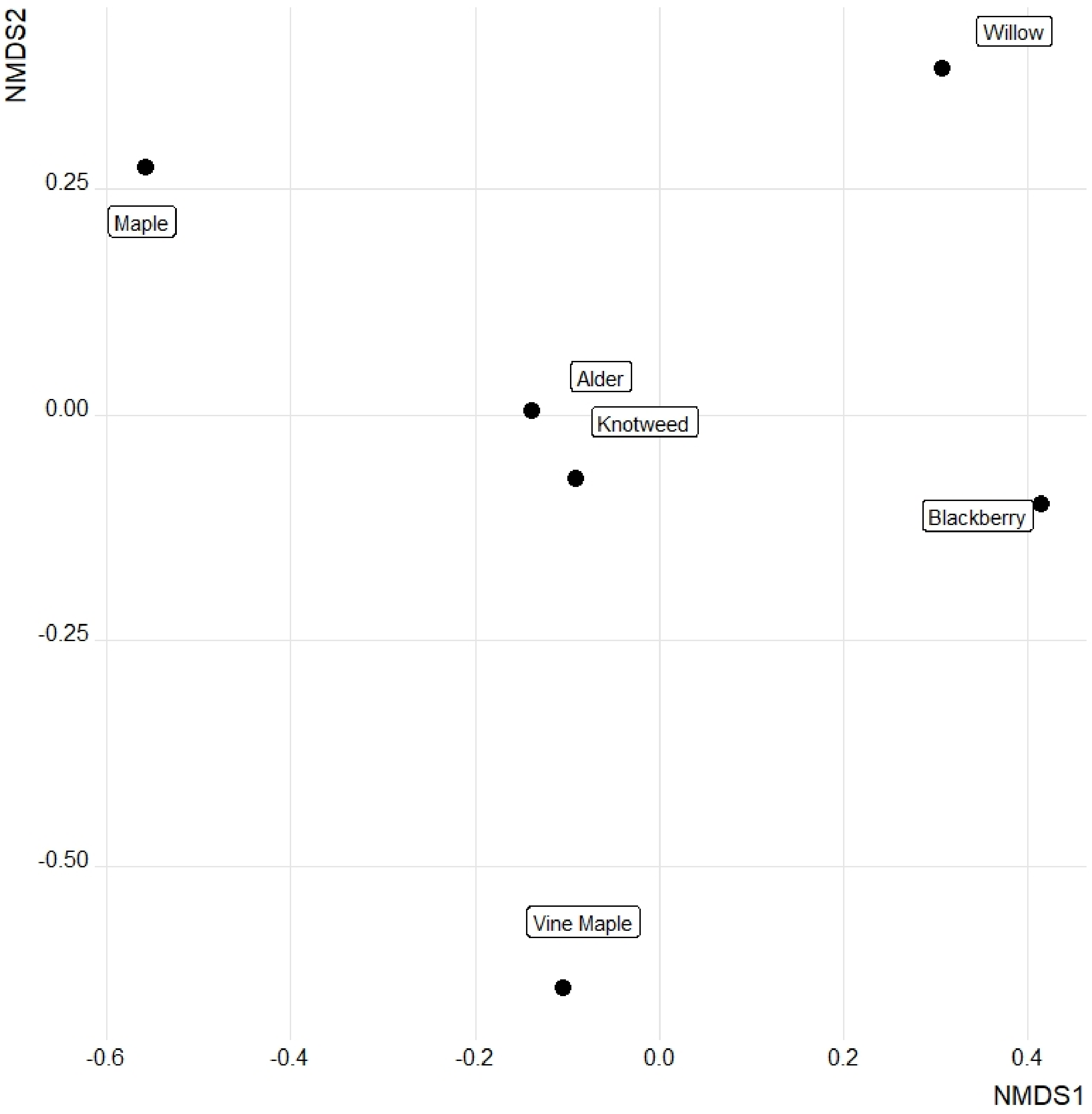


Figure 17. Dissimilarity of aquatic invertebrate communities on leaf species Non-metric multi-dimensional scaling (NMDS) of aquatic macroinvertebrate species assemblages associated with leaf litter packs.

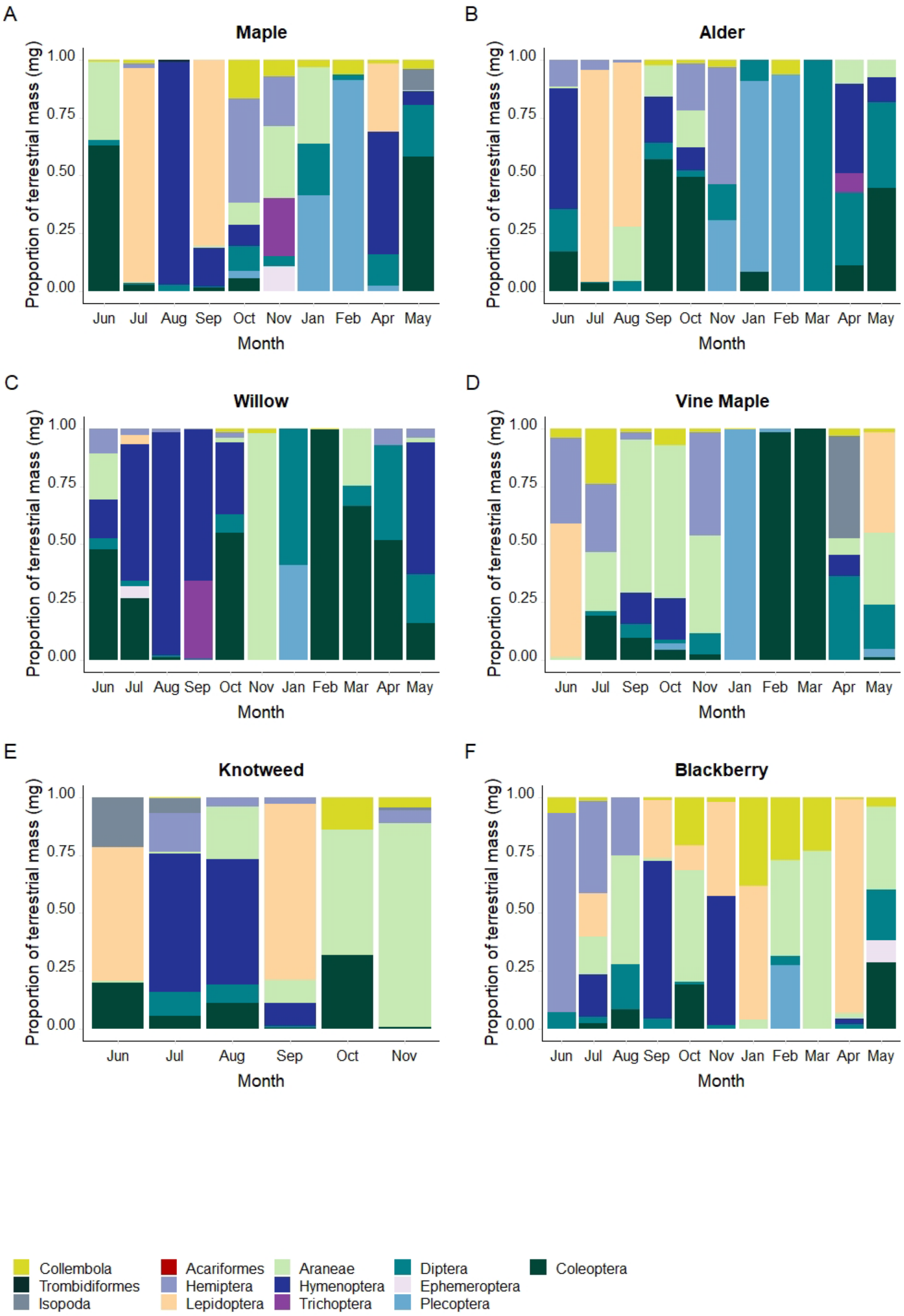


Figure 18. Invertebrates associated with terrestrial vegetation
Monthly proportion of invertebrates by order found in the terrestrial environment associated with six common riparian vegetation species: Bigleaf Maple (A), Red Alder (B), Sitka Willow (C), Vine Maple (D), Knotweed (E), and Blackberry (F).

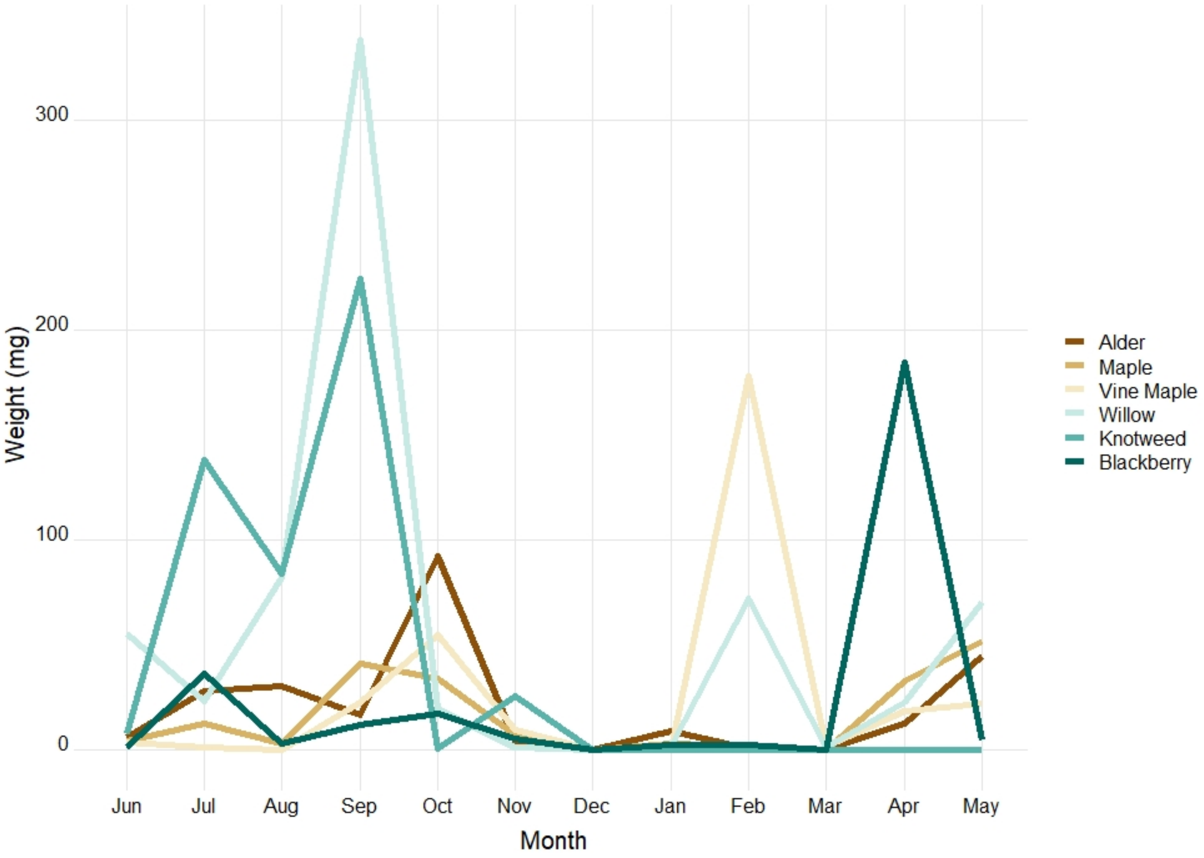


Figure 19. Monthly biomass of invertebrates associated with terrestrial vegetation
Monthly total weight of terrestrial invertebrates collected from beneath riparian plants, n=10 each species.

Table 9. Aquatic invertebrate diversity

Shannon's diversity index for aquatic invertebrate colonization of leaf litter packs.

	Shannon Diversity Index
Leaf Litter Alder	1.843271688
Leaf Litter Blackberry	1.934576093
Leaf Litter Knotweed	1.918056723
Leaf Litter Maple	1.903896859
Leaf Litter Vine	1.720620659
Leaf Litter Willow	2.043211378

Table 10. Aquatic invertebrate richness

Species richness (number of unique species) for aquatic invertebrate colonization of leaf litter packs.

	Species Richness (Number)
Leaf Litter Alder	9
Leaf Litter Blackberry	11
Leaf Litter Knotweed	10
Leaf Litter Maple	9
Leaf Litter Vine	8
Leaf Litter Willow	11

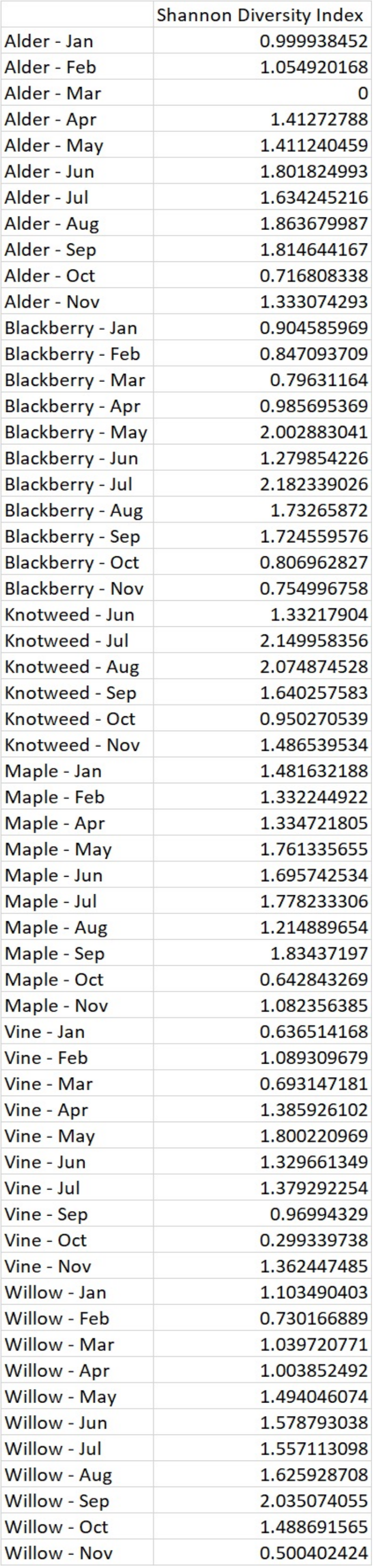
Table 11. Aquatic invertebrate evenness

Pielou’s species evenness for aquatic invertebrate colonization of leaf litter packs.

	Pielou's Species Evenness
Leaf Litter Alder	0.838909098
Leaf Litter Blackberry	0.806780894
Leaf Litter Knotweed	0.833001451
Leaf Litter Maple	0.866500802
Leaf Litter Vine	0.827443631
Leaf Litter Willow	0.852085327

Table 12. Terrestrial invertebrate diversity

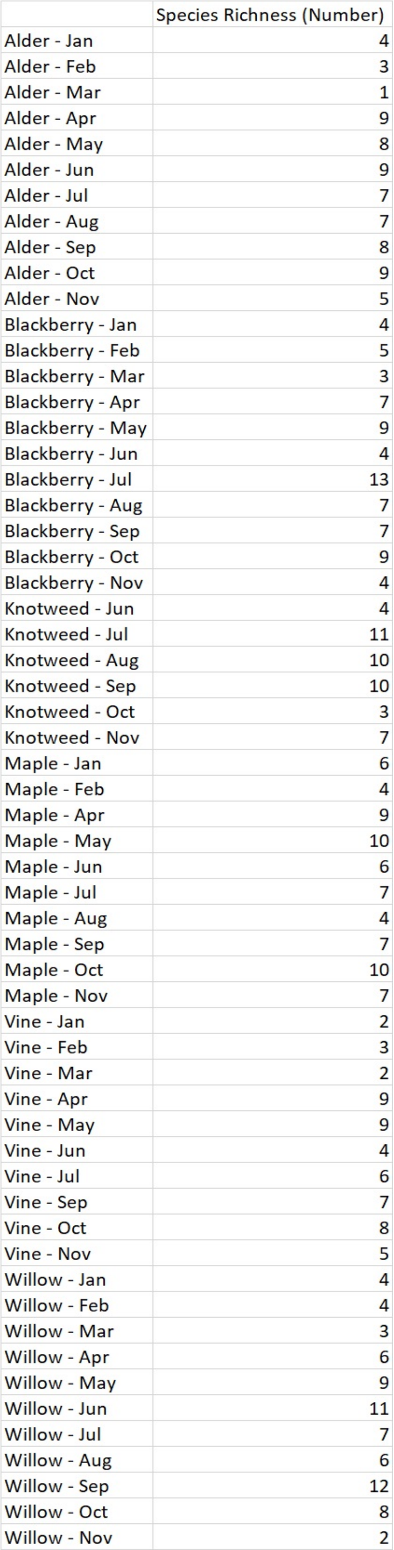
Shannon's diversity index for terrestrial invertebrate association with riparian plant species by month.



	Shannon Diversity Index
Alder - Jan	0.999938452
Alder - Feb	1.054920168
Alder - Mar	0
Alder - Apr	1.41272788
Alder - May	1.411240459
Alder - Jun	1.801824993
Alder - Jul	1.634245216
Alder - Aug	1.863679987
Alder - Sep	1.814644167
Alder - Oct	0.716808338
Alder - Nov	1.333074293
Blackberry - Jan	0.904585969
Blackberry - Feb	0.847093709
Blackberry - Mar	0.79631164
Blackberry - Apr	0.985695369
Blackberry - May	2.002883041
Blackberry - Jun	1.279854226
Blackberry - Jul	2.182339026
Blackberry - Aug	1.73265872
Blackberry - Sep	1.724559576
Blackberry - Oct	0.806962827
Blackberry - Nov	0.754996758
Knotweed - Jun	1.33217904
Knotweed - Jul	2.149958356
Knotweed - Aug	2.074874528
Knotweed - Sep	1.640257583
Knotweed - Oct	0.950270539
Knotweed - Nov	1.486539534
Maple - Jan	1.481632188
Maple - Feb	1.332244922
Maple - Apr	1.334721805
Maple - May	1.761335655
Maple - Jun	1.695742534
Maple - Jul	1.778233306
Maple - Aug	1.214889654
Maple - Sep	1.83437197
Maple - Oct	0.642843269
Maple - Nov	1.082356385
Vine - Jan	0.636514168
Vine - Feb	1.089309679
Vine - Mar	0.693147181
Vine - Apr	1.385926102
Vine - May	1.800220969
Vine - Jun	1.329661349
Vine - Jul	1.379292254
Vine - Sep	0.96994329
Vine - Oct	0.299339738
Vine - Nov	1.362447485
Willow - Jan	1.103490403
Willow - Feb	0.730166889
Willow - Mar	1.039720771
Willow - Apr	1.003852492
Willow - May	1.494046074
Willow - Jun	1.578793038
Willow - Jul	1.557113098
Willow - Aug	1.625928708
Willow - Sep	2.035074055
Willow - Oct	1.488691565
Willow - Nov	0.500402424

Table 13. Terrestrial invertebrate richness

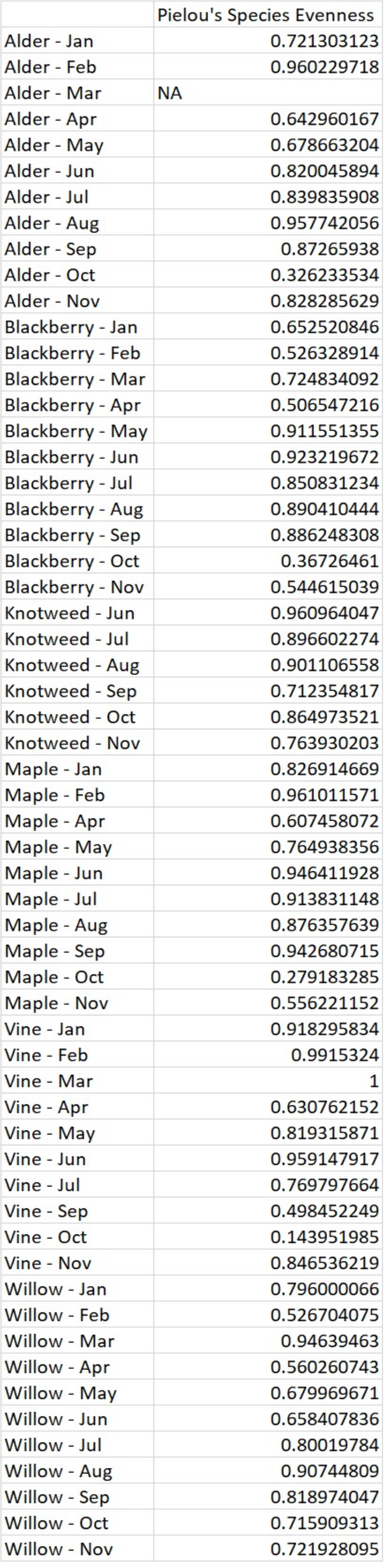
Species richness (number of unique species) for terrestrial invertebrate association with riparian plant species by month.



	Species Richness (Number)
Alder - Jan	4
Alder - Feb	3
Alder - Mar	1
Alder - Apr	9
Alder - May	8
Alder - Jun	9
Alder - Jul	7
Alder - Aug	7
Alder - Sep	8
Alder - Oct	9
Alder - Nov	5
Blackberry - Jan	4
Blackberry - Feb	5
Blackberry - Mar	3
Blackberry - Apr	7
Blackberry - May	9
Blackberry - Jun	4
Blackberry - Jul	13
Blackberry - Aug	7
Blackberry - Sep	7
Blackberry - Oct	9
Blackberry - Nov	4
Knotweed - Jun	4
Knotweed - Jul	11
Knotweed - Aug	10
Knotweed - Sep	10
Knotweed - Oct	3
Knotweed - Nov	7
Maple - Jan	6
Maple - Feb	4
Maple - Apr	9
Maple - May	10
Maple - Jun	6
Maple - Jul	7
Maple - Aug	4
Maple - Sep	7
Maple - Oct	10
Maple - Nov	7
Vine - Jan	2
Vine - Feb	3
Vine - Mar	2
Vine - Apr	9
Vine - May	9
Vine - Jun	4
Vine - Jul	6
Vine - Sep	7
Vine - Oct	8
Vine - Nov	5
Willow - Jan	4
Willow - Feb	4
Willow - Mar	3
Willow - Apr	6
Willow - May	9
Willow - Jun	11
Willow - Jul	7
Willow - Aug	6
Willow - Sep	12
Willow - Oct	8
Willow - Nov	2

Table 14. Terrestrial invertebrate evenness

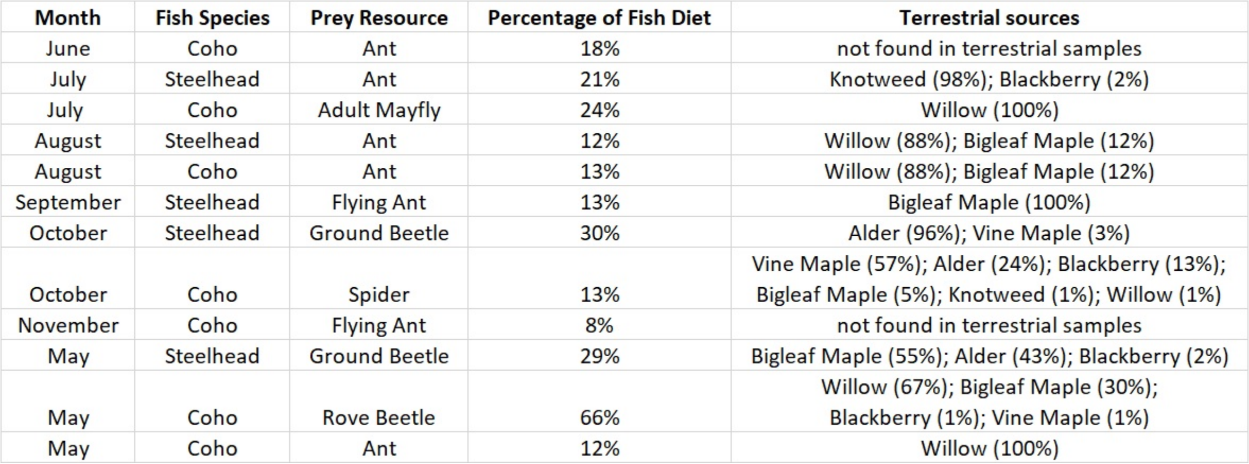
Pielou's species evenness for terrestrial invertebrate association with riparian plant species by month.



	Pielou's Species Evenness
Alder - Jan	0.721303123
Alder - Feb	0.960229718
Alder - Mar	NA
Alder - Apr	0.642960167
Alder - May	0.678663204
Alder - Jun	0.820045894
Alder - Jul	0.839835908
Alder - Aug	0.957742056
Alder - Sep	0.87265938
Alder - Oct	0.326233534
Alder - Nov	0.828285629
Blackberry - Jan	0.652520846
Blackberry - Feb	0.526328914
Blackberry - Mar	0.724834092
Blackberry - Apr	0.506547216
Blackberry - May	0.911551355
Blackberry - Jun	0.923219672
Blackberry - Jul	0.850831234
Blackberry - Aug	0.890410444
Blackberry - Sep	0.886248308
Blackberry - Oct	0.36726461
Blackberry - Nov	0.544615039
Knotweed - Jun	0.960964047
Knotweed - Jul	0.896602274
Knotweed - Aug	0.901106558
Knotweed - Sep	0.712354817
Knotweed - Oct	0.864973521
Knotweed - Nov	0.763930203
Maple - Jan	0.826914669
Maple - Feb	0.961011571
Maple - Apr	0.607458072
Maple - May	0.764938356
Maple - Jun	0.946411928
Maple - Jul	0.913831148
Maple - Aug	0.876357639
Maple - Sep	0.942680715
Maple - Oct	0.279183285
Maple - Nov	0.556221152
Vine - Jan	0.918295834
Vine - Feb	0.9915324
Vine - Mar	1
Vine - Apr	0.630762152
Vine - May	0.819315871
Vine - Jun	0.959147917
Vine - Jul	0.769797664
Vine - Sep	0.498452249
Vine - Oct	0.143951985
Vine - Nov	0.846536219
Willow - Jan	0.796000066
Willow - Feb	0.526704075
Willow - Mar	0.94639463
Willow - Apr	0.560260743
Willow - May	0.679969671
Willow - Jun	0.658407836
Willow - Jul	0.80019784
Willow - Aug	0.90744809
Willow - Sep	0.818974047
Willow - Oct	0.715909313
Willow - Nov	0.721928095

Table 15. Terrestrial links to important juvenile salmonid prey resources

Monthly importance of terrestrial contributions to juvenile coho salmon and steelhead trout diet (fish diet data obtained from Table 1 and Table 2 in Brady and Armstrong *In Draft*).



Month	Fish Species	Prey Resource	Percentage of Fish Diet	Terrestrial sources
June	Coho	Ant	18%	not found in terrestrial samples
July	Steelhead	Ant	21%	Knotweed (98%); Blackberry (2%)
July	Coho	Adult Mayfly	24%	Willow (100%)
August	Steelhead	Ant	12%	Willow (88%); Bigleaf Maple (12%)
August	Coho	Ant	13%	Willow (88%); Bigleaf Maple (12%)
September	Steelhead	Flying Ant	13%	Bigleaf Maple (100%)
October	Steelhead	Ground Beetle	30%	Alder (96%); Vine Maple (3%)
October	Coho	Spider	13%	Vine Maple (57%); Alder (24%); Blackberry (13%); Bigleaf Maple (5%); Knotweed (1%); Willow (1%)
November	Coho	Flying Ant	8%	not found in terrestrial samples
May	Steelhead	Ground Beetle	29%	Bigleaf Maple (55%); Alder (43%); Blackberry (2%)
May	Coho	Rove Beetle	66%	Willow (67%); Bigleaf Maple (30%); Blackberry (1%); Vine Maple (1%)
May	Coho	Ant	12%	Willow (100%)