Nutrient enrichment, trophic exchanges and feedback loops:
Effect of spawning salmon-derived nutrients on juvenile coho salmon

by

Michelle Catherine Nelson

M.E.S., York University, 2005

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY

Summer 2014

Approval

Name: **Michelle Catherine Nelson**

Degree: **Doctor of Philosophy (Biology)**

Title: ***Nutrient enrichment, trophic exchanges and feedback loops: Effect of spawning salmon-derived nutrients on juvenile coho salmon***

Examining Committee: **Chair:** Gerhard Gries
Professor

John Reynolds
Senior Supervisor
Professor

Wendy Palen
Supervisor
Assistant Professor

Rick Routledge
Supervisor
Professor
Department of Statistics and Actuarial Sciences

Michael Bradford
Supervisor
Research Scientist
Fisheries and Oceans Canada

David Green
Internal Examiner
Professor

Mark Wipfli
External Examiner
Professor
School of Fisheries and Ocean Sciences
University of Alaska, Fairbanks

Date Defended/Approved: July 11, 2014

Partial Copyright Licence

The author, whose copyright is declared on the title page of this work, has granted to Simon Fraser University the non-exclusive, royalty-free right to include a digital copy of this thesis, project or extended essay[s] and associated supplemental files ("Work") (title[s] below) in Summit, the Institutional Research Repository at SFU. SFU may also make copies of the Work for purposes of a scholarly or research nature; for users of the SFU Library; or in response to a request from another library, or educational institution, on SFU's own behalf or for one of its users. Distribution may be in any form.

The author has further agreed that SFU may keep more than one copy of the Work for purposes of back-up and security; and that SFU may, without changing the content, translate, if technically possible, the Work to any medium or format for the purpose of preserving the Work and facilitating the exercise of SFU's rights under this licence.

It is understood that copying, publication, or public performance of the Work for commercial purposes shall not be allowed without the author's written permission.

While granting the above uses to SFU, the author retains copyright ownership and moral rights in the Work, and may deal with the copyright in the Work in any way consistent with the terms of this licence, including the right to change the Work for subsequent purposes, including editing and publishing the Work in whole or in part, and licensing the content to other parties as the author may desire.

The author represents and warrants that he/she has the right to grant the rights contained in this licence and that the Work does not, to the best of the author's knowledge, infringe upon anyone's copyright. The author has obtained written copyright permission, where required, for the use of any third-party copyrighted material contained in the Work. The author represents and warrants that the Work is his/her own original work and that he/she has not previously assigned or relinquished the rights conferred in this licence.

Simon Fraser University Library
Burnaby, British Columbia, Canada

revised Fall 2013

Ethics Statement

Abstract

The movement of nutrients across ecosystem boundaries can affect recipient ecosystems at individual, population, and community levels. This is particularly the case when more productive systems subsidize less productive ones, where subsidies can sustain and enhance populations in nutrient-poor recipient environments. One prominent example of this is the annual migration of salmon from the marine environment into low-productivity freshwater streams for spawning. This thesis uses data collected from 47 near-pristine streams on the central coast of British Columbia to study spawning chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon and the ecological implications of their nutrient subsidy, focusing on stream-rearing juvenile coho salmon (*O. kisutch*). While considering a broad suite of habitat characteristics, the strongest predictors of juvenile coho size and abundance were spawning chum and pink salmon abundance. Streams with more spawning chum salmon had larger coho, while streams with more spawning pink salmon had higher coho populations. Further, the evidence suggested the negative association between juvenile coho and their intraguild predators/competitors, sculpin (*Cottus aleuticus and C. asper*), may be reduced as more spawning salmon nutrients became available. Altogether, this thesis shows strong impacts of marine-derived nutrient subsidies to freshwater ecosystems at multiple ecological scales. In general, it provides insights into the ecological mechanisms by which species interact with their environments, the potential for nutrient subsidies to affect recipient populations through changing food supply and predator-prey dynamics, and the role of multi-trophic interactions in subsidized trophic cascades. In specific, this research improves our understanding of the potential positive feedback between different species of salmon while incorporating the importance of multiple habitat characteristics. This has the potential to inform conservation and ecosystem-based management, particularly in light of the drastic decline in spawning salmon abundance in northern Pacific regions.

Keywords: nutrient subsidy, habitat-abundance relationships, indirect interactions, intraguild predation, spawning salmon, juvenile coho, freshwater streams

This work is dedicated to Sean Anderson, without whose statistical guidance I never would have completed it, and to Christopher Mull, for making me laugh while doing it.

Acknowledgements

My greatest thanks to Sean Anderson in the Earth To Ocean Research Group at Simon Fraser University for many hours of statistical guidance with this thesis, and for always being available when I needed help. Thank you to my senior supervisor, John Reynolds, for providing me the opportunity to conduct this research, supplying fieldwork funding, and for his skills in wordsmithing publications. Thank you to my supervisory committee for their time and comments, Rick Routledge, Mike Bradford and Wendy Palen, as well as very helpful administrative staff, Sandra Vishloff and Marlene Nguyen. I thank Raincoast Conservation Foundation for logistical and financial support, including Misty MacDuffee, Chris Darimont, Nicola Temple, Doug Brown and Mike Price. Thanks to Fisheries and Oceans Canada staff for technical and logistical support, including Darlene Gillespie, Shayne MacLellan, Kerry Parish, Ralph Nelson and Erland MacIsaac. I thank the members of the Heiltsuk and Kitasoo First Nations for their permission to undertake data collection on traditional territories, and the Heiltsuk Integrated Resource Management Department and Kitasoo Fisheries Program for their partnership in data collection, in particular Mike Reid, Randy Carpenter and Jeff McConnachie. I appreciate the support and guidance from the Earth to Ocean Group at SFU, in particular Sean Anderson, Andy Cooper and the stats discussion group, Mike Beakes, Corey Phillis, Melinda Fowler, and Rowan Atkinson from GTFO, and Kyle Artelle, Doug Braun, Jeanette Bruce, Rachel Field, Sean Godwin, Jenn Harding, Joel Harding, Morgan Hocking, Holly Kindsvater, Jane Pendray, Noel Swain, Jan Verspoor and Marlene Wagner from the Reynolds Lab. Thanks also to Svenja Bludau, Kyle Emslie, Ryan Midgely, Michelle Segal, Mark Spoljaric and Morgan Stubbs for field and laboratory assistance. My funding was provided by a Natural Sciences and Engineering Council of Canada industrial graduate fellowship with industrial support from Raincoast Conservation Foundation, and a Rix Family Leading Edge Student Award. All my love and thanks to my wonderful family members for their support and sometimes field assistance throughout this arduous process: my grandmother, Catherine Nelson, my mother, Jeri Nelson, my father, Rob Nelson, my uncle, Eric Nelson, my brother, Ryan Nelson, my sister, Alison Page, and my partner, Christopher Mull.

Table of Contents

List of Tables

List of Figures

1 General Introduction

Understanding what affects the abundance of populations has always been a central challenge in ecology. Several components may come into play, such as habitat characteristics, nutrient availability and predator-prey dynamics. In this thesis, I examine how each of these factors affects species abundance.

Effects of abiotic habitat characteristics on species abundance and distribution were recognized early on in ecology (e.g. Salisbury 1926, Chapman 1931, McArthur 1972), yet are still being explored for many species. Abundance can also be determined by food availability (Chapman 1966), and movement of nutrients across ecosystem boundaries can play a major role in determining species abundance in recipient environments (Polis et al. 1966, Nakano and Murakami 2001). Nutrient transport through geophysical processes and the movement of organisms themselves can link a wide range of environments, such as such as above- and below-ground terrestrial systems (Scheu 2001), sea ice and arctic islands (Roth 2002), and streams and forests (Nakano and Murakami, 2001). Spatial and temporal subsidies of nutrients can have various effects on recipient ecosystems' population abundance and distribution (Polis and Hurd 1996, Sanchez-Pintero and Polis 2000, Garcia et al. 2011), as well as individual growth and condition (Marczak and Richardson 2008, Young et al. 2011). Growth and condition can ultimately affect species abundances through migration timing (Giannico and Hinch 2007), fecundity (Wootton 1998), competitive and predatory success (Vincenzi et al. 2012) and survival (Groot et al. 1995). This has been demonstrated extensively on desert islands for example, where nutrient transfer through marine detritus and seabird guano supported much higher arthropod, lizard and rodent abundances on islands with subsidies than without (Strapp et al. 2002, Spiller et al. 2010, Piovia-Scott et al. 2011).

At the same time, species abundance may be controlled by interactions with other species through predation and competition (e.g. Paine 1966). Nutrient subsidies across ecosystem boundaries can affect predation and competition, and stimulate indirect effects and trophic cascades (Polis and Strong 1996). Trophic cascades fuelled by nutrient transfer can have important impacts on the dynamics between species (Nakano et al. 1999, Knight et al. 2005, Hocking and Reynolds 2011). In a fascinating example, the presence of fish in ponds increased the productivity of plants adjacent to those ponds by suppressing dragonfly larvae through predation pressure, which reduced predation of insect pollinators by adult dragonflies (Knight et al. 2005).

Nutrient subsidies are particularly relevant when productive systems subsidize nutrient-limited ones (Gravel et al. 2010), such as desert islands (Spiller et al. 2010, Piovia-Scott et al. 2011), temperate lakes (Graham et al. 2006) and freshwater streams (Richardson et al. 2010). In this case, subsidies can lead to higher species abundance, and generally higher productivity of normally low-productivity environments (Huxel and McCann 1998). The potential for subsidies to cause trophic cascades is also particularly pronounced in low productivity systems (Polis et al. 1996).

Freshwater streams are examples of nutrient-poor environments that receive large subsidies from adjacent habitats (Vannote et al. 1980). For example, terrestrial leaf litter (Wallace et al. 1997) and terrestrial arthropod inputs (Nakano et al. 1999) drive productivity and trophic cascades in stream food webs. Another important input of nutrients to freshwater streams occurs through the action of spawning salmon (*Oncorhynchus* spp.). The annual influx of spawning salmon nutrients provides a well-documented subsidy to freshwater streams along the temperate coasts of the northern Pacific Ocean (Naiman et al. 2002, Janetski et al. 2009). However, the full ecological effects of this subsidy are still not fully understood. Salmon gain >95% of their body mass in the ocean, but return to freshwater to spawn and then die (Janetski et al. 2009). The marine-derived nutrients they transport to nutrient-poor freshwater streams and lakes are considerable (Naiman et al. 2002, Schindler et al. 2003).

While the engineering effects of salmon spawning activities and the marine outmigration of salmon offspring result in some nutrient export (Scheuerell at al. 2005, Moore et al. 2007), research to date has shown that salmon nutrients can have both direct and indirect positive effects on the abundance of a number of freshwater taxa, including stream microorganisms (Wipfli et al. 1998, Verspoor et al. 2010), aquatic and terrestrial invertebrates (Wipfli et al. 1998, Verspoor et al. 2011, Hocking et al. 2013), and freshwater fish (Swain and Reynolds *in press*). One group of species that may be affected by the nutrient subsidies from spawning salmon are other species of salmon, particularly those that rear in freshwater streams for months or years before migrating to the ocean. For example, nutrients from salmon can contribute 20-40% of the nitrogen and carbon in stream-rearing juvenile coho (Bilby et al. 1996). Because of this potential interaction, it has been suggested that there may be positive feedback across generations of salmon (Michael 1995, Bilby et al. 1998). This concept has become so popular that it is now common practice for fisheries managers to add salmon carcasses from hatcheries into streams in order to enhance productivity, such as production of juvenile salmon (Harvey and Wilzbach 2010). However, the effects of this have not been rigorously tested.

We do know that juvenile salmonids and other stream fishes directly consume and preferentially select spawning salmon tissue and eggs (Bilby et al. 1998, Scheuerell et al. 2007, Armstrong et al. 2010). Further, they may benefit indirectly from spawning salmon nutrients from a general increase in stream primary productivity, as well as aquatic and terrestrial invertebrates (Wipfli et al. 1998, Hocking et al. 2013). However, bioturbation by large-bodied spawning salmon can also have negative effects on stream invertebrate biomass (Moore and Schindler 2008). Therefore, there has been little agreement of the net effects of spawning salmon on juvenile salmon at the individual and population levels in stream environments.

There is also the potential for spawning salmon to have community-level effects on juvenile salmonids. Spawning salmon nutrients could stimulate a trophic cascade among stream fishes. For example, spawning salmon tissue, eggs and fry could provide additional food for sculpins, which are both a competitor and predator of juvenile salmonids, thus reducing the negative impact of sculpin populations on those of juvenile salmonids.

In this thesis, I examine the effects of habitat, nutrients and predator-prey dynamics on population abundance, focusing on the cross-boundary nutrient subsidy provided to freshwater streams by spawning salmon as a model system. This thesis includes data from almost 50 near-pristine streams on the central coast of British Columbia, where the dominant spawning salmon are chum (*O. keta*) and pink (*O. gorbuscha*).

In Chapter 2, I explore the relationship between spawning chum and pink salmon and a wide range of habitat characteristics. Aside from the simple availability of habitat space (Chapman 1966), spawning salmon abundance can be affected by a number of other habitat features that affect ecological processes related to physiology and energetics, predation and egg incubation. For example, energy budgets for swimming fish are affected by water velocity, which is in turn affected by stream and riparian gradients (Fukushima and Smoker 1998, Sharma and Hilborn 2003). Physiological processes during spawning and egg incubation may be affected by water temperature, shading by overhead canopy, and substrate quality (Cooper 1965, Bjornn and Reiser 1991, Fukushima and Smoker 1998). Predation is another process that can be facilitated or reduced by features of habitat for spawning salmon, such as water depth, pool and large wood density, and undercut stream banks (Fukushima 2001, Gende et al. 2004, Deschenes and Rodriguez 2007, Braun and Reynolds 2011b). In this Chapter, I use a large comparison of streams to compare the importance of many habitat variables in predicting spawning chum and pink salmon abundance in order to assess the relevance of various underlying ecological phenomena.

In the third and fourth chapters, I examine the effect of the nutrient subsidy that spawning chum and pink salmon provide to juvenile salmonids rearing in freshwater streams. Coho salmon (*O. kisutch*) rear in freshwater for at least their first year before migrating to the ocean, whereas chum and pink salmon migrate directly to the ocean after emergence from the gravel in the spring (Groot and Margolis 1991). Thus, while juvenile chum and pink salmon cannot benefit from nutrients derived from spawning adults, juvenile coho could potentially be affected by the nutrients and engineering activities of spawning chum and pink salmon.

In Chapter 3, I first consider how body size and age proportion of juvenile coho salmon are affected by the availability of spawning chum and pink salmon nutrients, both directly and indirectly. Body size and the rate of growth affecting it are important for species abundance, through reproductive output (Wootton 1998), feeding success (Vincenzi et al. 2012), and ultimately survival (Groot et al. 1995). Previous research has shown condition and growth in juvenile salmonids (Scheuerell et al. 2007), and in particular juvenile coho (Bilby et al. 1998, Wipfli et al. 2003), were enhanced by the addition of salmon carcasses into streams. Further, nutrients from spawning salmon, traced by stable isotopes, were found to persist in streams from fall spawning events into the following growing season (Rinella et al. 2013). In this chapter, I seek to link the indirect effects of marine-derived nutrients from previous spawning events to the potential for direct consumption of salmon nutrients to affect the size and age proportion of juvenile coho across a range of naturally-occurring spawning salmon abundance. I also use a paired comparison within streams above and below barriers to spawning salmon. Studying the effects of naturally-occurring spawning salmon is important because live spawning salmon have different impacts on streams than experimental carcass additions (Janetski et al. 2009, Tiegs et al. 2011).

In Chapter 4, I look at how the abundance of juvenile coho is affected by spawning salmon nutrient availability, also in natural streams. Although previous research has found mixed results, either a positive effect of salmon carcass addition on juvenile coho abundance (Bilby et al. 1998) or no effect (Wilzbach et al. 2005), the literature has not yet clearly demonstrated an effect of naturally-occurring spawning salmon on the abundance of juvenile coho (cf. Michael 1995, Lang et al. 2006). Because we used natural streams differing in habitat characteristics, and we know juvenile coho abundance may also be strongly affected by habitat features, I compared the importance of habitat features to spawning salmon nutrient availability, including those related to predator refugia and food availability (Roni and Quinn 2001, Sharma and Hilborn 2001), and physiological tolerance (Holtby 1988), as well as habitat space itself (Bradford et al. 1997). I also explored a legacy effect of previous spawning events, encompassing nutrients from spawning salmon tissue, eggs and excreta, as well as the effects of engineering activities during redd digging by studying coho that had little to no direct contact with spawning salmon, as they emerged after the fall spawning event.

In my final data chapter, Chapter 5, I study the community-level effects of nutrient subsidies by examining the effect of spawning chum and pink spawning salmon on the relationship between juvenile coho and two species of sculpin, coastrange (*C. aleuticus*) and prickly (*C. asper*). While coho are rearing in freshwater, they compete for food and are directly preyed upon by sculpin (Hunter 1959). This triangular predator-prey relationship is an example of intraguild predation (Polis and Holt 1992), and can have critical impacts on intraguild prey populations (Brodeur and Roseheim 2000), in this case juvenile coho. In the absence of spawning salmon, coho and sculpin compete for invertebrate prey (Hunter 1959). However, during spawning events juvenile coho and sculpin both preferentially switch to abundant spawning salmon resources (Scheuerell et al. 2007, Swain et al. 2014). This may potentially reduce competition and predation of sculpin on coho, thereby causing an indirect effect between spawning salmon and juvenile coho abundance mediated by sculpin, or a trophic cascade. While the potential for nutrient subsidies to stimulate trophic cascades has been well documented, particularly in ecosystems with low productivity (Polis et al. 1996a), including freshwater systems (Shurin et al. 2002), the role of intraguild predation in inhibiting or facilitating trophic cascades is not yet clear (Huxel and McCann 1998, Finke and Denno 2005). In this chapter, I seek to add to our understanding of how multi-trophic interactions influence the ecological consequences of nutrient subsidies in food web ecology.

Identifying how environmental factors, nutrient availability and interspecies dynamics control species abundance are critically important issues in ecological theory and conservation. Insights into the ecological mechanisms by which these factors affect populations have the potential to enhance conservation and management, particularly as ecosystem-based management approaches become more common (Christiansen et al. 1996). In light of the concern over the vast reduction in the abundance of adult salmon transferring nutrients into low productivity streams, lakes and riparian areas during spawning (Gresh et al. 2000), knowledge of the ecological implications of their species-habitat relationships and the ramifications of marine-derived nutrient transfer may have great benefits to conservation and management efforts. I consider these implications further in my concluding chapter, Chapter 6.

2 Quantifying the effects of stream habitat on the abundance of breeding Pacific salmon[1]

2.1 Abstract

Recognizing the mechanisms by which environmental conditions drive population dynamics can greatly benefit conservation and management. For example, reductions in densities of spawning Pacific salmon (*Oncorynchus* spp.) have received considerable attention in research and management, but the role of habitat characteristics on population sizes of breeding salmon is not fully understood. We studied habitat-density relationships in spawning chum (O. *keta*) and pink (O. *gorbuscha*) salmon in 44 near pristine streams in the Great Bear Rainforest of coastal British Columbia, Canada. Our results indicate that a handful of habitat characteristics are important in predicting densities of spawning chum and pink salmon, namely pH for chum, and riparian slope and large wood volume for pink salmon. This is the largest multi-variable comparison to examine habitat-density relationships in adult spawning salmon, and may provide useful quantitative emphasis on a few key variables in comparison to a broad suite of abiotic characteristics in guiding management.

2.2 Introduction

Understanding species–environment relationships has always been a central challenge in ecology, with major implications in conservation and management. Physiological and ecological processes govern relationships between organisms and

---

[1] A version of this chapter has been submitted as Nelson, M.N., Hocking, M.D., Harding, J.N., Harding, J.M.S. and Reynolds, J.D. Quantifying the effects of stream habitat on the abundance of breeding Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* (August, 2014).

abiotic habitat characteristics (Elton 1927, Huey 1991). For example, abiotic habitat characteristics may influence competitive interactions, predator-prey relationships, energetic allocations, and reproductive success. As ecosystem-based management approaches become more common (Christiansen et al. 1996), insights into the mechanisms by which environmental conditions affect populations are increasingly in demand.

Considerable reductions in the abundance of some species of Pacific salmon in the North Pacific region (Gresh et al. 2000), is one of the foremost conservation concerns in North America (Ruckelshaus et al. 2002). Salmon require freshwater habitat to complete their life cycle and are susceptible to habitat degradation of spawning streams and surrounding riparian forests (Groot and Margolis 1991). As a result, billions of dollars have been invested in freshwater habitat restoration to improve conditions for salmonids, despite the fact that few quantitative assessments have been made of the effectiveness of such measures (Roni et al. 2008).

Because a full understanding of interactions between species and their environments is often lacking, researchers may develop models to inform management decisions that assess the impact of land use or environmental change (e.g., Guisman and Zimmermann 2000). Habitat-abundance models can be data-intensive, and the cost of data collection can be prohibitive, therefore the choice as to which variables to include is important. Further, increasing the number of variables studied leads to diminishing returns on information (Braun and Reynolds 2011a). A predictive model that requires a small number of variables is preferable, yet it is often difficult to assess which variables are more important than others (Bradford et al. 1997).

Several large-scale studies of habitat characteristics affecting juvenile salmonid populations have been explored (e.g., Bradford et al. 1997). Considering the importance placed on the ecology, behaviour and management of spawning adults, it is surprising how few systematic, quantitative assessments have been undertaken on habitat-abundance relationships for adult salmon that include a multivariate comparison of habitat characteristics. This is particularly true for chum and pink salmon. In the simplest case, the abundance of salmon can be limited by the amount of habitat space available

(Chapman 1966). However, there are other mechanisms that can influence population sizes; energy budgets for swimming during upstream migration and spawning are affected by stream and riparian gradients (Sharma and Hilborn 2003, Fukushima and Smoker 1998), and physiological processes during spawning and incubation may be affected by water temperature and pH (Crossin et al. 2008, Bjornn and Reiser 1991, Ikuta et al. 2003). Embryo survival may be positively affected by the availability of high quality spawning substrates (Fukushima and Smoker 1998, Fukushima 2001), while fine sediments may limit hatching success (Cooper 1965, Chapman 1988). Spawning salmon are also vulnerable to predation by bears and other animals (Gende et al. 2004), thus structures that provide cover may be beneficial, such as deep water, pools, large wood, undercut banks and dense vegetative cover (Fukushima 2001, Gende et al. 2004, Deschenes and Rodriguez 2007, Braun and Reynolds 2011b). Of the studies cited, only two specifically address habitat associations for adult pink salmon (Gende et al. 2004, Fukushima and Smoker 1998), one for juvenile pink and chum salmon (Rombough 1983), and none address habitat associations for adult chum salmon (Table 1).

In this study, we examine empirical relationships between 9 stream habitat characteristics and spawning chum and pink salmon abundance in 44 streams in a remote region on the central coast of British Columbia, Canada. These variables encompass ecological processes related to physiology and energetics, predation, and egg incubation. By using a large number of steams, we were able to assess the relative importance of a large number of habitat variables as predictors of salmon abundance. We use an information-theoretic approach to compare the importance of variables across a range of stream sizes (Table 2.1). Knowledge of key habitat factors influencing breeding pink and chum abundance could help reduce the effort involved in creating detailed habitat assessments, and inform conservation modeling tools and ecosystem-based management plans.

Table 2.1. **Predictions of the potential influence of habitat features on spawning chum and pink density**

Hypothesis	Variable	Mechanism	Direction	References
Predation	Maximum depth	Depth provides cover/predator refuge	Positive	Gende et al. 2004 (adult sockeye), Fukushima 2001 (adult Sakhalin taimen), Deschenes and Rodriguez 2007 (adult brook trout), Quinn et al. 2001 (adult sockeye)
Predation	Percent pool area	Pools provides cover/predator refuge	Positive	Braun and Reynolds 2011b (adult sockeye), Gende et al. 2004 (adult pink and sockeye), Fukushima 2001 (adult Sakhalin taimen)
Predation	Large wood density	Wood structures provides cover/predator refuge	Positive	Braun and Reynolds 2011b (adult sockeye), Gende et al. 2004 (adult pink and sockeye), Fukushima 2001 (adult Sakhalin taimen), Deschenes and Rodriguez 2007 (adult brook trout)
Predation	Percent undercut banks	Undercut banks provide cover/predator refuge	Positive	Braun and Reynolds 2011b (adult sockeye)
Embryo survival	Percent spawning substrate	More suitable habitat increases egg survival	Positive	Fukushima and Smoker 1998 (adult pink and sockeye); Fukushima 2001 (adult Sakhalin taimen)
Embryo survival	Percent fine sediments	Reduce oxygen availability for eggs	Negative	Chapman 1988 (all salmonids), Bjornn and Reiser 1991 (all salmonids)

Physiological tolerance	Water pH	Low pH can suppress reproductive behavior, increase egg mortality and cause aberrant alevin behavior	Positive	Ikuta et al. 2003 (adult sockeye), Rombough 1983 (juvenile chum and pink)
Physiological tolerance	Maximum weekly water temperature	High temperatures can impair physiological processes, reducing spawning success	Negative	Huey 1991 (ectotherms), Bjornn and Reiser 1991 (all salmonids, adults)
Energetics	Riparian slope	Increased run off causes extreme water velocities which increase energy expenditure	Negative	Sharma and Hilborn 2003 (juvenile coho)

2.3 Materials and Methods

2.3.1 Study sites and design

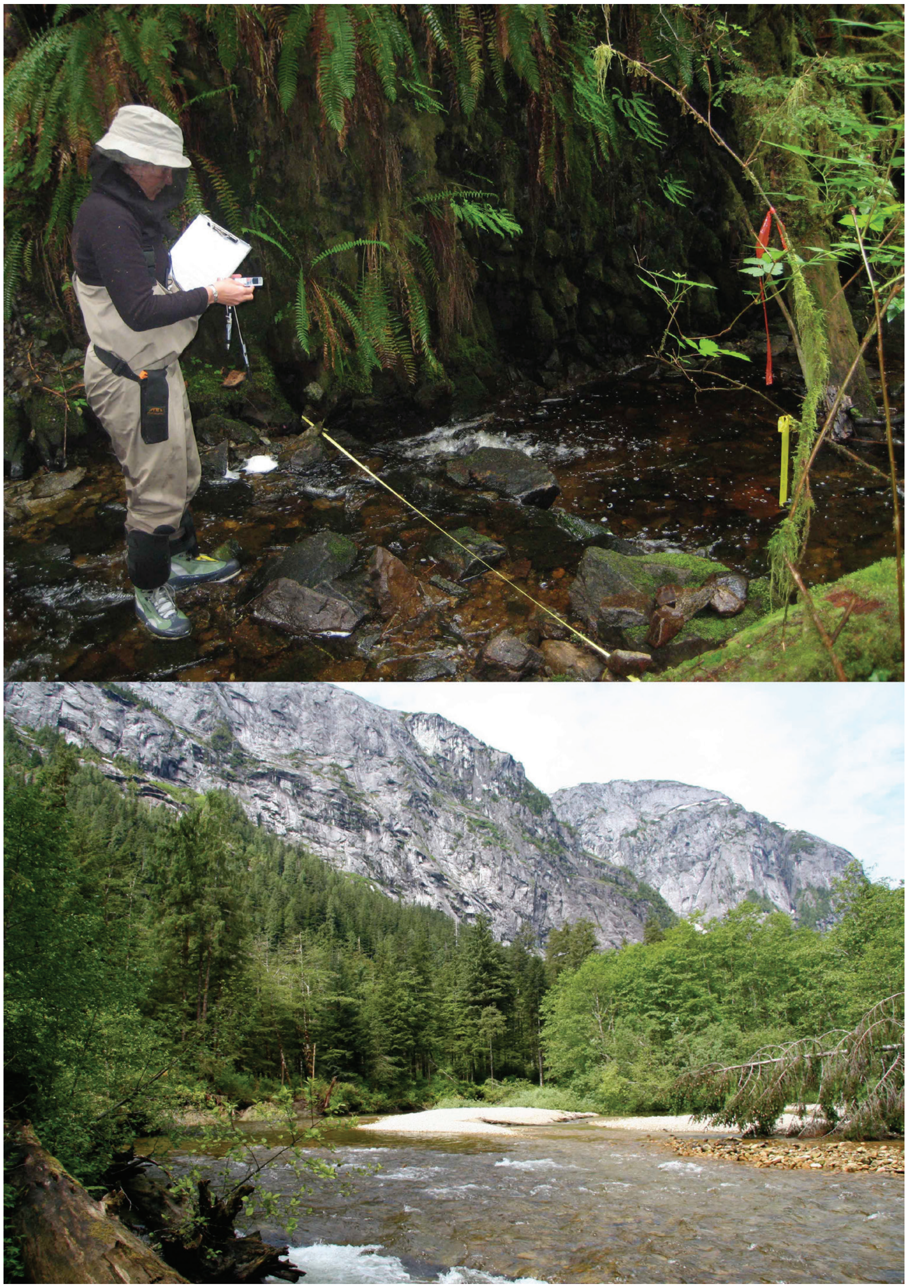
The study streams are located on the central coast of British Columbia near the coastal communities of Bella Bella and Klemtu (Table 2.2). All study sites were accessed by boat. The study area has no road networks, urban development or damming. Forestry and other land use have been limited, with selective logging prior to the 1950s (Hocking and Reynolds 2011).

Table 2.2. Stream characteristics and spawning chum and pink densities for streams in this study (n = 44).

Stream	Chum density (fish/m^2)	Pink density (fish/m^2)	pH	Riparian slope (degrees)	Large wood density (cm^3/m)
Ada Cove	0.298	0.082	5.68	32.0	0.062
Beales Left	0.116	0.340	7.44	18.9	0.526
Beales Right	0.038	0.168	5.51	26.1	0.058
Big Creek	0.009	0.804	-	3.5	0.323
Bolin Bay	0.012	0.192	-	7.2	0.056
Bullock Main	0.484	0.361	5.96	6.4	0.142
Bullock Square	0.172	0.105	5.45	10.7	0.218
Clatse	0.261	0.459	5.86	8.5	0.035
Codville	0.008	0.032	4.62	2.3	0.072
DeCosmos	0.127	0.071	4.99	11.9	0.255
Desbrisay	0.537	0.715	-	13.1	0.130
Duthie	0.114	0.454	-	12.2	0.034
Evans East	0.184	0.040	5.45	13.8	0.164
Fancy Head	0.368	0.161	5.45	13.0	0.238
Fancy Right	0.096	0.102	5.39	15.3	0.110
Fanny Left	0.160	0.304	5.39	7.0	0.106
Farm Bay	0.000	0.000	4.99	15.8	0.133
Gorilla	0.573	0.204	-	1.2	0.064
Hooknose	0.085	0.163	4.80	9.6	0.128
James Bay	0.012	0.411	-	1.3	0.124
Jane Cove	0.006	0.000	5.68	25.7	0.070
Kill Creek	0.558	0.203	6.60	12.0	0.154
Kunsoot Main	0.030	0.462	5.51	10.3	0.176
Kunsoot North	0.030	0.023	5.39	24.4	0.011
Kvai	0.000	0.044	-	3.3	0.103
Kynoch	0.122	0.197	-	0.0	0.020
Lard	0.050	0.008	-	11.5	0.075
Lee	0.233	0.035	5.77	11.8	0.036
Mosquito Left	0.097	0.292	5.55	3.2	0.101
Mosquito Right	0.152	0.228	5.48	7.6	0.127
Mussel	0.122	0.243	-	0.0	0.027
Nameless	0.060	0.087	-	10.0	0.259

Neekas	0.793	0.776	6.11	1.3	0.113
Port John	0.004	0.003	4.43	4.1	0.065
Quartcha	0.022	0.030	6.00	10.6	0.062
Rainbow	0.056	0.002	5.88	20.3	0.120
Roscoe Main	0.119	0.002	6.05	5.4	0.038
Roscoe Trib 1	0.141	0.107	5.59	15.1	0.124
Sagar	0.082	0.067	5.75	27.2	0.034
Salmon Bay	0.250	1.024	-	18.5	0.054
Spiller Trib 1	0.022	0.033	5.82	32.7	0.359
Troup North	0.002	0.000	4.80	17.0	0.227
Troup South	0.013	0.074	4.74	9.5	0.066
Windy Bay	0.005	0.013	-	13.3	0.073

Study streams all flow directly into the ocean, and the stream accessible to salmon for spawning ranged from 22 m to 15 km in length, and 3.3 m to 58 m in bank full width (Figure 2.1). Across all sites, riparian areas were forested, with vegetation typical of the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1987). Riparian tree composition is dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*) and red alder (*Alnus rubra*). Riparian shrub species are dominated by salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), false azalea (*Menziesia ferruginea*), and blueberry (*Vaccinium* spp.). Total annual precipitation in the region is a refreshing 3,000-4,000 mm/yr.



© Jennifer Harding and John Reynolds

Figure 2.1. Range in stream sizes from small (Jane Cove) to large (Roscoe Main).

Habitat surveys were conducted in 2007. The stream reach surveyed for environmental variables was scaled to average stream width (20 x stream width) (Bain and Stevenson 1999), and equally divided into 12 transects.

2.3.2 Environmental variables

We considered 10 habitat characteristics that we hypothesized to affect the abundance of spawning chum and pink salmon, categorized as representing various ecological processes (as shown in Table 2.1): stream depth, percent pool area, large wood density, percent undercut bank, pH, maximum stream temperature, riparian slope, percent suitable spawning substrate, percent fine substrate, and percent high stream gradient. Means and ranges of habitat variables are shown in Table 2.3.

Table 2.3. Mean and range of habitat characteristics (n = 44 streams for all variables except maximum stream temperature where n = 17).

Habitat characteristic	Mean ± Std Dev	Range
Maximum stream depth (m)	0.22 ± 0.11	0.06 - 0.56
Percent pool area (%)	12.0 ± 11.4	0.2 - 55.7
Large wood density (cm^3/m)	0.12 ± 0.1	0.011 - 0.53
Percent undercut bank (%)	53.9 ± 31.5	0 - 100
pH	5.57 ± 0.59	4.43 - 7.44
Maximum stream temperature (°C)	8.9 ± 1.4	6.6 - 11.5
Riparian slope (degrees)	12.0 ± 8.2	0 - 32.7
Percent suitable spawning substrate (%)	73.7 ± 19.4	21.7 - 98.3
Percent fine sediments (%)	4.9 ± 6.8	0 - 30.4

Stream depth was measured at each transect and the mean value calculated. Stream habitat types, including pools, riffles, runs, glides, cascades, rapids and stepped habitat, were identified according to Bain and Stevenson (1999). Percent pool area was calculated as the summed area of pools across the entire reach divided by the total area of that reach. All pieces of wood that were > 10 cm in diameter and > 1.5 m long that would be at least partially in the water at bank full water height were counted to calculate large wood pieces per 100 m (Roni and Quinn 2001). Percent undercut banks was determined as the number of transects with undercut banks divided by the total number of transects (occurred on both sides thus n = 24). Riparian slope was measured from the stream bank at each transect using a clinometer and averaged across transects. Substrate was measured on the intermediate axis of 10 stones along each transect (Wolman 1954), and categorized into fine sediments (0-1.2 cm), gravel (1.3-10.2 cm), small cobble (10.3-14.9 cm), large cobble (15.0-24.9 cm), boulder (>25.0 cm) or bedrock. Spawning substrate was percent gravel and small cobble combined.

Water pH was measured at three transects per stream. Stream temperature was recorded at a subset of streams (n = 17) using two waterproof ibutton data loggers (DS1922L) per stream, which recorded temperatures every two hours. Maximum temperature was calculated from weekly maximums.

2.3.3 Spawning pink and chum salmon abundance

Estimates of spawning salmon densities resulted from collaborative efforts between the Heiltsuk Integrated Resource Management Department, the Kitasoo Fisheries Program, Fisheries and Oceans Canada, and Simon Fraser University. We calculated mean pink and chum densities for our study period (2006-2011) using a minimum of two years per stream. Within each year, salmon abundance was estimated using area-under-the-curve, where three or more salmon counts existed (English et al. 1992). Peak (live+dead) counts were used when streams could not be accessed three times per season in a small proportion of streams (less than 10%). No substantive difference was found between these methods (Hocking and Reynolds 2011). Abundance in the spawning reach was divided by the area available for spawning to calculate density.

2.3.4 Data analysis

We used Akaike's information criterion adjusted for small sample sizes (AICc) and maximum likelihood estimation methods to assess relative importance of candidate models explaining chum and pink salmon densities (Burnham and Anderson 1998, Zuur et al. 2009). Spawning chum and pink salmon densities, percent pool area, large wood density and percent fine sediments were $\log_{10}$ transformed. We used all possible model combinations, including a null model with an intercept only, although we only allowed a maximum of four habitat variables per model to avoid over-fitting (Burnham and Anderson 2002). ΔAICc values, which are the difference between model i and the top-ranked model, are reported for our candidate model set (all models with ΔAICc < 2) (Burnham and Anderson 2002, Grueber et al. 2011). Model diagnostics did not reveal problems with heteroscedasticity, over-leveraging of data points, nor normality and independence of residuals.

AICc did not reveal maximum temperature to be an important predictor of either chum or pink density at the subset of streams where temperature data were available (n = 17), therefore maximum temperature was not included in the final model selection which used the full set of streams (n = 44).

Given the potential for multicollinearity between many of the habitat variables considered, we used the variance inflation factor (VIF) to identify and remove highly collinear variables with VIF scores greater than 3 (Zuur et al. 2010). All variables had VIF scores of less than 3, which indicates a low level of collinearity. Correlations between variables are shown in Table 2.4.

All statistical analyses were performed using R (R Development Core Team 2009), including the MuMIn package (Barton 2012).

Table 2.4. Bivariate correlations, r, between variables for all streams (n = 44 for all variables except maximum stream temperature where n = 17).

	Pink density	Stream depth	Percent pool area	Large wood density	Percent undercut bank	Percent spawn substrate	Percent fine sediment	pH	Maximum stream temp	Riparian slope
Chum density	0.52	-0.13	0.00	0.09	-0.06	0.16	-0.06	0.40	-0.29	-0.1
Pink density	-	-0.08	0.04	0.40	0.02	0.24	0.03	0.16	-0.09	-0.26
Stream depth	-	-	-0.37	0.02	-0.22	-0.14	0.26	0.08	-0.09	-0.33
Percent pool area	-	-	-	-0.05	0.32	0.01	0.17	0.16	0.05	-0.09
Large wood density	-	-	-	-	-0.24	0.01	-0.08	0.26	-0.07	0.2
Percent undercut banks	-	-	-	-	-	0.49	0.24	-0.15	0.12	-0.33
Percent spawn substrate	-	-	-	-	-	-	-0.13	-0.01	-0.03	-0.43
Percent fine sediment	-	-	-	-	-	-	-	0.03	-0.12	-0.31
pH	-	-	-	-	-	-	-	-	-0.08	0.17
Maximum stream temp	-	-	-	-	-	-	-	-	-	0.01

2.4 Results

Water pH was the single best predictor of spawning chum density after all other variables were taken into account across models (Figure 2.3), although the positive relationship between chum density and water pH was not very strong on its own (r^2 =

0.16; Figure 2.2). pH was in every top model predicting chum density (ΔAICc < 2; Table 2.5), and the addition of the next best predictor, riparian slope, to pH only increased by 0.04 (Table 2.5). Although riparian slope appears in three of the six top models for chum density (Table 2.5), has the second highest relative variable importance and second largest (negative) scaled coefficient value, the uncertainty around the estimate make the effect of riparian slope on chum density unclear (Figure 2.3).

Pink salmon density was most strongly correlated with large wood volume and riparian slope. Large wood volume and riparian slope were in all top models for pink density (ΔAICc < 2; Table 2.5). Large wood volume was a clear positive correlate of pink density, while riparian slope was a clear negative correlate (Figure 2.3). Although pH was present in all the top models for pink density (Table 2.5), meaning some unique variation in pink density was explained by pH; however, the strength of the effect of pH on pink density was not strong, as shown by a low coefficient estimate (Figure 2.2).

The relationship between stream size, as approximated by area available for spawning, and the top habitat characteristics identified by AICc was less than 0.1 (r^2 = 0.07, 0.08 and 0.001 for pH, riparian slope and large wood density, respectively).

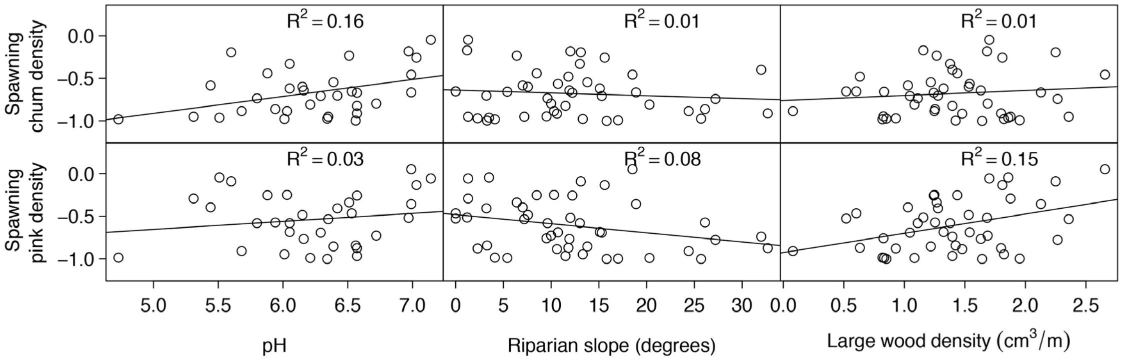


Figure 2.2. Relationships between the density of spawning chum and pink salmon and top habitat characteristics identified by AICc. Spawning chum and pink densities and large wood volume have been log transformed.

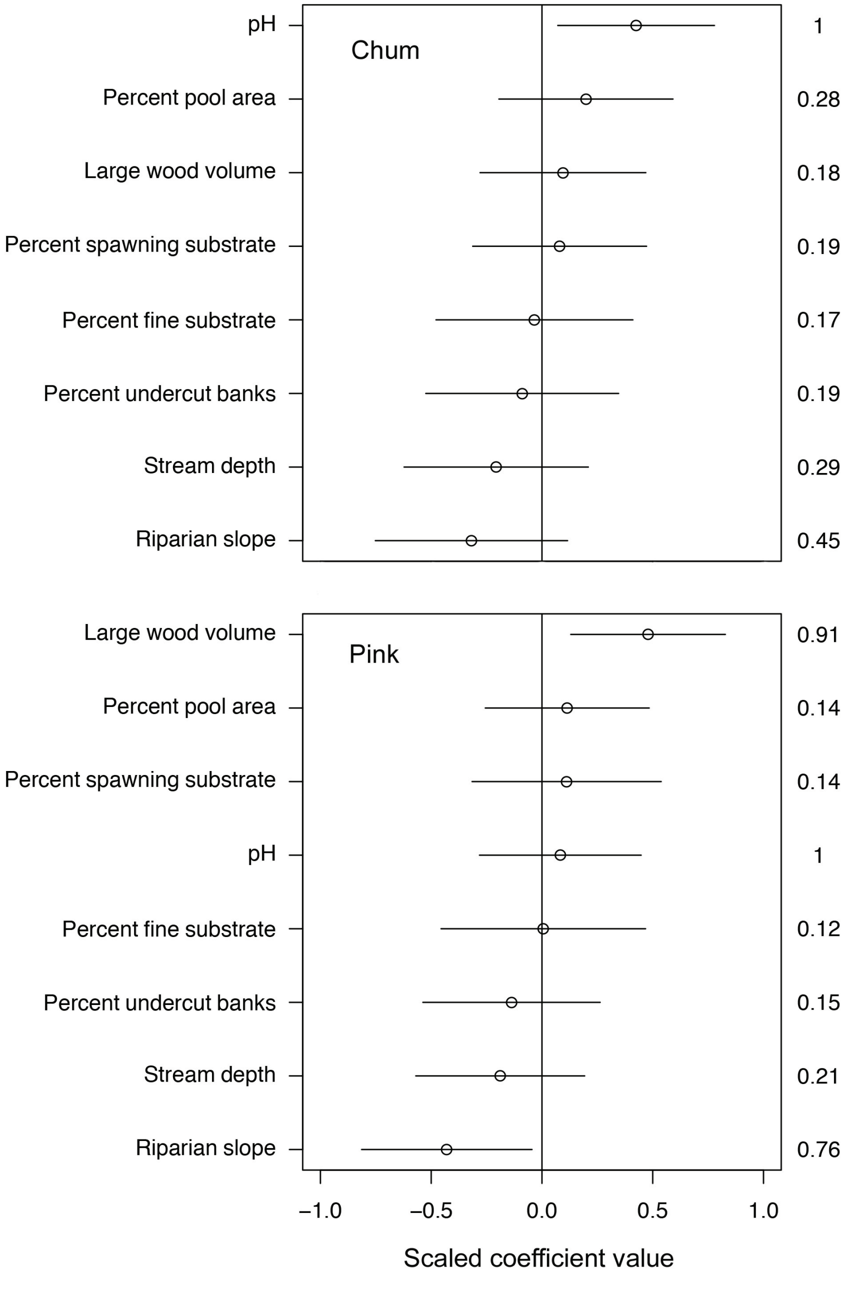


Figure 2.3. Parameter estimates (circles) with 95% confidence intervals (lines) from averaged linear models predicting chum salmon density (top) and pink salmon density (bottom). The estimates are scaled and ranked from highest positive value to lowest negative value. Relative variable importance values for each variable are indicated on the right and are scaled from 0 to 1.

Table 2.5. Summary of linear regression models with the greatest support (Δ AICc < 2.0) for spawning chum and pink salmon abundance for all streams (n = 44). AICc = Akaike's information criterion corrected for small sample size, K = model parameter number, R2 = model coefficient of determination, Δ AICc = difference in AICc score from top model, wi = AICc model weight. The models are ordered by descending wi.

	Model parameters	K	R^2	ΔAICc	w_i
Chum	pH	3	0.16	0.00	0.10
	pH + riparian slope	4	0.21	0.78	0.07
	pH + riparian slope + stream depth	5	0.27	0.92	0.07
	pH + pools	4	0.19	1.49	0.05
	pH + riparian slope + pools	5	0.25	1.59	0.05
	pH + stream depth	4	0.18	1.92	0.04
Pink	large wood + riparian slope + pH	5	0.36	0.00	0.25
	large wood + riparian slope + pH + water depth	6	0.40	0.99	0.15
	large wood + riparian slope + pH + pools	6	0.38	1.86	0.10

2.5 Discussion

This is the first study to examine relationships between stream habitats and breeding chum and pink salmon across a large number of streams. We found several habitat characteristics were important predictors, including pH for chum salmon, and riparian slope and large wood density for pink salmon.

Water pH was the most important and positive predictor of chum density. This was consistent with our prediction that lower pH would negatively affect fish physiology. Low water pH is known to suppress reproductive behaviour including nest digging and upstream migration in salmonids, and this occurs at pH levels at the lower end of the streams in this study (pH 5.8-6.4, Ikuta et al. 2003). Low pH can also increase egg and fry mortality, and chum seem to be most sensitive to this effect compared to other salmonid species (Rombough 1983). Further, even mildly acidic water (pH under 6.0) can cause aberrant behaviour in newly hatched chum fry (Rombough 1983), which is the mid to lower pH range of our study streams.

Streams with steep riparian slopes had lower pink salmon density. This may reflect a negative impact of high water velocity and extreme flooding events due to increased run-off in steeper areas. Higher stream gradients have been associated with lower breeding salmon abundance due to increased energy expenditure during spawning (Fukushima and Smoker 1998, Healey et al. 2003). A negative effect of valley slope on juvenile salmonid density has also been found and attributed to extreme water velocities (Sharma and Hilborn 2001). A clear negative relationship between water velocity and adult salmon has been established (Deschenes and Rodriguez 2007).

Large wood density was positively related to pink salmon density. Previous studies have identified cover structures including large wood, pools, deep water, and undercut banks as important positive correlates of spawning sockeye (Gende et al. 2004, Braun and Reynolds 2011b), and resident brook trout populations (Deschenes and Rodriguez 2007), which was attributed to reduced predation pressure due to the fish having more areas of refuge. While we also expected to find similar effects from pools, deep water and undercut banks, these variables were not as important as large wood in the streams we studied. These study streams were relatively pristine, and may not span the lower range of pools and undercut banks that could influence predation pressure on salmon. A study of juveniles showed that relationships between cover and salmon density only holds when cover is rare (Inoue et al. 1997).

Because we found low correlations between stream size and the top habitat characteristics identified by AICc, namely pH, riparian slope and large wood density, it is unlikely stream size is simply driving these relationships.

Our results indicate that a handful of habitat characteristics are important in predicting densities of spawning chum and pink salmon, namely pH for chum, and riparian slope and large wood for pink salmon. While quantitative evaluations of habitat can be used to prioritize streams for conservation, the choice of which habitat variables to measure is often difficult to make. Identifying the importance of these few variables in comparison to a broad suite of abiotic characteristics may make creating predictive models of spawning pink and chum densities more straightforward.

3 Effects of subsidies from spawning chum and pink salmon on juvenile coho salmon body size and age proportion[2]

3.1 Abstract

Organisms transporting nutrients from highly productive ecosystems can subsidize food webs and alter ecosystem processes. For example, the carcasses and eggs of migratory Pacific salmon (*Oncorhynchus* spp.) provide a high-quality food source that could potentially benefit other species of salmon rearing in fresh water. We investigated relationships between spawning chum (*O. keta*) and pink (*O. gorbuscha*) salmon density, and the body size and age of juvenile coho salmon (*O. kisutch*) in 17 streams on the central coast of British Columbia, Canada. Chum salmon density was the most consistently important and positive correlate of coho body size, in comparison with pink salmon density, juvenile coho salmon density, and numerous characteristics of habitats. This was shown by comparisons both among and within streams, and between sites above and below natural barriers to spawning chum and pink salmon. In addition, streams that had higher chum and pink salmon spawning densities had a higher proportion of age 0 coho (less age 1), suggesting earlier juvenile coho migration to the ocean with increased spawning salmon nutrient availability. Most of the coho sampled had little or no direct contact with spawning chum and pink salmon, which suggests an indirect, time-delayed influence on coho body size.

---

[2] A version of this chapter has been accepted as Nelson, M.N. and Reynolds, J.D. Effects of subsidies from spawning chum and pink salmon on juvenile coho salmon body size and migration timing. *Ecosphere* (July, 2014).

3.2 Introduction

Geophysical processes and organisms can transport nutrients across ecological boundaries, thus linking an array of environments, such as above- and below-ground terrestrial systems (Scheu 2001), sea ice and arctic islands (Roth 2002), and streams and forests (Nakano and Murakami, 2001). Productive systems can subsidize nutrient-limited ones (Gravel et al., 2010), such as when nutrients move from the marine environment to desert islands (Spiller et al., 2010) and freshwater streams (Richardson et al., 2010). These subsidies can have a wide range of effects, including the growth and body size of organisms in recipient food webs (Marczak and Richardson, 2008; Young et al., 2011). Growth and body size can affect migration timing (Giannico and Hinch 2007), fecundity (Wootton 1998), competitive and predatory ability (Vincenzi et al. 2012) and, ultimately, survival (Groot et al. 1995).

Transport and concentration of nutrients can occur both spatially, such as in avian nesting colony aggregation, and temporally, such as through annual migrations. One example that constitutes both a spatial and temporal aggregation of nutrients occurs through the annual migration of spawning salmon (*Oncorhynchus* spp.) along the temperate coasts of the northern Pacific Ocean. Because salmon gain >95% of their body mass in the ocean, return to freshwater to spawn and then die, the marine-derived nutrients they transport can be substantial to nutrient-poor freshwater streams and lakes (Naiman et al. 2002, Schindler et al. 2003; Janetski et al. 2009). While most research has focused on import of nutrients (e.g. Verspoor et al. 2011, Hocking et al. 2013), it is noteworthy that salmon can also drive export of nutrients from streams through the engineering effects of spawning adults, which can flush invertebrates downstream (Moore et al. 2007). In addition, nutrients are exported by young salmon migrating downstream toward the sea, especially if they have been feeding for some time in freshwater (Scheuerell at al. 2005). Thus, we cannot automatically assume that salmon cause a net increase in nutrients in any particular component of a freshwater ecosystem.

One group of organisms that can be affected by spawning salmon subsidies is other species of salmon, particularly species that stay in freshwater for many months before migrating to the ocean. For example, nutrients from salmon can contribute 20-

40% of the nitrogen and carbon in stream-rearing juvenile coho (Bilby et al. 1996). This can come from direct consumption of adult salmon tissue and eggs (Kline et al. 1990) and indirectly through increased aquatic (Wipfli et al. 1998, Verspoor et al. 2011) and terrestrial invertebrates in the presence of spawning salmon (Hocking et al. 2013), which provide potential prey for juvenile salmonids. The presence of spawning salmon increased energy intake of juvenile rainbow trout (Scheuerell et al. 2007), and coho salmon (Heintz et al. 2003; Armstrong et al. 2010). Furthermore, nutrients from spawning salmon have been linked to improved condition and growth rate of juvenile coho in a number of carcass addition experiments (e.g. Bilby et al. 1998; Wipfli et al. 2010). However, bioturbation during redd-digging could also reduce food availability through reduced invertebrate biomass (Moore and Schindler, 2008).

Most previous research has been limited to experimental carcass addition, which does not take non-carcass nutrients or engineering activities into account. No previous research has examined effects on juvenile coho age composition, nor has there been consideration of the mediating effects of habitat characteristics that are known to affect juvenile salmonids (Tiegs et al. 2008). For example, juvenile coho salmon can be affected by habitat and food availability, cover or refugia from predation, and temperature (e.g. Sharma and Hilborn 2001, Bradford 1997). We predicted the density of overhead canopy may affect the degree to which spawning salmon nutrients subsidize primary productivity in a stream, or structural complexity may affect retention of nutrients. In addition, the presence and density of juvenile conspecifics can also affect growth (Roni and Quinn, 2001).

Here, we provide the first investigation of the impacts of naturally-occurring salmon-derived nutrients on size and age proportion of juvenile salmon. Specifically, we study the prediction that nutrients from spawning pink and chum salmon will lead to larger juvenile coho salmon, and higher proportion age 0 (less age 1) which may indicate earlier seaward migration timing by those fish. Whereas chum and pink juvenile emerge from stream substrate and migrate to the ocean within weeks, juvenile coho spend at least one year in freshwater streams (Groot and Margolis, 1991). We predicted chum salmon would have greater positive effects on juvenile coho body size than pink salmon due to their larger body size and egg deposition, although there is the potential for greater negative effects of chum than pink through more bioturbation during nest digging due to the larger body size of chum, as well as potentially aggressive behavior towards juvenile coho during nest guarding (Nelson and Reynolds 2014a). We incorporate the potential for each of these effects by looking at the number of chum and pink spawning salmon, and the potential for each species to have different effects by modeling them separately. Our study incorporates natural variation in numbers of spawning pink and chum salmon in 17 streams in a remote region of the central coast of British Columbia, Canada. We also make comparisons within four streams above and below barriers to spawning fish. Most of the coho that we studied were young of year (age class 0) and had emerged in the spring just prior to sampling, and would therefore have had no direct exposure to spawning salmon. Therefore, for those fish in age class 0, any impacts of spawning pink and chum on juvenile coho body size are indirect effects from previous spawning events. On the other hand, body size in age class 1 fish would encompass both indirect effects and may benefit directly through consumption of spawning salmon tissues and eggs, and potentially chum and pink fry. They may also be affected by spawning engineering activities.

3.3 Materials and Methods

3.3.1 Study sites and design

We surveyed streams on the central coast of British Columbia, Canada, in the Great Bear Rainforest (Table 3.1). The dominant spawning salmon species are chum and pink, and juvenile coho are present in all streams. Sites are accessible only by boat, and land use has been very limited in the area. Coho spawn in the upper tributaries of the streams, whereas chum and pink spawn in the lower reaches. Densities of spawning coho at the five streams in our study area where data were available (50-204 females/km) exceed that which are thought to fully saturate the habitat with juveniles (19 females/km; Bradford et al. 2000). At four of our sites a natural barrier to chum and pink spawners was present, which coho spawners were able to pass, resulting in juveniles on both sides of the barrier.

Study streams all flow directly into the sea, range from mid-gradient exterior coastal sites to lower gradient coastal fiords, and had bank full widths from 1.2 to 22.8 m. This region is in the Coastal Western Hemlock biogeoclimatic zone (Pojar et al., 1987), with forests dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). Riparian zones are dominated by red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), false azalea (*Menziesia ferruginea*), and blueberry (*Vaccinium* spp.). Annual precipitation in the region is pleasantly high, at 3,000-4,000 mm/yr.

Juvenile coho and physical habitat were studied in the fall (September-October) of 2007 and 2008. Spawning salmon counts were undertaken across the entire spawning length of the stream for returning chum and pink salmon from 2006-2011, to provide an overall index for comparing average differences among streams (methods in Hocking and Reynolds, 2011). Average stream width was used to scale the length of area sampled for habitat characteristics (30 x stream width).

Table 3.1. Stream characteristics, spawning salmon chum and pink population data (2006-11), and juvenile coho salmon density and body size (fork length) at ages 0 and 1 for the 17 streams in this study. Sample sizes of fish measured are in brackets.

Stream	Length (m)	Bankfull width (m)	Spawning chum density (fish/m^2)	Spawning pink density (fish/m^2)	Juvenile coho density (fish/m^2)	Juvenile coho age 0 body size (cm)	Juvenile coho age 1 body size (cm)
Ada Cove	6,480	11.1	0.296	0.081	0.167	7.9 (7)	9.9 (3)
Beales Left	3,360	10.9	0.116	0.340	0.244	7.5 (5)	-
Bullock Main	2,420	10.9	0.480	0.358	0.362	6.9 (8)	-
Clatse	6,820	22.8	0.260	0.458	-	9.1 (5)	-
Evans East	4,200	13.3	0.184	0.040	-	9.6 (5)	11.9 (2)
Fanny Left	4,270	12.8	0.160	0.304	2.126	6.0 (10)	-
Hooknose	2,970	16.9	0.085	0.163	0.644	6.8 (7)	11.1 (6)
Jane Cove	1,380	4.6	0.007	0.000	0.082	6.2 (5)	5.5 (2)
Kill Creek	980	3.5	0.550	0.199	0.347	7.7 (8)	-
Kunsoot Main	3,670	13.1	0.030	0.462	0.559	6.3 (6)	-
Kunsoot North	760	7.2	0.029	0.023	-	7.6 (5)	8.7 (2)
Mosquito Left	3,250	4.0	0.056	0.123	0.021	5.9 (4)	7.6 (2)
Port John	2,540	3.3	0.004	0.003	0.230	5.5 (7)	6.4 (2)
Quartcha	9,300	21.7	0.022	0.030	-	7.3 (4)	-
Sagar	5,200	15.5	0.082	0.066	0.677	6.6 (5)	6.2 (2)
Troup North	440	4.4	0.002	0.000	0.322	6.6 (3)	8.2 (5)
Troup South	1,050	4.1	0.013	0.073	-	7 (2)	9.0 (4)

3.3.2 Environmental variables and juvenile coho density

We measured the following habitat characteristics that have been shown to affect body size and growth of juvenile coho salmon: stream bank full width, stream length, amount of large wood in streams, pools, pool to riffle ratio, undercut banks, gradient, canopy cover, percent fine substrate, pH, temperature and dissolved nutrients (ammonia, nitrate and soluble phosphorous). We also calculated the density of conspecific juvenile coho, as explained below. This large variable set was reduced for model testing analyses (see Data Analysis, below).

Stream bank full width is the maximum width without flooding, which was measured at 12 transects. iMapBC was used to calculate stream length (Field and Reynolds, 2011). Large wood was included if it would be in the water at bank full, and was >10 cm in diameter and >1.5 m long (Roni and Quinn 2001). Habitat types were identified as pool, riffle, run, glide or rapid (Bain and Stevenson 1999), and area measured for pool to riffle ratio. Pool depth was also measured at the deepest point for pool volume. Undercut banks were measured as a percentage of the length of stream banks on both sides, divided by 2. A clinometer was used to measure gradient at each transect, and a spherical densiometer to measure vegetative canopy cover on each side and the centre of the stream at each transect. Substrate was categorized into percentages of fines (0-12 cm), gravel (1.3-10.2 cm), small cobble (10.3-14.9 cm), large cobble (15.0-24.9 cm), boulder (>25.0 cm) or bedrock (Wolman 1954). Water pH was measured at three transects per stream each year, and the mean between years ranged from 4.8 to 6.9. Maximum weekly averaged temperature was measured over two years using data taken every two hours from ibutton data loggers (DS1922L). Fisheries and Oceans Canada Cultus Lake Research Facility analyzed three water samples collected from each stream prior to and during spawning for ammonium (NH_3^+), nitrate (NO_3) and soluble reactive phosphorous according to American Public Health Association methods (APHA 1989).

To calculate juvenile coho density, triple-pass depletion was completed with a two-meter wide pole seine. Sections were chosen randomly within the area sampled for environmental variables with a seine section length of 8 x bankfull width, with stop nets at the upper and lower ends of the sampling area. Sampled areas were left undisturbed for a minimum of one hour between passes, with the same methods used for each pass.

Density was calculated using maximum likelihood modeling (Schnute 1983).

3.3.3 Spawning chum and pink salmon density

At six of the 17 streams in this study, on-foot visual estimates of spawning salmon abundance were available for spawning chum and pink salmon from Fisheries and Oceans Canada. Additional on-foot stream counts were used for the remainder of sites, undertaken in partnership with the Heiltsuk First Nation's Integrated Resource Management Department. During the period 2006-2011, all streams were counted for a minimum of two years and up to six years. An average of these values was used to get a general characterization of each stream. Exploratory AICc modeling did not distinguish a difference between using mean 2006-2011 spawning chum and pink densities compared to using individual years, therefore only mean (2006-2011) densities are reported.

Three or more salmon counts were completed at each stream during spawning. For most streams, total abundance was estimated using the area-under-the-curve method (English et al. 1992). Peak counts (live+dead) were used for some streams that were not accessible three times during the spawning season (less than 10% of streams). At a subset of streams using both methods, there was no difference in spawning salmon calculations (Hocking and Reynolds, 2011). Estimates of the total number of fish were divided by stream spawning area to calculate spawning salmon density (chum and pink density per m^2) to account for differences among streams in the length where spawning occurred. The stream length available for spawning was measured during visual spawning salmon counts and multiplied by average stream width to estimate stream spawning area

3.3.4 Juvenile coho salmon body size and age determination

All coho collected in pole seines were sampled for body size by measuring fork length, or the distance from tip of snout to fork in tail.

Scales were collected from five fish per stream (3 scales per fish) during each sampling event to determine age in order to categorize fish into age classes. The majority (84.4%) of fish sampled were young of year (age class 0) and the remainder age class 1.

We tested for an effect of sampling date on juvenile coho response variables, as streams were sampled over a period of four to six weeks. No effect was found, therefore sampling date was not considered in further analyses.

3.3.5 Data analysis

We used two approaches to assess the effect of spawning chum and pink salmon densities on juvenile coho body size. First, we used information theoretic and partial correlation approaches to evaluate the correlations between chum and pink salmon densities to young of year (age 0) and age 1 coho body size, compared to a broad suite of habitat variables across a gradient of spawning salmon densities at 17 streams. We used Akaike's information criterion adjusted for small sample sizes. AIC provides a comparison of model fits that includes a penalty for models with larger numbers of parameters to be estimated (Burnham and Anderson 1998). We also examined a linear regression of age composition at the same streams. Second, we used natural barriers including waterfalls in streams, which excluded chum and pink but not coho salmon from upstream locations to test paired sites with and without spawners for 4 streams.

In our first analysis, given the number of streams we surveyed and the large number of potentially inter-related environmental variables assessed, we conducted an exploratory analysis informed by *a priori* hypotheses to identify the habitat or coho density variables that best described each coho body size response variable across the 17 streams, using AICc (AIC adjusted for small samples sizes) according to the methods suggested by Zuur et al. (2010). We retained only the top 2 habitat variables based on ΔAICc values for each response variable to avoid over-fitted models and uphold the principle of parsimony (Burnham and Anderson 2002). These included stream width and pool volume for age 0 body size, and canopy cover and undercut banks for age 1 body size. We used variance inflation factor (VIF) to test for multicollinearity among the explanatory variables (Zuur et al. 2010). For the final models, no variable exceeded a value of two, which suggests multicollinearity among variables was not of concern.

We then assessed the relative importance of pink density, chum density, and the top habitat features as identified in exploratory AICc analysis as explanatory variables on age 0 and age 1 body size. Because we predicted that the behavioral and ecological effects of pink and chum spawning salmon would differ between species, we retained them as separate parameters. However, an exploratory combined analysis showed similar results, with the strength of combined effects somewhere in between the effects of each species individually. Linear models were constructed to represent our *a priori* hypotheses. Because we hypothesized the density of canopy might mediate the effects of spawning salmon on juvenile coho through affecting primary productivity, and pool volume and undercut banks might affect carcass retention, we included interaction terms for them. However, initial analyses prior to final AIC testing revealed that interactions were not important. Therefore, they were excluded from the final analysis. A null model was included in each candidate set, and we included year as a fixed effect to account for systematic differences between the two years of data.

After selecting our independent variables and interactions based on a priori hypotheses and exploratory analyses (Zuur et al. 2009 and 2010), we created a set of models in all combinations limited to a maximum of three variables per model to avoid over-fitting (Burnham and Anderson 2002). We used mixed models to incorporate the hierarchical nature of our data set, including individual body size data for juvenile coho and stream scale data for environmental variables. As such, stream was included as a random effect, while year was included as a fixed effect. We computed candidate models using maximum likelihood estimation (Zuur et al. 2009), and inspected diagnostics for heteroscedasticity, over-leveraging of data points, and normality and independence of residuals. To rank the relative importance of explanatory variables, we used model averaging with summed model weights incorporating all candidate models (Anderson 2008). ΔAICc values, or the difference between model *i* and the top ranked model, are reported for all models with ΔAICc < 3 for reference but only those with ΔAICc < 2 are discussed (Burnham and Anderson, 2002; Grueber et al., 2011). We then used partial correlation analysis to determine the unique contribution of chum and pink density on juvenile coho age 0 and age 1 body size after taking the effect of the top habitat variables (identified by AICc, as above) into account (Cohen et al. 2003).

We also examined the effect of spawning chum and pink density on the proportion of age 0 compared to age 1 fish across the 17 streams. Because there was no significant difference between years (2007 and 2008) for proportion age 0 ($p > 0.05$), we pooled the data to increase the number of fish at each stream used to calculated age proportion (maximum five fish per stream per year). We used an arcsine square root transformation of the ratio of age 0 to age 1 coho and a log transformation of chum and pink density, and used AICc to compete linear regression models in the same way we did for body size. The top habitat variables included for age proportion analysis were gradient and large wood.

For the second part of our analysis, we compared age 0 juvenile coho body size at paired locations above and below a natural barrier to chum and pink spawning in 2008 in each of four streams. Below the barrier juvenile coho had access to chum and pink salmon nutrients, while above the barrier juvenile coho were present because their parents are able to pass the barrier during spawning, but the juvenile coho had no access to chum and pink nutrients. There were no significant differences in the habitat variables identified above and below barriers ($p > 0.05$). We used t-tests to compare differences in juvenile coho body size above and below barriers at each site. We then used linear regression to examine the relationship between the magnitude of difference in juvenile coho body size above and below barriers, and chum and pink biomass density below barriers at each stream. We were unable to separate the effect of species nutrient deposition, either chum or pink, at the sites with spawning salmon (below barrier) and without (above barrier) in this comparison, thus we combined pink and chum densities for the second part of the analysis. Due to difference in body size and thus nutrient load, we used salmon biom ass density based on mean values of chum body mass 3.5k g, and pink body mass 1.2 kg (Hocking and Reynolds, 2011).

All statistical analyses were performed using R (R Development Core Team, 2009), including the MuMIn package (Barton, 2012).

3.4 Results

The body size of the younger age class (age 0) of coho salmon was correlated more strongly with spawning chum salmon density than with pink density (r-squared = 0.31 and 0.02 for chum and pink, respectively; Table 3.2). The positive correlation was also stronger than with any of the habitat variables, or juvenile coho density. An additional 1/4 chum per m^2 was associated with a full centimeter increase in age 0 coho length (Figure 3.1). The model containing spawning chum density in combination with stream width and pool volume was the top model, which improved r-squared by 0.2 compared to the next top model, which was chum by itself (ΔAICc < 2, relative importance 0.87; Table 3.3, Figure 3.2). The resulting relationship between chum density and juvenile coho body size was still relatively strong after taking the effect of the top habitat variables into account, and there was no relationship with pink density (partial r-squared = 0.28 and 0.01, respectively).

Chum density was the only variable in the top model for size of age 1 fish, whereas pool volume and stream width joined chum density in the top model for age 0 fish (Table 3.3, Figure 3.2). These relationships remained the same when habitat variables were taken into account (partial r-squared = 0.28 and 0.36 for age 0 and age 1 body size, respectively). There was a trend towards a stronger relationship between chum density and juvenile coho body size in age 1 coho compared to age 0 (Figure 3.1). Thus, juvenile coho that had had direct contact with spawning chum the previous fall, and had longer in streams for indirect effects to occur, had stronger relationships with spawning chum than juvenile coho that had very little direct contact. Our results suggest that pink salmon density has a positive effect on age 1 coho, though the parameter estimates overlap zero (r-squared 0.23, relative variable importance 0.32; Figure 3.2). This relationship was stronger once the top habitat variables were taken into account (partial r-squared = 0.32 compared to 0.23). There was no strong effect of habitat, either canopy cover or undercut banks (Figure 3.2).

In our analysis above and below barriers to chum and pink spawning salmon, age 0 juvenile coho were significantly larger below the barriers at the two sites with the highest spawning salmon biomass density (Figure 3.3). As salmon biomass density below barriers increased across the four streams, the difference in body size of juvenile coho also increased (r-squared = 0.82; Figure 3.4).

Streams that had more chum and pink salmon had more age 0 compared to age 1 coho (r-squared = 0.29 and 0.28 for pink and chum respectively, $p < 0.03$; Figure 3.3). The effect of chum and pink salmon on proportion age 0 fish was stronger than any habitat variable or juvenile coho density (Table 3.3; Figure 3.5). The untransformed data showed an asymptotic relationship, where the proportion of age 0 coho approached 1, or 100%, at fairly low spawning chum and pink densities (0.15 and 0.2 fish/m^2, respectively; Figure 3.3).

The relationships between habitat variables and each of the three salmon species (Table 3.2) were weaker than the relationships between coho and the two species of spawning salmon (Table 3.3). As expected, the dissolved inorganic nitrogen (ammonia and nitrate) and soluble reactive phosphorus in the streams during spawning in fall were correlated with the density of spawning chum and pink salmon (Table 3.4). However, these relationships generally did not persist through the non-spawning season to summer (Table 3.4), nor were dissolved nutrients among the top habitat variables for juvenile coho body size in the AICc analyses (not shown). In addition to the habitat variables considered in the AICc analyses, chum density was somewhat correlated with the percentage of the substrate that was small cobble (r-squared = 0.21), and pink density with gravel (r-squared = 0.18). These substrate characteristics were not correlated with coho body size (r-squared < 0.1). This suggests that relationships between coho and the other salmon species were not being driven by separate responses to habitat features.

Table 3.2. Bivariate correlations, r, between variables used in the AICc analyses with the data from 2007 and 2008. For age 0 juvenile coho salmon body size, n = 17 streams; and for age 1, n = 7 streams for each year.

		Coho body size, age 0		Coho body size, age 1		Coho percent age 0	Chum density	Pink density	Coho density	Stream width	Canopy density	Pool volume	Percent undercut bank
		2007	2008	2007	2008								
Coho body size, age 0	2007	-	0.34	0.95	0.69	0.27	0.49	0.19	-0.33	0.21	0.49	-0.5	-0.22
	2008	-	-	NA (n=2)	0.28	0.30	0.74	0.03	-0.42	0.51	0.51	-0.09	-0.13
Coho body size, age 1	2007	-	-	-	NA (n=2)	0.23	0.89	0.20	-0.03	0.71	0.86	0.33	-0.59
	2008	-	-	-	-	0.15	0.51	0.65	0.86	0.45	0.34	0.25	0.91
Coho percent age 0		-	-	-	-	-	0.39	0.39	0.04	0.48	0.50	0.02	-0.16
Chum density		-	-	-	-	-	-	0.41	0.03	0.06	0.61	-0.28	0.27
Pink density		-	-	-	-	-	-	-	0.21	0.41	0.48	0.20	0.05
Coho density		-	-	-	-	-	-	-	-	-0.12	-0.03	0.36	0.11
Stream width		-	-	-	-	-	-	-	-	-	0.50	0.50	-0.22
Canopy density		-	-	-	-	-	-	-	-	-	-	-0.02	-0.24
Pool volume		-	-	-	-	-	-	-	-	-	-	-	-0.07

Table 3.3. Summary of Akaike's information criterion linear regression models with the greatest support for body size of age 0 and age 1 juvenile coho salmon. K is the number of model parameters, R^2 is the model correlation coefficient, ΔAICc of model i is the change in model i AICc score from the top model, w_i is the AICc model weight.

	Model parameters	K	R^2	ΔAICc	w_i
Age 0 body size	Chum + pools + stream width	5	0.51	0	0.41
	Chum	3	0.31	2.33	0.13
Age 1 body size	Chum	3	0.36	0	0.41
	Chum + pink	4	0.44	2.23	0.14
	Pink	3	0.23	2.59	0.11
	Null	2	0	2.93	0.1
Proportion age 0	Chum + pink	4	0.50	0	0.21
	Chum	3	0.34	0.95	0.13
	Chum + large wood	4	0.47	1.01	0.13
	Pink	3	0.32	1.32	0.11
	Chum + pink + gradient	5	0.59	1.41	0.10
	Chum + gradient + large wood	5	0.57	2.02	0.08
	Chum + pink + large wood	5	0.56	2.49	0.06
	Chum + gradient	4	0.4	2.97	0.05

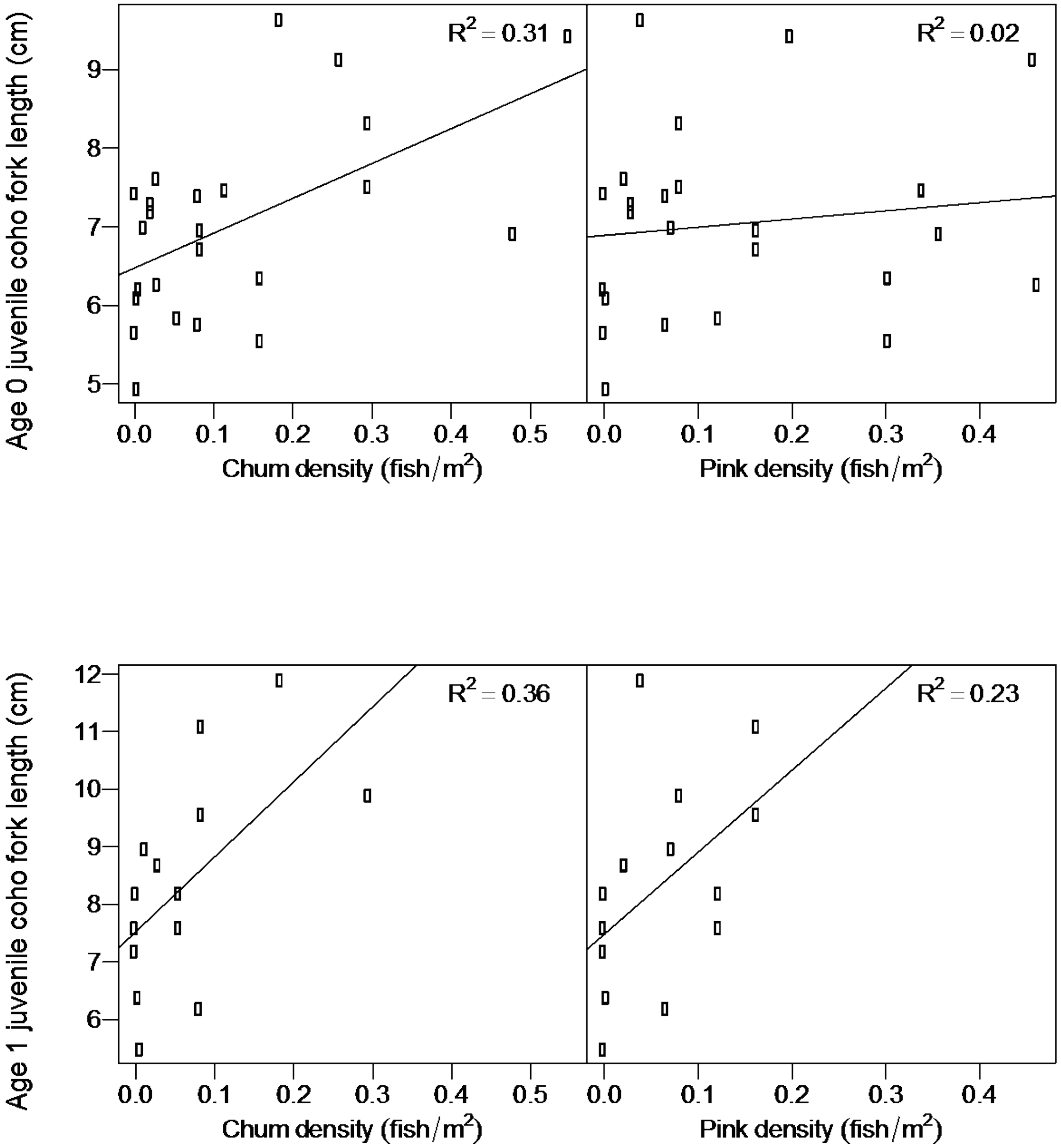


Figure 3.1. Relationships between the density of spawning chum and pink salmon and juvenile coho salmon age 0 body size (top), and age 1 body size (bottom). Each data point represents a stream, in either 2007 or 2008.

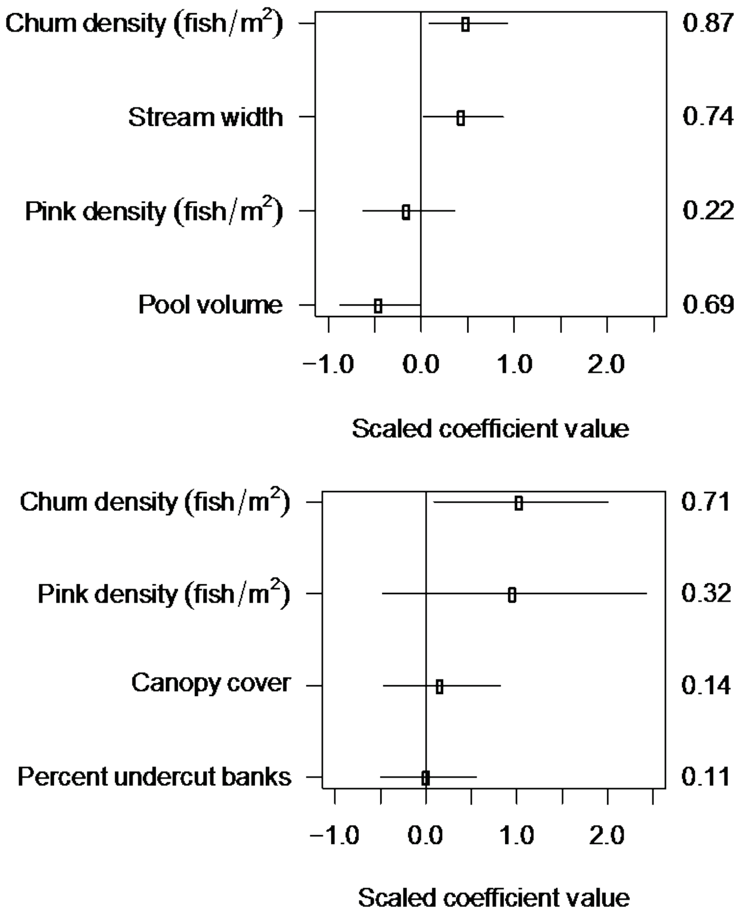


Figure 3.2. Scaled model parameter estimates (circles) with 95% confidence intervals (lines) from averaged predictive linear models describing age 0 coho salmon body size (top), and age 1 coho salmon body size (bottom). The variables are ordered from the highest positive scaled coefficient value to lowest negative value. The relative importance of variables to the averaged model (indicated on the right) is scaled from 0 to 1.

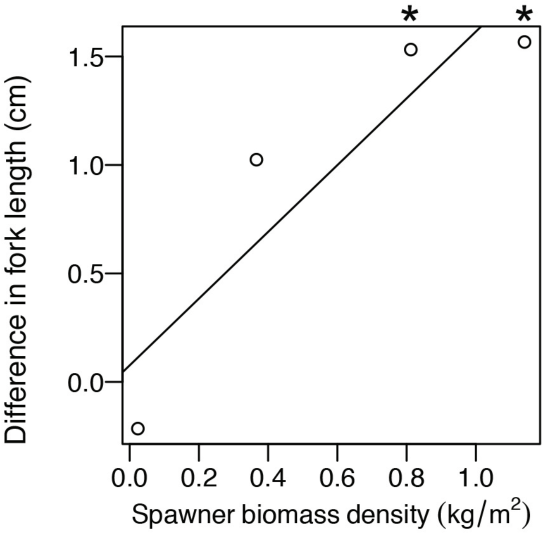


Figure 3.3. Relationship between spawning chum and pink biomass density and the difference in body size of juvenile coho salmon above and below barriers to spawning chum and pink. (*) denote streams with significant differences in juvenile coho body size above and below barriers

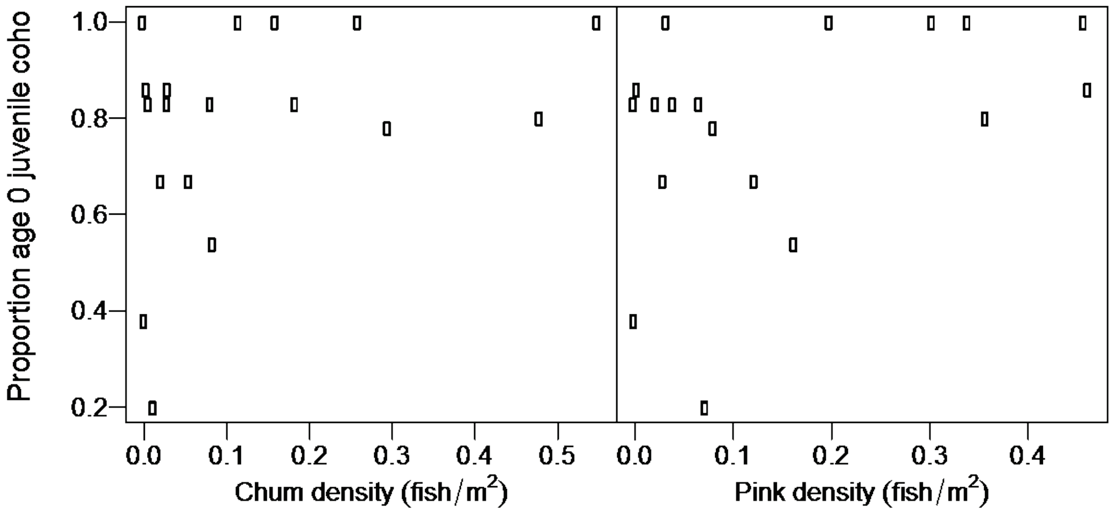


Figure 3.4. Relationship between the density of spawning chum and pink salmon and proportion of age 0 juvenile coho salmon. Each data point represents a stream, in either 2007 or 2008.

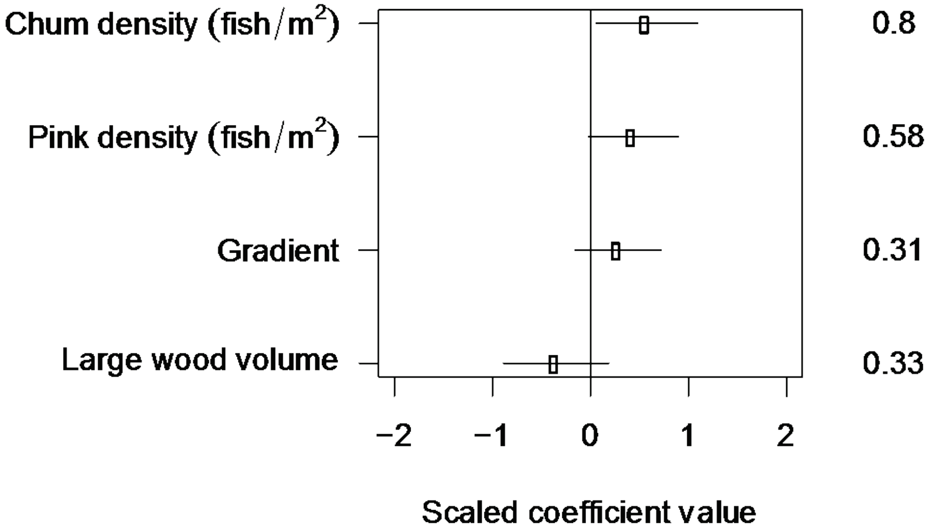


Figure 3.5. Scaled model parameter estimates (circles) with 95% confidence intervals (lines) from averaged predictive linear models describing proportion age 0 coho salmon. The variables are ordered from the highest positive scaled coefficient value to lowest negative value. The relative importance of variables to the averaged model (indicated on the right) is scaled from 0 to 1.

Table 3.4. Bivariate correlations, r, between individual nutrient variables and spawning chum and pink salmon density.

	Nitrate		Ammonia		Soluble phosphorous	
	Summer	Fall	Summer	Fall	Summer	Fall
Chum density	0.24	0.52	0.14	0.59	0.15	0.71
Pink density	0.43	0.57	0.21	0.52	0.02	0.47

3.5 Discussion

We found larger juvenile coho in streams with higher densities of spawning chum salmon, and larger juvenile coho below natural barriers to spawning chum and pink compared to above barriers at high spawning salmon density streams. For age 0 coho, these positive impacts are due to indirect effects. We also found that higher densities of both chum and pink resulted in proportionally fewer age 1 coho compared to age 0, suggesting higher spawning salmon nutrients may result in earlier seaward migration of juvenile coho.

Our findings suggest an indirect carry-over effect from previous spawning events because the majority of coho we sampled were young-of-the-year fish that would have had little to no access to salmon nutrients at the time of sampling. The relationship between juvenile coho body size for age class 1 fish and spawning chum salmon was stronger than for young-of-the-year fish, which may indicate a potential additional benefit from direct access to spawning salmon nutrients or accumulated indirect effects over a longer time period. Our comparison of differences above and below a barrier to spawning pink and chum salmon support the among-stream comparisons, indicating a positive effect of nutrients from spawning fish on juvenile coho body size, with the magnitude of the benefit increasing with the density of spawning fish.

Indirect effects on young-of-the-year coho salmon may have come through increased aquatic and terrestrial invertebrate prey availability linked to spawning salmon (Wipfli et al. 1998, Verspoor et al. 2011, Hocking et al. 2013). These resources are readily used by juvenile salmonids (Scheuerell et al. 2007, Denton et al. 2009). A concurrent study of many of the same streams that we used found spawning salmon biomass predicted primary productivity better than habitat characteristics, and that aquatic invertebrates used both nitrogen and carbon resources from spawning salmon (Harding and Reynolds in prep). While dissolved nutrients may be a key player for this bottom-up mechanism, they were not strongly related to juvenile coho body size. Nutrients may be taken up by primary and secondary producers or are flushed out of the stream. Further study on nutrient and food web dynamics would be helpful to explicitly elucidate the mechanisms behind the relationships described here.

Our results suggest that body size in age 1 coho had stronger relationships with adult chum salmon than body size in young-of-the-year fish, which may reflect greater benefits when salmon nutrients are available directly to the juvenile fish, through preferential diet switching to eggs and tissue (Scheuerell et al. 2007, Hicks et al. 2005). These diets can have dramatically improved energy rations compared to diets not containing eggs (Armstrong et al. 2010). Salmon eggs are 2-3 times more energy dense than benthic invertebrates (Moore et al. 2008). This may explain why salmon subsidies have been shown to have strong effects in stream food webs even though they are available for a short period of time. Furthermore, older age classes of juvenile coho can prey upon newly-hatched pink and chum fry (Hunter 1959), as well as invertebrates that have been stirred up by adult salmon digging nests an fighting for space and mates. They may also benefit from blowfly larvae on salmon carcasses in streams, which are a preferred food source for juvenile salmonids (Scheuerell et al. 2007, Denton et al. 2009).

We found few to no age 1 coho in streams at the upper range of spawning chum and pink densities (Figure 4). This matches our prediction that nutrient subsidies and resulting larger coho body size could lead to migration from the stream to the ocean at an earlier age. Further, our data suggest a threshold effect of spawning salmon density where the majority of age 0 fish migrate to the ocean rather than remaining in freshwater for an additional year, and this threshold is fairly low within the range of the streams included in this study (Figure 4). Although other studies have found stream temperature to affect whether coho outmigration occurs in a given year (e.g. Spence and Dick 2013), we did not find this to be the case. Instead, chum and pink densities were better correlates of juvenile coho age proportion than any habitat characteristic. Note that it is also possible that chum salmon cause displacement of juvenile coho during spawning, as suggested in a subsequent chapter, where we found that the positive effect of spawning chum on juvenile coho abundance was reduced in the fall compared to summer (Nelson and Reynolds 2014a).

Previous research has also found a positive effect of spawning salmon nutrients on juvenile salmonids, with the majority of studies utilizing experimental carcass additions. For example, carcass addition positively affected juvenile coho body condition (Bilby et al. 1998, Wipfli et al. 2010), juvenile coho mass and body size (Wipfli et al.

2003), juvenile coho growth (Wipfli et al. 2010, Giannico and Hinch 2007, Lang et al. 2006), and biomass of juvenile Atlantic salmon (Williams et al. 2009). On the other hand, two studies did not find positive effects of carcass addition on juvenile cutthroat trout and steelhead: specific growth rate was less with carcasses than without (Wilzbach et al. 2005) and growth did not change with carcass addition (Harvey and Wilzbach et al. 2010). Notably, this study design does not take the full effect of spawning salmon into account (Tiegs et al. 2011). For example, many of these studies do not include eggs, which are preferred by juvenile salmonids (Hicks et al. 2005, Scheurell et al. 2007). Exceptions that did include egg provision were studies by Wipfli et al. (2010) and Lang et al. (2006). In addition, carcass experiments do not include the effect of dissolved nutrients through excretions, or the potential engineering effects of spawning activities (Moore and Schindler 2008). A study using stable isotopes has shown that juvenile coho were not able to take up significant amounts of marine-derived nitrogen from sites with only carcass additions, whereas they were enriched in salmon nutrients from sites with naturally-occurring spawning salmon, which would have included the combined effects of carcass, egg and excretory nutrient benefits and engineering activity (Shaff and Compton 2009).

Our findings complement those by Rinella et al (2012), who showed increased growth rate in juvenile coho, as indexed by RNA-DNA ratios, across 11 streams of increasing naturally-occurring spawning salmon. Although the authors showed carry-over effects into the non-spawning season, we are the first to show an entirely indirect effect of spawning salmon on juvenile coho body size by studying age 0 coho. Another study looking at naturally-occurring spawning salmon found increased growth rate in dolly varden in seven ponds increasing in spawning salmon biomass (Denton et al. 2009). Our study is the first to separate effects by age class (including age 0 with no direct contact and age 1 with direct contact with spawning salmon), to examine effects on coho age composition, and to include the comparative influences of habitat characteristics. Contrary to our expectation and indications from previous research (Tiegs et al. 2008, Armstrong et al. 2010), we found habitat characteristics did not mediate the relationship between spawning chum and pink, and juvenile coho. This may be related to a comparatively high density of spawning fish obscuring any effects of habitat.

We attempted to address the potential issue of spurious results in our correlative study by taking a broad range of habitat variables into account explicitly and analyzing them with information theoretic and partial correlation approaches. For example, a spurious correlation may come out if all three species of salmon respond similarly to an unmeasured habitat characteristic. We included stream width at bank full, stream length, large wood, pools, pool:riffle ratio, undercut banks, gradient, canopy cover, percent fines, pH, substrate, temperature, dissolved nutrients and the density of conspecifics, and found the relationships between spawning chum and pink salmon and juvenile coho were stronger than those between any of the three salmon species and habitat characteristics.

This study suggests that spawning salmon can have positive effects on other species of juvenile salmonids. Since growth and production of stream-rearing salmonids can be limited by food availability (Chapman 1966) these findings imply that cross-boundary nutrient inputs may be important for fisheries. Understanding these cross-species interactions can also help inform ecosystem-based management (Bilby et al. 2001, Wipfli and Baxter 2010, Levi et al. 2012).

4 Time-delayed subsidies: Interspecies population effects in salmon[3]

4.1 Abstract

Cross-boundary nutrient inputs can enhance and sustain populations of organisms in nutrient-poor recipient ecosystems. For example, Pacific salmon (*Oncorhynchus* spp.) can deliver large amounts of marine-derived nutrients to freshwater ecosystems through their eggs, excretion, or carcasses. This has led to the question of whether nutrients from one generation of salmon can benefit juvenile salmon from subsequent generations. In a study of 12 streams on the central coast of British Columbia, we found that the abundance of juvenile coho salmon was most closely correlated with the abundance of adult pink salmon from previous years. There was a secondary role for adult chum salmon and watershed size, followed by other physical characteristics of streams. Most of the coho sampled emerged in the spring, and had little to no direct contact with spawning salmon nutrients at the time of sampling in the summer and fall. A combination of techniques suggest that subsidies from spawning salmon can have a strong, positive, time-delayed influence on the productivity of salmon-bearing streams through indirect effects from previous spawning events. This is the first study on the impacts of nutrients from naturally-occurring spawning salmon on juvenile population abundance of other salmon species.

---

[3] A version of this chapter has been accepted as Nelson, M.N. and Reynolds, J.D. Time-delayed subsidies: Interspecies population effects in salmon. *PLoS one* (March, 2014).

4.2 Introduction

Movement of nutrients across ecosystem boundaries can contribute to the productivity of recipient ecosystems (Polis et al. 1997, Nakano and Murakami 2001). This can have a wide range of effects, including individual condition and growth (Marczak and Richardson 2008), population abundance and distribution (Garcia et al. 2011), and community dynamics (Knight et al. 2005, Hocking and Reynolds 2011). Subsidies are particularly important to nutrient-limited systems, such as desert islands (Piovia-Scott et al. 2011), temperate lakes (Graham et al. 2006), and freshwater streams (Richardson et al. 2010).

The annual influx of spawning salmon (*Oncorhynchus* spp.) along the temperate coasts of the northern Pacific Ocean constitutes a substantial contribution of marine-derived nutrients to nutrient-poor freshwater streams and lakes (Naiman et al. 2002, Janetski et al. 2009). At the same time, the engineering effects of salmon spawning activities and the marine outmigration of salmon offspring result in some nutrient export (Scheuerell at al. 2005, Moore et al. 2007). Reductions in salmon populations in the North Pacific region, which are as high as 95% in some areas (Gresh et al. 2000), have created concern that reduced nutrient availability or streambed engineering by spawning fish may alter the species and communities in freshwater and adjacent terrestrial ecosystems. In fact, the decline of Pacific salmon represents one of the key current environmental issues in North America (Ruckelshaus et al. 2002). Yet without quantifying relationships between salmonids and their ecosystems, it is difficult to inform ecosystem-based management or make holistic management decisions (Sharma and Hilborn 2001).

Since some species of Pacific salmon spend a year or more as juveniles in the same streams that receive nutrients from adult carcasses, it has been suggested that there could be positive feedback across generations of salmon (Michael 1995, Bilby et al. 1998). For example, coho (*O. kisutch*) spawn far upstream, but juveniles move downstream into areas where high densities of other species of salmon are spawning, such as pink (*O. gorbuscha*) and chum (*O. keta*). Analysis of 8 years of data indicated a positive relationship between the abundance of spawning pink salmon and subsequent spawning adult coho abundance two years later (Michael 1995). This idea has taken such a strong hold that it is now common practice for fisheries managers to consider adding salmon carcasses from hatcheries into streams in order to enhance productivity, including growth or survival of juvenile salmon (Harvey and Wilzbach 2010). However, the effects of such a practice have not been rigorously tested. We do know that stream-rearing juvenile salmonids directly consume spawning adult tissue and eggs (Bilby et al. 1998, Armstrong et al. 2010), and they preferentially switch to these resources when they are available (Scheuerell et al. 2007). They may also benefit indirectly from spawning salmon nutrients which increase primary productivity (Wipfli et al. 1998, Verspoor et al. 2010) and aquatic and terrestrial invertebrates (Wipfli et al. 1998, Verspoor et al. 2011, Hocking et al. 2013). However, bioturbation by large-bodied spawning salmon can also have negative effects on stream invertebrate biomass (Moore and Schindler 2008). Therefore, there remains little evidence of population-level linkages among populations of salmonids.

Nutrients from marine-derived sources, measured by stable nitrogen isotopes, were found to persist in stream salmonids from fall spawning events into the following growing season (Rinella et al. 2013), and marine-derived nutrient signatures were best explained by spawning events in the previous year (Reisinger et al. 2013). Studies have shown increased spawning salmon resource availability is linked to improved condition and growth in juvenile salmonids (Scheuerell et al. 2007), and coho in particular (Bilby et al. 1998, Lang et al. 2006, Wipfli et al. 2003). However, the effect of spawning salmon on juvenile salmonid abundance is not yet clear, with some studies showing positive effects (Bilby et al. 1998) and others no strong effects (Wilzbach et al. 2005, Harvey and Wilzbach 2010). Notably, most previous research has been limited to experimental carcass addition (cf. Lang et al. 2006), which may have different impacts on streams than do live spawning salmon (Tiegs et al. 2011).

Abundance of coho juveniles also depends on habitat characteristics, including cover and predator refugia in the form of pools (Sharma and Hilborn 2001), large wood and undercut banks (Roni and Quinn 2001). Coho may also be affected by habitat related to food availability, such as riffle area, fine substrate, gradient (Hawkins et al. 1983), and overhead canopy density (Wilzbach et al. 2005). Juvenile coho can be limited by physiological tolerances related to temperature (Holtby 1988) and pH (Degerman et al. 1986). Additionally, stream size is an important predictor of juvenile coho production (Bradford et al. 1997).

In this study we investigate whether juvenile coho salmon benefit from adult pink and chum salmon. Coho spend at least their first year of life rearing in freshwater streams, whereas pink and chum salmon migrate to the ocean within weeks of emerging from the stream substrate (Groot and Margolis 1991). Therefore, juvenile pink and chum have little potential to benefit from salmon nutrients in the stream, whereas their nutrients or engineering effects could affect juvenile coho. Most of the coho that we studied were young of year, and would therefore not have had any direct exposure to spawning salmon in fall at the time of summer sampling because they emerged only the previous spring. At the time of fall sampling, some egg or tissue consumption may have occurred during the spawning period (at most a few weeks of exposure). However, while this may affect individual attributes such as condition and body size immediately, we feel this is apt to have had minimal effects on population abundance in such a short time period. Coho adults spawn much further upstream in our study streams than pink and chum salmon, and at less than 5% of pink and chum density, so there are likely little to no carcass implications from adult coho.

We conducted a multi-stream comparison to examine the relationship between spawning pink and chum abundance and juvenile coho abundance, and considered a suite of habitat variables that have been shown to be associated with juvenile coho. We also tested whether these habitat variables could have independent effects on the three salmon species. Because the vast majority of coho we sampled were young-of-the-year, any effects would be due to spawning events from previous years. We predicted that chum salmon would have greater effects than pink salmon due to their larger body size and egg deposition (Groot and Margolis 1991). By using naturally-occurring salmon in a wide range of streams, this study encompasses the combination of carcasses, eggs and excreta, as well as engineering effects on the abundance of juvenile salmonids.

4.3 Materials and Methods

4.3.1 Study sites and design

We surveyed 12 streams on the central coast of British Columbia in the Great Bear Rainforest, in Heiltsuk First Nation traditional territory (Table 4.1). Pink and chum are the dominant spawning salmon, and juvenile coho were present in all streams. All sites were accessible only by boat. Land use has been very limited in the area, with some selective logging prior to the 1950s (Hocking and Reynolds 2011).

In order to account for the effect of spawning coho adults on the density of juvenile coho, it may be helpful to have data for adult coho in streams. However, there were very little historical data available on spawning coho numbers at our streams, nor was it possible to assess this in the field due to the inherent difficulties in estimating spawning coho abundance (Irvine et al. 1992). However, a consistent relationship between spawning coho and coho smolt abundance has been difficult to find because smolt production is regulated by the availability of rearing habitat in the stream, rather than adult spawning coho abundance (e.g. Bradford et al. 1997), unless spawning densities are very low. Furthermore, where data were available within our study area (five streams with spawning coho counts available since 2000), the densities of spawning coho (50-204 females/km) exceed the number of spawning adults that are thought to saturate the habitat with juveniles, which ranges from 4-44 females/km with an average of 19 (Bradford et al. 2000). Expected juvenile production, calculated as 85 juveniles per spawning female (Bradford et al. 2000) for the five streams (mean = 11,800) was far in excess of the observed number of juveniles (mean = 3,592), which further indicates juveniles are limited by something other than spawning coho abundance.

Study streams ranged in bank full width from 1.2 to 22.8 m, and they all flow directly into the sea. The watersheds range from high gradient exterior coastal sites to lower gradient habitats in coastal fjords. Stream riparian areas are forested within the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1987), with a dominant canopy of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and

Sitka spruce (*Picea sitchensis*). Riparian trees and shrubs are dominated by red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), false azalea (*Menziesia ferruginea*), and blueberry (*Vaccinium* spp.). Total annual precipitation in the region is amongst the highest in North America, at 3000-4000 mm/yr.

Study streams were sampled for juvenile coho when the pink and chum salmon were spawning in September-October, 2008, as well as prior to spawning in May-June, 2008. Data were available for numbers of adult pink and chum returning to spawn from 2006-2011 across the entire spawning length of each stream. The length of area sampled for environmental variables was scaled to average stream width (30 x stream width), and divided into 12 transects. A random subsample of this area was sampled for juvenile coho (8 x stream width), as per below.

Table 4.1. Stream characteristics, spawning salmon population data (2006-11) and mean juvenile coho abundance (summer and fall, 2008) for streams (n = 12) in this study. Coho salmon abundance and density were log transformed for the analyses.

Stream	Length (m)	Bank full width (m)	Mean pink abundance	Mean chum abundance	Mean coho abundance	Mean coho density (fish/m^2)
Ada Cove	6,480	11.1	318	1,160	756	0.193
Beales Left	3,360	10.9	1,030	351	1,111	0.367
Bullock Main	2,420	10.9	1,515	2,030	752	0.178
Fanny Left	4,270	12.8	5,008	2,646	48,936	2.97
Hooknose	2,970	16.9	2,970	1,537	13,530	0.632
Jane Cove	1,380	4.6	0	12	214	0.122
Kill Creek	980	3.5	289	797	731	0.505
Kunsoot Main	3,670	13.1	5,800	376	9,272	0.74
Mosquito Left	3,250	4	203	92	10	0.006
Port John	2,540	3.3	2	3	164	0.241
Sagar	5,200	15.5	634	779	9,409	0.988
Troup North	440	4.4	1	2	505	0.422

4.3.2 Environmental variables

We measured a large set of variables that have been shown or hypothesized to affect abundance of juvenile coho salmon (Table 4.2). These were: stream catchment area, stream width at bank full, stream length, maximum stream depth, stream wetted width, large wood, pools, pool:riffle ratio, undercut banks, gradient, canopy cover, percent fines, maximum weekly temperature, pH, and dissolved nutrients (nitrate, ammonia and soluble reactive phosphorous). These variables were combined for model testing (see Data Analysis, below).

Table 4.2. Predictions of the potential influence of habitat features on juvenile coho abundance.

Variable	Mechanism	Direction	References
Stream length	Available habitat increases as stream length increases	Positive	Bradford et al. 1997
Stream width	Smaller streams have more structural complexity	Negative	Rosenfeld et al. 2000
Large wood	Structures provide cover/predator refuge	Positive	Roni and Quinn 2001
Undercut banks	Provide cover/predator refuge	Positive	Roni and Quinn 2001
Pools	Provide cover/predator refuge	Positive	Sharma and Hilborn 2001
Pool:riffle ratio	Optimum combination of cover (pools) to invertebrate production (riffles)	Negative outside optimal range	Kershner and Snider 1992
Fine sediment	Reduces proportion of drift invertebrates, and reduces cover availability by filling spaces between large substrates and structures	Negative	Hawkins et al. 1983
Gradient	High gradient reduces riffles for intertebrate production, and increases effects of extreme flow events	Negative outside optimal range	Hawkins et al. 1983
Canopy cover	Provides habitat for terrestrial invertebrates composing drift, but reduces light penetration for primary productivity-feeding aquatic invertebrates	Positive or negative	Nakano and Murakami 2001, Wilzbach et al. 2005
pH	Physiological tolerance	Positive (slightly acidic streams)	Degerman et al. 1986
Temperature	Physiological tolerance	Negative (for maximum temperatures	Holtby 1988

Stream width was measured in two ways. First we measured the width at water level at the time of sampling, or wetted width. Second, we measured the width at the maximum width without flooding, or bank full width. Both stream width measurements were averaged across 12 transects. Depth was measured at each transect and the highest value used to represent maximum depth. Stream length and catchment area were calculated using iMapBC (Field and Reynolds 2011).

Stream temperature was characterized as the maximum weekly average temperature (MWAT) averaged over the two years during which data were collected. Temperatures were measured using two waterproof ibutton data loggers (DS1922L) at two standard transects per stream near the top and bottom of the study reach, which were fastened below the lowest water level to iron rods, and which recorded temperatures every two hours. Water pH was measured at three standard transects per stream throughout the study reach, and ranged between 4.8 and 6.9.

Stream habitat types (pool, riffle, run, glide, rapid) were identified according to Bain and Stevenson (1999). The length and width of each habitat unit was measured, giving a measure of pool:riffle ratio for the stream. Pool depth was also measured at the deepest point, giving an estimate of pool volume for the stream. All pieces of wood that would be in the water at bank full and which were >10 cm in diameter and >1.5 m long were measured for length and diameter to calculate large wood volume for the stream (Roni and Quinn 2001). Undercut bank percentage for the stream was calculated as the mean length of stream bank undercut on either side, divided by the stream length. Gradient was measured using a clinometer, and vegetative cover using a spherical densitometer at 12 transects per stream. Substrate was measured at 12 transects per stream on the intermediate axis on 10 stones along each transect (Wolman 1954), and categorized into fines (0-1.2 cm), gravel (1.3-10.2 cm), small cobble (10.3-14.9 cm), large cobble (15.0-24.9 cm), boulder (>25.0 cm) or bedrock.

Three water samples were collected at three standard transects at each stream throughout the study reach prior to and during spawning for dissolved nutrients. Dissolved phosphorous (soluble reactive phosphorous) and dissolved inorganic nitrogen (ammonium NH_3^+ and nitrate NO_3^-) were analyzed by personnel at the Fisheries and

Oceans Canada Cultus Lake Research Facility following the American Public Health Association methods (APHA 1989).

4.3.3 Spawning pink and chum salmon abundance

Visual surveys by observers walking up streams were available from Fisheries and Oceans Canada for spawning pink and chum abundance at half of the streams in this study for between one and six years while the study was being undertaken (2006-2011). These data were supplemented using the same survey protocol in partnership with the Heiltsuk First Nation's Integrated Resource Management Department. Fish in all streams were counted for at least two years and up to six years (2006-2011) by either Fisheries and Oceans Canada, Heiltsuk First Nation's Integrated Resource Management Department or Simon Fraser University staff, with an average taken (sum of spawning salmon counts/number of times counted) in order to generally characterize each stream and reduce the influence of annual temporal variation. Akaike's information criterion adjusted for small sample sizes (AICc) results were similar using mean 2006-2011 adult abundance compared with the spawning year prior to sampling, 2007, thus only mean 2006-2011 adult abundance results are reported in order to reduce the effect of inter-annual variation.

At least three spawning salmon counts were undertaken at each stream in each spawning season, and total abundance was estimated using the area-under-the-curve method (English et al. 1992). When we could not access the stream three times within a spawning season, the peak (live+dead) counts were used. There was no substantive difference between methods at a subset of cases using both methods (Hocking and Reynolds 2011).

4.3.4 Juvenile coho salmon abundance

In May-June and September-October, 2008, juvenile coho were collected by triple-pass depletion of a stop-netted section. Due to the remoteness of our sites and the complexity of streams, we elected to use a two-meter wide pole seine to collect juvenile coho (e.g. Swain and Holtby 1989). Sampled areas were left undisturbed for a minimum of one hour between passes, with the same methods used for each pass. Sections were chosen randomly within the area sampled for environmental variables with seine section length standardized as 8 x bank full width. In order to ensure stable and representative coho density throughout the entire section, the sampled area included representation from all habitat types (pools, riffles, glides, and runs) with an average area sampled for coho density of 231.9 m^2. Resulting coho density (juvenile coho/m^2) was used to calculate abundance (juvenile coho/stream) in the spawning reach for each stream.

Maximum likelihood modeling was used with the three pass depletion data to estimate total abundance (Schnute 1983). A comparison between a standard multinomial method (Zippin 1956), maximum likelihood (Schnute 1983), and a hierarchical approach (Dorazio et al. 2005) for estimating abundance from depletion found no significant difference in abundance estimates between methods (ANOVA, n=12, $p > 0.05$). As streams were sampled consecutively over a period of six weeks, we tested for an effect of sampling date within season on abundance. No effect was found, therefore sampling date was not included in further analyses within each season.

Age analysis of scales from a small subset of individuals (n = 5 at each stream) revealed the vast majority (87.8% in summer and 81.0% in fall) were young of year (hatched in spring of the same year of sampling) and the remainder hatched the previous spring. We were unable to separate the remaining fish by age class, nor were we able to model abundance for age classes separately, thus our abundance values include both age classes.

4.3.5 Data analysis

Given the large number of potentially inter-related environmental characteristics assessed (Table 4.2), we used principal components analysis (PCA) to reduce 17 habitat variables into orthogonal axes. All axes explaining more than 5% of the variance were extracted for further analysis (McGarigal et al. 2000). These axes explained 64.8% of the variation in habitat characteristics among streams in three principal components; watershed size (PC1), habitat structure (PC2), and dissolved nutrients (PC3) (Table A.1, Appendix A). The component representing watershed size (PC1) includes catchment area, stream length, bank full width and wetted width, as well as dissolved phosphorous. The component mainly representing habitat structure (PC2) includes percent undercut bank, large wood volume, and gradient, as well as pH. The component representing dissolved nutrients (PC3) includes maximum temperature, dissolved nitrate and dissolved phosphorous (Table A.1).

Next, we assessed the relative importance of pink salmon abundance, chum salmon abundance, and the habitat principal components as explanatory variables of juvenile coho salmon abundance in summer and fall. Linear models were constructed to represent our *a priori* hypotheses. Although it is possible habitat characteristics, such as those affecting nutrient retention or availability, may mediate the relationships between spawning pink and chum and juvenile coho abundance (e.g. Tiegs et al. 2008), we did not include interaction terms in order to avoid over-parameterization (Burnham and Anderson 2002). However, preliminary correlation analyses between habitat variables and spawning pink and chum abundance did not reveal strong interactions (r-squared < 0.25). A null model was included in each candidate set. To account for the lack of independence from data from 2007 and 2008, we included year as a fixed effect in our models. Coho abundance was $\log_{10}$ transformed to reduce over-leveraging of outlying data points.

Akaike's information criterion adjusted for small sample sizes (AICc) was used to evaluate the relative importance of the candidate sets of linear models for juvenile coho abundance as the response variable. AIC evaluates the predictive power of models with different combinations of variables based on the principle of parsimony, which balances optimal fit with the number of variables used in the model (Burnham and Anderson 1998). We used all model combinations with a maximum of three variables per model to avoid over-fitting (Burnham and Anderson 2002). Candidate models were computed using the maximum likelihood estimation method (Zuur et al. 2009). We inspected model diagnostics for heteroscedasticity, over-leveraging of data points, and normality and independence of residuals. Model averaging was then used to quantify and rank the importance of individual explanatory variables for each response variable using summed model weights (Anderson 2008). We incorporated all of the candidate models (including those with ΔAICc > 2) into the model averaging for each response variable. ΔAICc values, which represent the difference between model *i* and the top ranked model, are reported for all models with ΔAICc < 3 (Burnam and Anderson 2002, Grueber et al. 2011).

We wanted to determine whether stream size could drive patterns of juvenile salmon abundance. Therefore, the principal component representing these variables was included in AICc model testing, with coho abundance as the response variable. An alternative would have been to calculate fish densities instead of abundance, i.e. juvenile coho, and spawning pink and chum per unit stream size (Figure A.1, Appendix A). We found similar results, and we have chosen to present the abundance results with stream size as a separate parameter in order to see the independent effects of stream size rather than combine it with spawning salmon. We also used partial correlation analysis to determine the unique contribution of pink and chum abundance to coho abundance after the influence of stream size and other habitat characteristics (principal components) had been removed.

All statistical analyses were performed using R (R Development Core Team 2009), including the MuMIn package (Barton 2012).

4.4 Results

High summer juvenile coho abundance was associated with high pink and chum abundance and large watershed size (PC1, Figure 4.1). These three variables were the only important correlates of summer coho salmon abundance, (ΔAICc < 2, relative importance 0.58, 0.4 and 0.59, respectively; Figure 4.2). After taking the effect of habitat components, including watershed size (PC1), into account, the resulting positive relationship between pink and chum abundance and juvenile coho abundance was still clear (partial r-squared = 0.35 and 0.55 for pink and chum, respectively). Note that the remaining correlation between chum and coho was stronger than pink and coho when the effect of habitat was controlled statistically, which was consistent with our prediction.

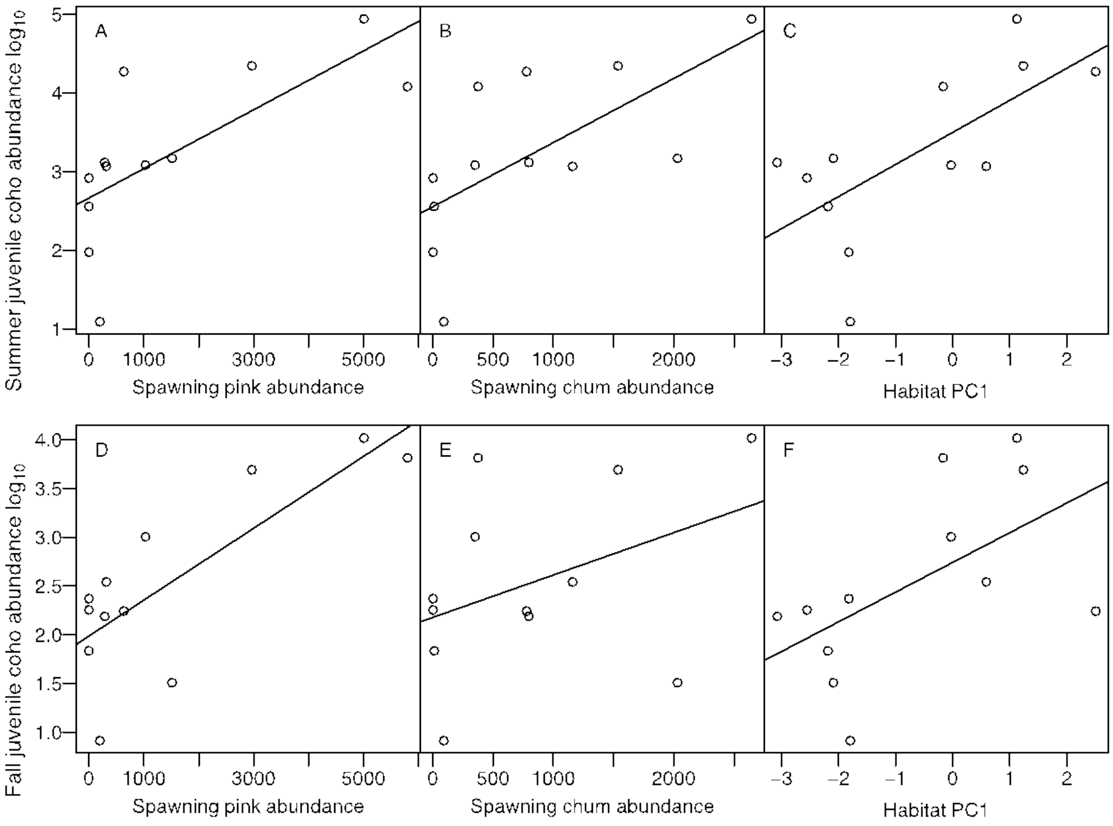


Figure 4.1. Relationships between the abundance of spawning pink and chum salmon and habitat principal components, and abundance of juvenile coho salmon in summer prior to spawning (a-c) and during spawning in fall (d-f). Large values of PC1 correspond to variables related to large watersheds.

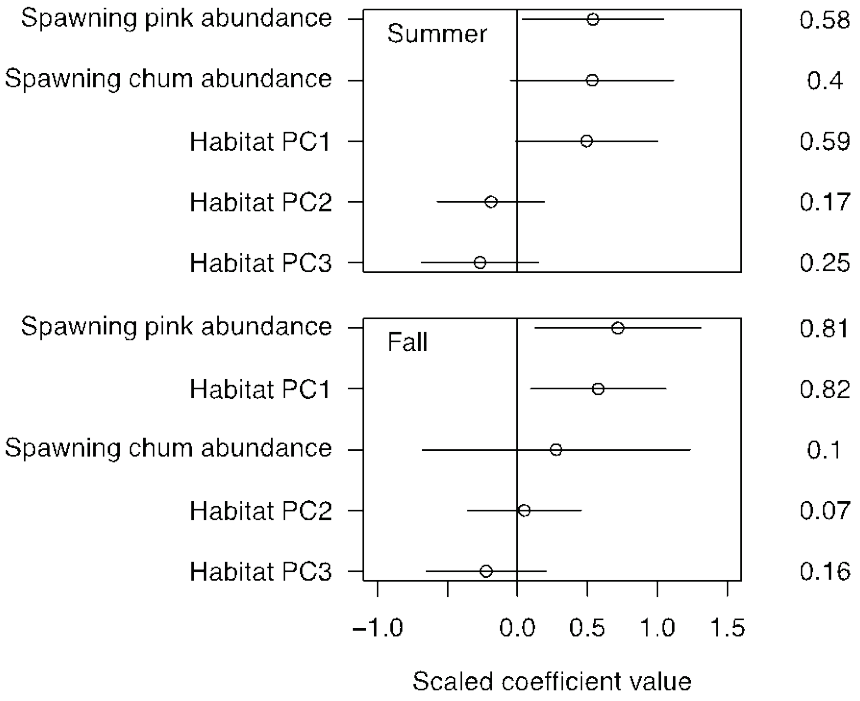


Figure 4.2. Scaled model parameter estimates (circles) with 95% confidence intervals (lines) from averaged predictive linear models describing juvenile coho salmon abundance in summer (top) and fall (bottom). The variables are ordered from the highest positive scaled coefficient value to lowest negative value. The relative importance of variables to the averaged model (indicated on the right) is scaled from 0 to 1.

For fall coho abundance, spawning pink salmon abundance and watershed size (PC1) explained differences in juvenile coho abundance better than chum abundance, habitat structure (PC2), or dissolved nutrients (PC3) (Table 4.3). Every 1,000 pink salmon adults were associated with 1,500 more juvenile coho salmon (Figure 4.1). The model containing spawning pink abundance and watershed size was the only model with ΔAICc < 2 (relative importance = 0.81 and 0.82 for pink abundance and watershed size, respectively; Figure 4.2). The relationship between pink abundance and fall coho abundance remains after taking the effect of habitat components into account (partial r-squared = 0.59), while no relationship remains between chum abundance and coho abundance in fall (partial r-squared = 0.04).

Table 4.3. Summary of linear regression models with the greatest support (ΔAICc < 3.0) for juvenile coho salmon abundance in summer and fall. AICc = Akaike's information criterion with a correction for small sample size, K = number of model parameters, R^2 = model correlation coefficient, ΔAICc = change in AICc score from top model, w_i = AICc model weight. The models are ordered by decreasing w_i.

	Model parameters	K	R^2	ΔAICc	w_i
Summer juvenile coho abundance	Pink + PC1	4	0.73	0.00	0.23
	Pink	3	0.61	1.20	0.13
	Chum + PC1	4	0.68	2.34	0.07
	Chum + PC3	4	0.68	2.38	0.07
	PC1	3	0.57	2.50	0.07
	Chum	3	0.56	2.74	0.06
	Chum + PC1 + PC3	5	0.77	2.91	0.05
Fall juvenile coho abundance	Pink + PC1	4	0.76	0.00	0.50

Streams that had the greatest loss of juvenile coho between summer and fall had larger numbers of chum adults (r = 0.49; Figure 4.3). However, there was no relationship with the abundance of pink salmon (r = -0.06).

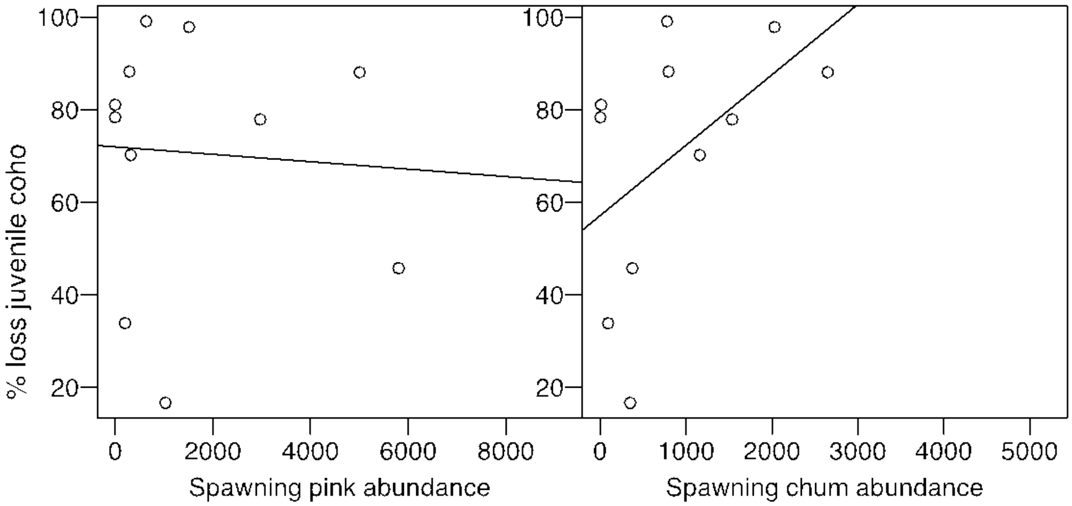


Figure 4.3. Relationships between the percent loss of juvenile coho salmon between summer and fall and the abundance of spawning pink and chum salmon.

The relationships between the broad suite of habitat variables measured (Table 4.2) and coho abundance were weaker than the relationships between pink and chum abundance and coho abundance (Tables 4.3 and 4.4). Pink and chum abundance were also correlated with the percentage of the substrate that was small cobble (r^2 = 0.52 and 0.48, respectively). Small cobble was not correlated with coho abundance (r^2 < 0.1).

Table 4.4. Bivariate correlations, r, between variables used in the analyses. Coho salmon abundance has been log transformed.

	Summer coho abundance	Fall coho abundance	Pink abundance	Chum abundance	Habitat PC1	Habitat PC2	Habitat PC3
Summer coho abundance	-	0.79	0.78	0.75	0.75	-0.16	-0.21
Fall coho abundance	-	-	0.76	0.56	0.74	0.02	-0.31
Pink abundance	-	-	-	0.55	0.61	0.02	-0.16
Chum abundance	-	-	-	-	0.66	0.08	0.17
Habitat PC1	-	-	-	-	-	0.00	0.00
Habitat PC2	-	-	-	-	-	-	0.00

4.5 Discussion

We found that streams containing higher more spawning pink salmon had more juvenile coho salmon. Juvenile coho were also more abundant in streams that had more spawning chum salmon, though this was true only in the summer period prior to the arrival of spawning adult chum. Because over 80% of the coho sampled in the pre-spawning portion of this study were recently hatched and had no direct contact with spawning adults of any species, our findings suggest a legacy effect of salmon nutrient subsidies through indirect effects. Other studies have shown marine-derived nutrients to persist in aquatic invertebrates and stream salmonids from fall into summer (Rinella et al. 2013) and a legacy signature of marine-derived nutrients in juvenile coho that is best explained by spawning salmon run size the previous year (Reisinger et al. 2013).

Watershed size was as important in explaining juvenile coho abundance as pink and chum abundance, whereas watershed size and spawning salmon abundance were much better at predicting juvenile coho abundance than the broad suite of other habitat characteristics considered. This multi-stream comparison also complements a study of one stream with 8 years of data suggesting that adult coho abundance is positively related to the abundance of adult pink salmon (Michael 1995).

Several mechanisms may explain the strong and positive indirect effects of spawning pink and chum on juvenile coho abundance. For example, there could be a bottom-up trophic pathway if dissolved nutrients from spawning salmon enhance primary productivity. It is also possible that salmon subsidize invertebrates feeding directly on carcasses, which could be eaten by juvenile coho. Both mechanisms have been shown, with enhanced primary production (Wipfli et al. 1998, Verspoor et al. 2010) and increased invertebrate biomass (Wipfli et al. 1998, Verspoor et al. 2011). Indeed, at the streams in this study, other research has found spawning salmon biomass to be the best predictor of summer biofilm and chlorophyll a, and salmon-derived nitrogen in biofilm to be 2-3x higher in sites below barriers to pink and chum compared to above (Harding et al. 2014). Furthermore, at these same streams, spawning salmon biomass was an important predictor of salmon-derived nitrogen and carbon in aquatic invertebrates (Harding and Reynolds in prep). Although dissolved nutrients were not strong predictors of coho abundance, they were more strongly related to spawning pink and chum in fall than during summer (Habitat PC3, Table 4.4), suggesting these nutrients do not persist in the water for long after spawning events.

Previous studies have tested for impacts of salmon on densities of juvenile salmonids using experimental additions of carcasses. Bilby et al. (1998) showed an increase in the density of juvenile coho following the addition of adult coho carcasses to two natural streams. Lang et al. (2006) found a general pattern of greater coho density in ponds connected to spawning habitat by hyporheic flow, which is consistent with our findings. Other studies have found no change in juvenile salmonid density with the addition of carcasses to three natural streams (Wilzbach et al. 2005, Harvey and Wilzbach 2010). While carcass addition studies can examine the effects of direct consumption of carcass tissue, they do not take into account the full effect of spawning salmon (Tiegs et al. 2011), including the influence of nutrient provision in the form of eggs, and these nutrients are readily used by juvenile salmonids (Hicks et al. 2005, Scheurell et al. 2007), nor do they include the effect of dissolved nutrients through excretions (Levi et al. 2011), or the potential engineering effects of spawning activities (Moore and Schindler 2008). In addition, live fish excrete nutrients that have higher bioavailability than carcasses and may be more effective in stimulating primary productivity, particularly in nutrient-limited systems (Levi et al. 2011). Furthermore, older juvenile coho can prey upon newly-hatched pink and chum fry (Hunter 1959).

A potential issue with comparisons of natural variation among streams is that habitat variables could confound the results. For example if all three species of salmon respond in the same way to the same habitat variables, that could lead to spurious correlations. However, by taking a broad range of habitat variables found to be associated with juvenile coho into account explicitly and using an information theoretic model comparison, we have attempted to minimize the chance of this occurring. Specifically, we measured 17 habitat characteristics known to be correlated with abundance of juvenile coho. The relationships between spawning salmon and juvenile coho were stronger than the relationships between any of the three species and habitat characteristics, though the relationship with watershed size was high, which we attempted to isolate using a partial correlation approach. We also note that habitat usage by coho is very different from the others. Adult coho travel much further upstream, and the young spend a year or more in freshwater, favoring pools and large wood structures (Table 2, see also Sharma and Hilborn 2001, Roni and Quinn 2001). In contrast, pink and chum salmon spawn lower down in the stream, and their juveniles leave for the ocean immediately after they emerge in the spring.

The relationship between juvenile coho abundance and adult chum salmon was strong in the summer before adults arrived but there was no relationship in the fall, when the fish were spawning. We also found the percent reduction in coho abundance from summer to fall was positively related to chum abundance but not to pink abundance. These effects may be due to more aggressive behavior of chum displacing juvenile coho (personal observation), or stronger bioturbation by chum, which are considerably larger than pink salmon. Although no previous studies have looked at the effect of aggressive behavior of chum on juvenile coho, we do know that juvenile coho may be negatively affected by aggressive behavior of conspecifics. For example, Bradford et al. (2000) estimated 60-90% of newly hatched coho become displaced and move downstream into the marine environment in their first spring due to intraspecific aggression and high water flows, resulting in mortality. Furthermore, bioturbation could reduce foraging success of juveniles through reduced invertebrate biomass (Moore and Schindler 2008) and thus mediate the positive effect of the nutrient subsidy to primary and invertebrate production (Wipfli et al. 1998, Verspoor et al. 2010 and 2011), although bioturbation may also increase drifting invertebrates which may increase foraging success of juveniles. Bioturbation can also increase the availability of salmon eggs to other species (Scheuerell 2007), but only approximately 20% of the coho in our study would have had access to eggs. Further data on primary and invertebrate productivity would be required to fully elucidate the importance of a bioturbation mechanism in our system. Additionally, comparing diets of juvenile coho in summer prior to spawning and fall during spawning may illuminate underlying trophic mechanisms at play.

This study advances our understanding of the strength and persistence of nutrient subsidies in resource-limited systems such as freshwater streams while taking important habitat characteristics into account. There is a great deal of interest in the importance of such cross-ecosystem subsidies in fisheries and ecosystem-based management (Bilby et al. 2001, Hocking and Reynolds 2011, Levi et al. 2012). Our results suggest that spawning salmon have indirect but significant influences on stream-rearing juvenile salmonid populations that persist in the environment, creating a legacy effect of marine nutrient subsidy.

5 Nutrient subsidies drive a trophic cascade in an intraguild predator-prey relationship in freshwater fishes

5.1 Abstract

Nutrient subsidies across ecosystem boundaries can stimulate indirect effects and trophic cascades, particularly in nutrient-poor systems such as freshwater streams. Predator-prey dynamics in recipient ecosystems are particularly important in determining the strength and effects of such cascades, yet the role of intraguild predation is poorly understood. We investigated the effects of nutrient subsidies to freshwater streams on the intraguild predator-prey relationship between two stream fishes, juvenile coho salmon (*Oncorhynchus kisutch*) and their competitor and predator, sculpin (*Cottus aleuticus* and *C. asper*). We studied whether the effect of the size and density of sculpin on juvenile coho density was affected by nutrients from spawning pink and chum salmon in 13 streams on the central coast of British Columbia, Canada. We found negative associations between sculpin body size and coho density, which may reflect competitive or predatory interactions. At sites with high spawning salmon densities and thus resource availability, this relationship weakened, which may indicate reduced competitive and predatory effects. These results suggest that nutrient subsidies to both species in an intraguild predation relationship can stimulate a trophic cascade whereby the prey benefits from reduced predation or competition from the predator.

5.2 Introduction

Species abundance may be controlled either from the bottom up through the availability of food (e.g. Chapman 1966) or from the top down through predation and competition (e.g. Paine 1966). Changes in competition and predation can potentially cause trophic cascades. Although there is some debate as to how the term trophic cascade should be used, we are using it as defined by Polis et al., as indirect effects between two species mediated through trophic interactions with a third species (2000). The important point is that these indirect effects can be important in structuring food webs (Wootton 1994). The movement of nutrients across ecosystem boundaries can stimulate indirect effects and trophic cascades (e.g. Polis and Strong 1996), thus altering the strength of interactions among species in recipient communities (Polis and Holt 1992). For example, the effects of subsidies on predatory fish can cascade through food webs to alter primary productivity through both direct and indirect interactions (Power 1990).

The potential for spatial subsidies to cause trophic cascades may be particularly pronounced in aquatic ecosystems (Shurin et al. 2002) and those with low productivity (Polis et al. 1996). For example, freshwater streams can be nutrient-poor and receive large subsidies from adjacent terrestrial habitats (Vannote et al. 1980, Richardson et al. 2010). Access to spatial subsidies can strongly affect predator-prey dynamics (Holt 1984), particularly in ecosystems where more energy enters the food web as subsidies than is produced within it (Huxel and McCann 1998). Several stream trophic levels are linked to terrestrial leaf litter inputs (Wallace et al. 1997) and terrestrial arthropod inputs drive trophic cascades in stream food webs (Nakano et al. 1999). Nutrient subsidies to nutrient-poor systems are particularly important because they can lead to higher productivity, carrying capacity and consumer abundance (Huxel and McCann 1998).

Spawning salmon provide a well-documented subsidy to freshwater streams (Janetski et al. 2009), although the full ecological effects of this subsidy are still not fully understood. Salmon nutrients have been linked to direct and indirect positive effects on the abundance of a number of freshwater taxa, including stream biofilm (Wipfli et al. 1998, Harding et al. 2014), aquatic invertebrates (Wipfli et al. 1998, Verspoor et al. 2011), salmonids (Bilby et al. 1998), and sculpin (Swain and Reynolds *in prep*). An indirect positive effect of spawning salmon nutrients on the abundance of riparian birds was found due to an increase in stream invertebrates (Nakano and Murakami 2001). Indirect effects from previous spawning events have been found to affect juvenile coho abundance and growth (Nelson and Reynolds,*2014*a, b).

There is potential for a trophic cascade among stream fishes from spawning salmon nutrients if the subsidy affects one species of fish in a way that alters its impact on another competitor or prey species. Juvenile coho spend at least their first year after emergence in freshwater before migrating to the ocean (Groot and Margolis 1991). In streams, they are subject to competition for food from sculpin, as well as direct predation by sculpin (Hunter 1959). Both coho and sculpin directly consume spawning salmon eggs and fry (Bilby et al. 1998, Swain et al. 2014), which provide a high quality food source (Moore et al. 2008). Increased spawning salmon abundance has been linked with increased abundance of both juvenile coho (Nelson and Reynolds *2014a*) and sculpins (Swain and Reynolds *in prep*). Further, sculpin diets switch from prey fish to salmon eggs when they are available (Swain et al. 2014). However, the indirect effects of spawning salmon nutrients on juvenile coho abundance through sculpin, has not been investigated.

Because coho and sculpins belong to the same ecological guild, in that they compete for similar resources (Polis and Holt 1992), yet are also engaged in predator-prey interactions, their ecological interaction is known as intraguild predation (Polis, Meyers and Holt 1989). This triangular trophic configuration (Figure 5.1) is a widespread phenomenon (Holt and Polis 1997) that plays a role in maintaining ecological function (Polis and Holt 1992). Importantly, intraguild predation can have major impacts on intraguild prey populations (Brodeur and Rosenheim 2000). Stable coexistence of intraguild predator-prey may not be possible unless certain conditions are met (Polis and Holt 1992), such as an intermediate, but not high, level of environmental productivity (Holt and Polis 1997). The effect of spatial resource subsidies on intraguild predation is not yet clear. Intraguild predation may inhibit (Finke and Denno 2005) or facilitate (Huxel and McCann 1998) trophic cascades potentially stimulated by nutrient subsidies, and thus environmental productivity. Understanding the implications of multi-trophic interactions such as intraguild predation is important in understanding the ecological ramifications of nutrient subsidies in food web ecology (e.g. Finke and Denno 2005).

In this study, we investigate whether an intraguild predator-prey relationship either inhibits or facilitates a trophic cascade due to a spatial resource subsidy. We conducted a multi-stream comparison on the central coast of British Columbia to examine the relationship between two species of sculpin, coastrange (*C. aleuticus*) and prickly (*C. asper*), and juvenile coho salmon (*O. kisutch*), as mediated by the availability of nutrient subsidies from spawning pink (*O. gorbuscha*) and chum (*O. keta*) salmon. We predicted more and larger sculpins would negatively impact coho densities through their intraguild predator-prey dynamic in which sculpin both prey upon juvenile coho and compete with them for limited resources. As sculpin body size increases so does their ability to prey on coho and the coho content in their diets (Tomaro 2006). However, where abundant resources were available in the form of spawning salmon nutrients, we predicted the predation and competitive pressure of sculpins on coho may be reduced, thus creating a trophic cascade.

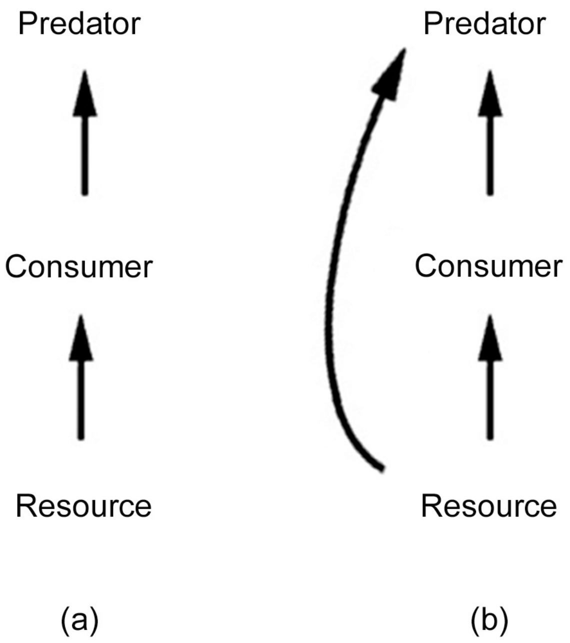


Figure 5.1. Food webs without (a) and with (b) intraguild predation.

5.3 Materials and Methods

5.3.1 Study sites and design

We surveyed 13 streams on the central coast of British Columbia, Canada, in the Great Bear Rainforest (Table 1). Chum and pink salmon were the dominant spawning species, and juvenile coho were present in all streams. Land use has been limited in the area and sites were accessible only by boat.

Streams in this study all flow directly into the ocean, mainly consist of mid-gradient exterior coastal sites, and had bank full widths from 3.3 to 22.8 m. This region is in the Coastal Western Hemlock biogeoclimatic zone (Pojar et al., 1987), with forests dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). Riparian zones are dominated by red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), false azalea (*Menziesia ferruginea*), and blueberry (*Vaccinium* spp.). Annual precipitation in the region is 3,000-4,000 mm/yr.

Table 5.1 Stream spawning salmon density (pink and chum combined), sculpin density, sculpin body size, and juvenile coho salmon density for the 13 streams in this study.

Stream	Juvenile coho density (fish/m^2)	Spawning salmon density (fish/m^2)	Coastrange sculpin density (fish/m^2)	Coastrange sculpin body size (cm)	Prickly sculpin density (fish/m^2)	Prickly sculpin body size (cm)	Watershed size (km^2)
Ada Cove	0.30	0.38	3.92	7.83	0.19	-	9.8
Bullock Main	0.35	0.84	-	7.00	0.27	-	3.3
Clatse	11.50	0.72	7.45	4.69	-	-	24.3
Fanny Left	5.30	0.46	-	-	0.14	6.83	16.4
Hooknose	1.22	0.25	1.98	-	0.18	8.46	1.2
Jane Cove	0.21	0.01	-	7.55	0.44	8.83	1.3
Kill Creek	0.90	0.75	0.96	5.95	0.00	-	0.5
Kunsoot Main	0.96	0.49	0.38	6.93	0.10	9.78	4.9
Neekas	4.28	1.56	6.56	5.55	0.26	9.55	16.0
Port John	0.14	0.01	0.37	-	-	-	1.9
Quartcha	0.27	0.05	2.33	7.43	-	-	29.4
Sagar	1.96	0.15	-	-	-	9.10	1.6
Troup North	0.69	0.00	1.69	9.10	0.03	9.58	1.6

5.3.2 Spawning salmon density

Pink and chum spawning salmon counts were available at six of the 13 streams in this study from Fisheries and Oceans Canada. Data for the remainder of sites were derived from stream counts conducted on foot between 2006 and 2011, undertaken in partnership with the Heiltsuk First Nation's Integrated Resource Management Department. The same protocols were used by all. Three or more spawning salmon counts were undertaken at each stream in each year. Total abundance was then estimated using the area-under-the-curve method (English et al. 1992). However, for some streams that we could not visit three times during the spawning season, peak counts (live+dead) were used (< 10% of streams). There was no difference in spawning salmon calculations at a subset of streams tested using both methods (Hocking and Reynolds, 2011). Spawning salmon densities were calculated by adding pink and chum abundance together, and dividing the total number of fish by spawning area for each stream (per m^2). Density estimates were averaged across years for each stream in order to generally characterize spawning salmon densities in streams. Tests with Akaike information criterion corrected for small sample sizes (AICc, see below) showed similar results for a mean value and those of individual years.

5.3.3 Juvenile coho salmon and sculpin density and body size

Juvenile coho and sculpin were collected by multiple-pass depletion surveys of a stop-netted section of stream using a two-meter wide pole seine (coho) or Smith-Root LR-24 and 12-B backpack electrofishing apparatus (sculpin). Coho were collected in 2007 and 2008, and sculpin were collected in 2009 and 2010, both in summer when no spawning pink or chum salmon were present. Sections were chosen randomly within the area sampled for environmental variables as 8 x bank full width. Seined areas included all stream habitat types (pools, riffles, glides, runs), the same methods were used for each pass, and sections were left undisturbed for a minimum of one hour between passes.

Maximum likelihood modeling was used with the depletion data to estimate coho and sculpin density (Schnute 1983). A comparison between a standard multinomial method (Zippin 1956), maximum likelihood (Carle and Strub 1978), and a hierarchical approach (Dorazio et al. 2005) for estimating coho density from depletions found no significant difference in density estimates between methods (ANOVA, $n=13$, $p > 0.05$). The density of coho between years (2007 and 2008) was correlated ($r = 0.7$) for the 10 streams where comparable data were available for both years. Sculpin data were available at only three streams for both years of sculpin sampling, so a correlation was not calculated. Freshwater sculpins are relatively long-lived and typically exhibit site fidelity (Goto 1998, Gray et al. 2004, McPhail 2007). Few studies have adequately compared sculpin population densities and size structures among years. Those studies that exist have concluded that temporal variation was lower than variation among sampling sites and streams (Brown et al. 1995, Edwards et al. 2007). Therefore, while we were unable to assess inter-annual variation in sculpin populations due to our limited number of re-surveyed streams, it seems reasonable to assume that patterns observed among streams in our study are relatively consistent across time. All coho and sculpins collected were measured for fork length (mean = 38.3 coho, 6.1 prickly and 5.7 coastrange sculpin per stream).

The majority (84.4%) of coho sampled were young of year (age class 0) and the remainder age class 1, as determined by scale analysis of 5 coho per stream. In order to eliminate potential confounding effects with varying mortality or outmigration across sites, we have looked at only age 0 coho in the analyses, by including only individuals with the lowest 84% of fork lengths.

As streams were sampled consecutively over the study periods, we tested for an effect of sampling date on the response variable, juvenile coho density. No effect was found, therefore date was not included in further analyses. We also did not find any relationship between coho body size (for all fish sampled) and coho density, thus size was also not included in the analyses.

5.3.4 Data analysis

We used an information theoretic approach to examine the relationships among spawning salmon, sculpins, and juvenile coho, including the effects of spawning salmon on the relationship between juvenile coho and sculpins, represented by interaction terms. We predicted a negative relationship between juvenile coho density and sculpin density and body size, reflecting negative predatory and competitive effects of more and larger sculpins on juvenile coho populations. Further, we predicted these negative relationships would be weakened when more spawning salmon resources were available (higher spawning salmon densities), which would be reflected by negative interactions involving sculpin density and size with salmon density.

Coho density ~ sculpin density + sculpin size + salmon density + sculpin density*salmon density + sculpin size*salmon density

Because we caught both species of sculpin in only four streams, we modeled the effects of each sculpin species separately, using the same predictions for each species. We combined spawning pink and chum densities into spawning salmon density to reduce the number of model parameters. In preliminary tests we found very similar trends for pink and chum salmon, as well as for relationships with spawning salmon biomass density. We did not include juvenile coho body size as a parameter in our models. However, previous research at these study sites did not reveal juvenile coho body size to be strongly related to juvenile coho abundance (Nelson and Reynolds in press). We constructed linear models to represent our *a priori* hypotheses, including interaction terms between sculpin variables and spawning salmon density (as above). We show the bivariate correlations between variables in Table 5.2.

Akaike's information criterion adjusted for small sample sizes (AICc) was used to compare the fit of models while including a penalty for models with more parameters (Burnham and Anderson 1998). We used maximum likelihood estimation for all possible model combinations with a maximum of three variables to avoid over-fitting (Zuur et al. 2009). Model diagnostics were inspected for heteroscedasticity, over-leveraging of data points, and normality and independence of residuals. All variables were log-transformed to meet model assumptions of normality, and scaled to allow comparison between variables (Gelman 2008). Model diagnostics showed that our data met model assumptions reasonably well. ΔAICc values, or the differences between a given model and the top-ranked model, are reported for all models with ΔAICc < 2 (Burnam and Anderson, 2002; Grueber et al., 2011). We then used model averaging to calculate scaled coefficient values to compare the predictive ability of individual variables (Anderson 2008).

All statistical analyses were performed using R (R Development Core Team, 2009), including the MuMIn package (Barton, 2012).

Table 5.2. Bivariate correlations, r, between variables used in the analyses.

	Spawning salmon density (fish/m^2)	Coastrange sculpin density (fish/m^2)	Coastrange sculpin body size (cm)	Prickly sculpin density (fish/m^2)	Prickly sculpin body size (cm)
Juvenile coho density (fish/m^2)	0.63	0.4	-0.83	-0.1	-0.3
Spawning salmon density	-	0.36	-0.74	0.15	-0.17
Coastrange sculpin density	-	-	-0.32	0.61	-0.36
Coastrange sculpin body size	-	-	-	0.18	0.17
Prickly sculpin density	-	-	-	-	-0.06

5.4 Results

Streams that had larger coastrange sculpin had lower densities of juvenile coho salmon ($R^2 = 0.69$; Figure 5.2). Sculpin body size was the top model explaining juvenile coho density in the coastrange sculpin model set and showed the strongest negative effect (Table 5.3 and Figure 5.3). The negative relationship between coastrange sculpin size and juvenile coho density was weaker in streams with higher densities of spawning pink and chum salmon (Figure 5.3). This inference is supported by three results. First, the strength of this interaction was relatively strong, and the confidence intervals do not cross zero (Figure 5.3). Second, the fit of the model increased with the addition of the interaction term (R^2 increased from 0.69 to 0.9). Third, the modeled interactions predicted a strong negative correlation between coastrange sculpin body size and juvenile coho density at the highest quartile of spawning salmon density, and no relationship at the lowest quartile of spawning salmon density (Figure 5.4). However, AICc (AIC adjusted for small sample sizes) adds an additional penalty for a low sample size (n = 10),, and did not indicate high support for the interaction (Table 5.3).

The best correlate of juvenile coho salmon density for the prickly sculpin model set was sculpin body size, followed by the model containing sculpin body size and spawning salmon density (Table 5.3). While prickly sculpin body size may explain some unique variation in coho density, the fit of the linear relationship between sculpin body size and juvenile coho density is not very high (R^2 = 0.09; Figure 5.5). The addition of spawning salmon density improved the model fit considerably (R^2 = 0.53; Table 5.3), and only spawning salmon density had a clear correlation with coho density (Figure 5.3). Similarly to coastrange sculpins, the negative influence of larger sculpins on juvenile coho density was reduced as spawning salmon density increased, however the uncertainty around the interaction estimates makes this effect unclear (Figure 5.3).

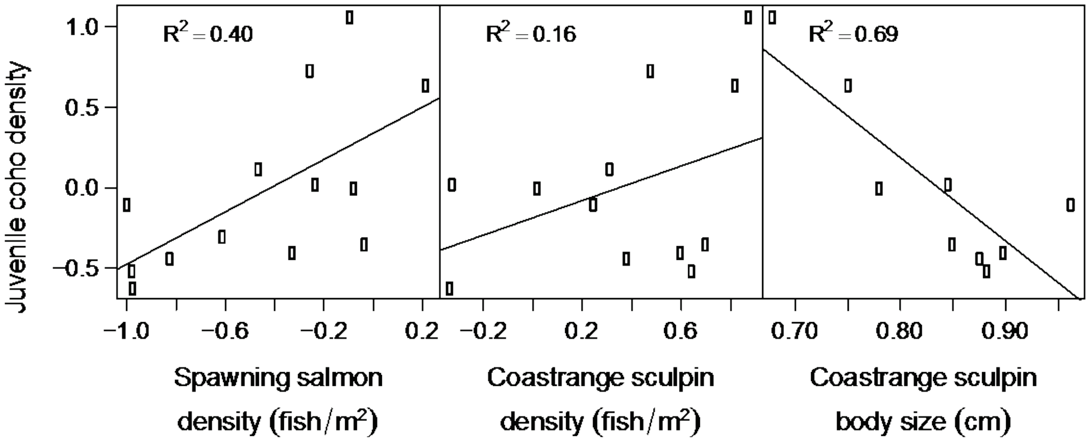


Figure 5.2. Bivariate plots showing relationships for the coastrange sculpin model set between spawning salmon, sculpin body size and density, and juvenile coho salmon density. Each data point represents a stream. Variables have been log transformed.

Table 5.3. Summary of Akaike's information criterion linear regression models with the greatest support for juvenile coho salmon density. All models with ΔAICc > 2 are shown. K is the number of model parameters, R^2 is the model coefficient of determination, ΔAICc value of zero indicates that the model is the top one from those considered, w_i is the AICc model weight.

Sculpin species tested	Model parameters	K	R^2	ΔAICc	w_i
Coastrange sculpins	Sculpin body size	3	0.69	0.00	0.91
Prickly sculpins	Sculpin body size	3	0.09	0.00	0.48
	Sculpin body size + spawning salmon density	4	0.53	1.27	0.26

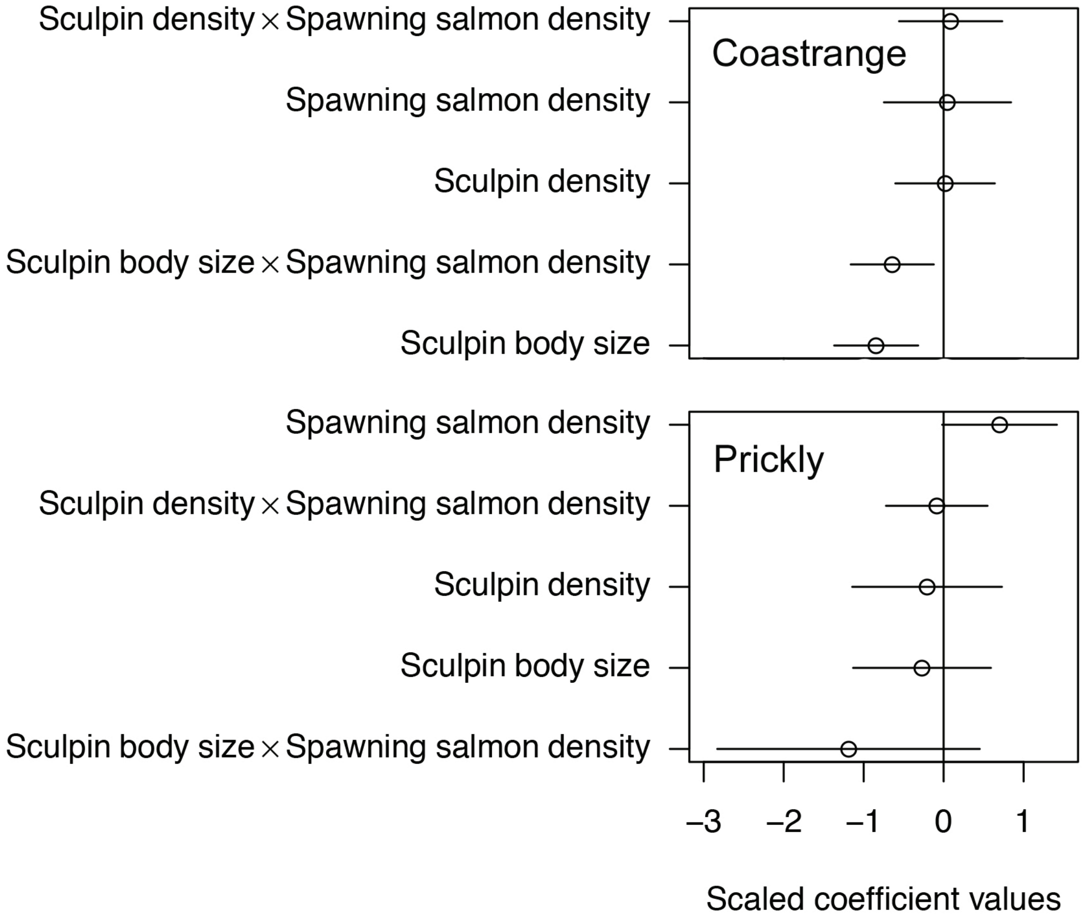


Figure 5.3. Scaled model parameter estimates (circles) with 95% confidence intervals (lines) from averaged predictive linear models describing juvenile coho salmon density for coastrange (top) and prickly (bottom) sculpin model sets. The variables are ranked beginning with the highest positive scaled coefficient.

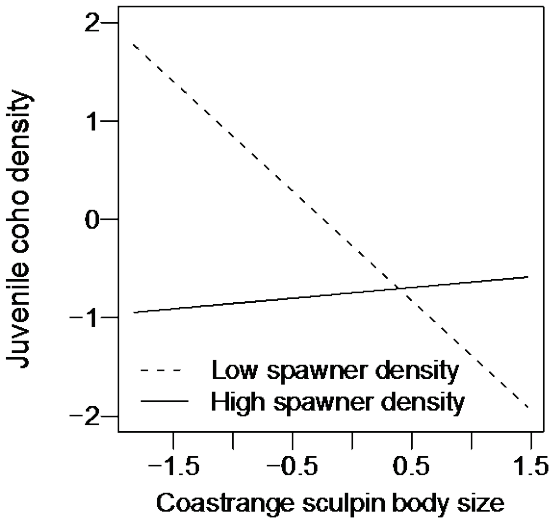


Figure 5.4. Interaction plot showing relationships between coastrange sculpin body size and juvenile coho salmon density, at lowest and highest quartile spawning pink and chum salmon density.

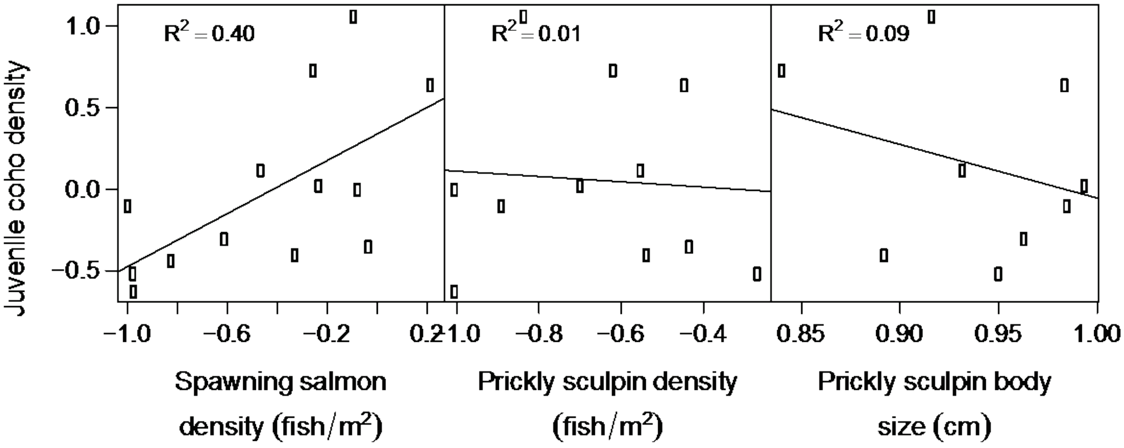


Figure 5.5. Bivariate plots showing relationships for the prickly sculpin model set between spawning salmon, sculpin body size and density, and juvenile coho salmon density. Each data point represents a stream. Variables have been log transformed.

5.5 Discussion

We found negative associations between sculpin body size and juvenile coho salmon densities. As the density of spawning salmon increased, we found these associations were less strong. This may indicate that spatial subsidies, in the form of spawning salmon, reduce competitive and predatory effects of larger sculpin on juvenile coho populations. If that is the case, this example would illustrate a trophic cascade between spawning pink and chum salmon and juvenile coho salmon, mediated through an intraguild predation relationship with stream sculpin (Figure 5.6).

While Finke and Denno (2005) found intraguild predation to dampen the effects of trophic cascades in an empirical study of a coastal marsh community, our results support theoretical work by Huxel and McCann (1998), who modeled a nutrient subsidy on a tri-trophic predator-prey relationship similar to ours and predicted a trophic cascade. If the effect we detected is real, it is possible that the system we are testing improved the detection probability, because of the fairly simple trophic interactions, low diversity and low redundancy of freshwater stream fishes in our systems, all of which tend to strengthen trophic cascades (Polis et al. 2000, Shurin et al. 2002). Our results suggest an impact of the intraguild predator on the population of the intraguild prey during a period of high environmental productivity. Although empirical evidence is still lacking, ecological theory on intraguild predation suggests coexistence between species involved will not be stable in highly productive environments (Holt and Polis 1997), particularly where species feeding preferences favor subsidized resources (Huxel and McCann 1998). However, stable coexistence even in highly productive environments has been found if a temporal refuge from the intraguild predation interaction exists, even of small duration (Amarasekare 2008). In our case, the temporal heterogeneity of the nutrient subsidy provided by spawning salmon may mimic such a refuge, leading to stable coexistence.

Several mechanisms may explain an indirect effect of spawning pink and chum salmon on juvenile coho through sculpin. For example, the additional food source that spawning salmon provide sculpins through direct consumption of tissue and eggs may reduce the predation pressure of sculpins on juvenile coho. For example, Swain et al. (2014) found sculpin diets switched from invertebrates and juvenile salmonid prey to salmon eggs during spawning events, and as the abundance of spawning salmon increased across streams, so did marine-derived nutrient isotope signatures in sculpin tissues. Cross-boundary nutrient inputs have been found to reduce the prey suppression functions of predators (Polis et al. 1996). It is also possible that more abundant spawning salmon tissue and eggs, which are a shared food source between sculpin and juvenile coho, reduce the competition between these species for other prey. Juvenile coho and sculpin share a similar predatory trophic position in freshwater streams, and compete for food in the absence of spawning salmon nutrients, such as aquatic invertebrates and drifting terrestrial invertebrates (Hunter 1959, Foote and Brown 1998). It is well known that juvenile coho are negatively affected by intraspecific aggression, based both on density and body size (Roni and Quinn 2001). It has been estimated that these intraspecific aggressive interactions, coupled with high water flows, lead to the displacement of 60-90% of emergent coho fry, which then move downstream into the marine environment, resulting in mortality (Bradford et al. 2000).

We found the negative associations between juvenile coho with coastrange sculpins were stronger than with prickly sculpins. This might be explained by different habitat preferences of the two sculpin species (McPahil 2007). Further, the prickly sculpin in our samples were more limited in body size range, which would reduce the potential to detect an effect.

This study suggests that nutrient subsidies may affect intraguild predation relationships. Incorporating multi-trophic interactions and intraguild predation is an important challenge in the study of nutrient subsidies and food web ecology (Finke and Denno 2005), as is incorporating factors such as omnivory in the occurrence and strength of aquatic trophic cascades (Polis and Strong 1996a). Experimental manipulations would be a useful way to confirm the trophic cascade suggested here. An interesting direction for future research is the implications of the temporal heterogeneity of the spawning salmon subsidy to freshwater streams, which may play an important role in structuring stream communities (Huxel and McCann 1998, Richardson et al. 2010). Because biotic interactions tend to fluctuate seasonally (Polis et al. 1995), the implications of intraguild predation between fish species and the strength of trophic cascades may change based on the seasonal nature of spawning salmon nutrient inputs. Examining the changing dynamics through time may be key to understanding the mechanisms that allow intraguild predation interactions to be maintained (Amarasekare 2008).

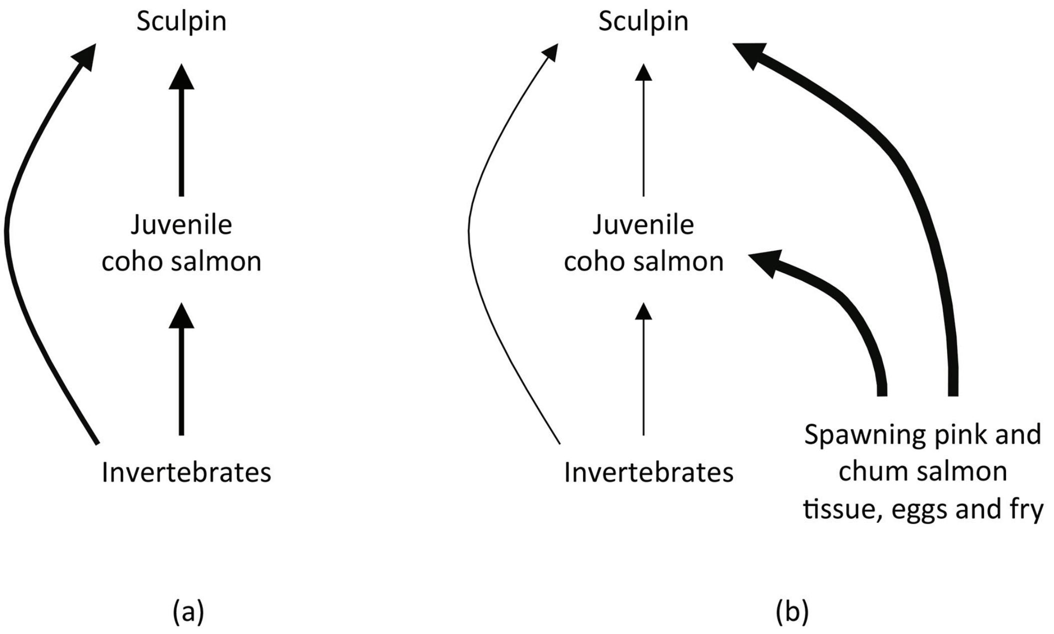


Figure 5.6. Intraguild predation relationship between sculpins and juvenile coho salmon without (a) and with (b) resource subsidy

6 General Discussion

In this thesis, I explored the effects of habitat characteristics, nutrient availability, and predator-prey dynamics on species abundance. Using spawning salmon in freshwater streams as a model system, I studied how habitat features affect salmon abundance and how the nutrient subsidy provided by spawning salmon affects the recipient ecosystem at individual, population and community levels by studying juvenile coho salmon size, age proportion and abundance as well as intraguild predation interactions with stream sculpin across streams with a range of spawning salmon densities.

I found that habitat characteristics related to space, energetics and predation best explained spawning chum and pink salmon abundance. Notably, stream size mediated the effect of some of the other habitat characteristics, suggesting the dominance of differing ecological mechanisms at different scales. The importance of habitat characteristics was then taken into account in exploring the effects of spawning salmon on juvenile coho size, age proportion and abundance. While habitat space was a consistently good predictor, as expected, there was also a role for density of spawning salmon, followed by other features of habitats. Spawning chum salmon abundance best explained juvenile coho size across streams with a range of spawning salmon abundances, and coho were larger at sites below natural barriers to spawning chum and pink salmon than above them. Streams with more spawning salmon had a higher proportion of age 0 to age 1 coho, suggesting that larger coho in streams with more spawning salmon may be more likely to migrate to the ocean in their first year than in their second. Further, spawning pink salmon abundance was the best predictor of juvenile coho abundance, better than any feature of habitat.

The vast majority of the coho studied were young of year, and had little to no direct contact with spawning chum and pink salmon at the time of sampling. Therefore, these results suggest an indirect, time-delayed influence of spawning chum and pink on juvenile coho at the individual and population levels. Furthermore, those fish sampled that were in their second year in the stream and had the potential to directly consume spawning salmon tissue, eggs, or emerging fry showed the strongest influence of spawning salmon on juvenile coho size.

The results here also suggest an impact of spawning salmon nutrient subsidies at the community level, although further research would be required to confirm these findings. The negative impact of larger intraguild predators, coastrange and prickly sclupin, on juvenile coho salmon was reduced in streams where more salmon nutrients were available, suggesting weakened competitive and predatory effects.

The findings in this thesis are relevant to fisheries and stream management, and may be particularly useful as ecosystem-based management approaches become more in demand. For example, we pointed to the importance of habitat features which reduce extreme water flows and scouring events, and which moderate high temperatures for spawning chum and pink salmon.

While habitat features were important for spawning chum and pink salmon and juvenile coho, I found the nutrients provided by the spawning adults were more important than the habitat features that I measured for juvenile coho, at the individual and population level. The use of a fairly large sample size of streams and my statistical techniques (AICc) allowed me to directly compare the effect of many habitat variables with spawning salmon, and spawning salmon were clearly the best predictors of juvenile coho size and abundance. This size of comparison had not been made previously. Further, I was able to use naturally-occurring spawning salmon, which is uncommon in the literature, and is more realistic than previous carcass addition studies because this approach includes the full effects of spawning salmon, such as nutrients from tissues, eggs and excreta, as well as bioturbation and engineering effects from spawning activities. We found stronger evidence of an effect of spawning salmon on juvenile coho than previous artificial carcass additions, and this may be because studying naturally-occurring spawning salmon provides a better picture of the real ecological implications of spawning salmon.

The implications of these findings to fisheries and stream management may be significant considering the investment of resources currently being made in habitat restoration for juvenile salmonids. Improving spawning salmon returns through changing fisheries management strategies may have greater impacts on juvenile salmonid production. In addition, the time-delayed influence of spawning salmon I found in stream food webs may have important implications for fisheries management by considering how different species of salmon affect each other.

Further, where this thesis illustrates the effects of spawning salmon nutrients at multiple ecological scales, it suggests extensive multi-trophic impacts on stream food webs through indirect interactions. This must be taken into consideration, particularly if ecosystem-based management is being implemented. Further research into the full ecological implications and integration into management may be useful. In addition, while our streams were fairly pristine, it would be useful to also study a range of habitat quality that encompasses disturbed streams, such as those under pressure from forestry or urban development, to determine if spawning salmon nutrient subsidies are as important. It is possible that in streams with lower habitat quality, juvenile coho size or abundance may be not be limited by spawning salmon nutrient availability. For example, in streams with very little protection in the form of pools and large wood, juvenile coho may be limited by predation pressure, while additional nutrients from spawning salmon may not have a strong effect. Further study would help inform management in areas of high land use and development pressure.

I found the influence of the marine nutrient subsidy and potential engineering effects by spawning salmon in freshwater streams had both direct and indirect effects at multiple ecological scales, which suggests far-reaching effects on stream food webs. These interactions have not been fully elucidated, and freshwater streams may provide a fascinating model system for research on the ecological implications of spatial and temporal nutrient subsidies. Further, I found some evidence of a trophic cascade stimulated by nutrient subsidies through an intraguild predation relationship. While the impact of nutrient subsidies on food web ecology has been explored, the incorporation of multi-trophic interactions has been fairly limited, as has the role of multi-trophic interactions in trophic cascades.

Because freshwater stream fish communities are fairly simple, and can have fairly low productivity, this system again may provide a very useful model for advancing our understanding of the full ecological effects of nutrient subsidies. For example, while salmon nutrient subsidies may affect species abundance through a bottom-up mechanism by increasing stream primary productivity, I also found some evidence of a top-down (or side-ways) mechanism through their effect on an intraguild predation (competition) relationship. The importance of bottom up and top down effects on the occurrence and strength of trophic cascades is still unclear, and may be elucidated with further study in this system. The theory around the maintenance and stability of intraguild relationships is still being explored as well, and current theory suggests it is related to ecosystem productivity (Huxel and McCann 1998). Spatial and temporal nutrient subsidies, such as those provided by spawning salmon to freshwater streams, may provide a natural experiment to further study these complex food web relationships.

References

Amarasekare, P. 2008. Coexistence of intraguild predators and prey in resource-rich envrionments. Ecology. 89:2786-2797.

American Public Health Association, American Waterworks Association and Water Pollution Control Federation. 1989. *Standard methods for the examination of waste and wastewater.* 17th Ed. American public health association, Washington, DC.

Anderson, D.R. 2008. *Model based inference in the life sciences: a primer on evidence.* Springer, New York.

Archord, S., Levin, P.S., and Zabel, R.W. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? *Ecology Letters*. 6:335-342.

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

Bain, M. and Stevenson, N. 1999. *Aquatic habitat assessment: common methods*. American Fisheries Society, Bethesda, Md.

Barton, K. 2012. Multi-model inference (MuMIn). GPL-2.

Bilby, R.E., Fransen, B.R. and Bisson, P.A. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can. J. Fish. Aquat. Sci*. 53:164-173.

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

Bilby, R.E., Fransen, B.R., Walter, J.K., Cedarholm, J. and Scarlett, W.J. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific Salmon. *Fisheries*. 26:6-14

Bjornn, T.C. and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. In *Influences of forest and rangeland management of salmonid fishes and their habitat.* Eds. W. Meehan. Am. Fish. Sock. Spec. Pub, Bethesda, Md.

Bradford, M., Taylor, G. and Allen, J. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. *Transactions of the American Fisheries Society*. 126:59-64.

Bradford, M., Myers, R.A. and Irvine, J.R. 2000. Reference points for coho salmon (Oncorynchus kisutch) harvest rates and escapement goals based on freshwater production. *Canadian Journal of Fisheries and Aquatic Sciences*. 57:677-686.

Braun, D.C. and Reynolds, J.D. 2011a. Cost-effective variable selection in habitat surveys. *Methods Ecol. Evol*. 3:388-396.

Braun, D. C. and Reynolds, J. D. 2011b. Relationships between habitat characteristics and breeding population densities in sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci*. 68:758-767.

Brodeur, J and Rosenheim, J.A. 2000. Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata*. 97:93-108.

Burnham, K.P. and Anderson, D.R. 1998. *Model selection and multimodel inference: a practical information-theoretic approach.* Spring Science + Business Media Inc., New York.

Burnham, K.P. and Anderson, D.R. 2002. *Model selection and multi-model inference, 2nd Ed*. Springer, New York, USA.

Carle, F.L., Strub, M.R. 1978. A new method for estimating population size from removal data. *Biometrics*. 34:621–630

Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Research Board of Canada*. 19:1047-1080.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. *American Naturalist*. 100:345-357.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Trans. Am. Fish. Soc*. 117:1-21.

Chapman, R.N. 1931. *Animal Ecology.* McGraw-Hill, New York.

Christensen, N. L., Bartuska, A., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., and Moodmansee, R.G. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecol. Appl*. 6:665-691.

Cohen, J., West, S.G., Aiken, L. and Cohen, P. 2003. *Applied multiple regression/correlation analysis for the behavioral sciences*. Lawrence Erlbaum Associates, Mahwah, New Jersey.

Compton, J.E., Andersen, C.P., Phillips, D.L., Brooks, J.R., Johnson, M.G., Church, M.R., Hogsett, W.E., Cairns, M.A., Rygiewicz, P.T., McComb, B.C. and Shaff, C.D. 2006. Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. *Front. Ecol. Envrion*. 4:18-26.

Cooper, A.C. 1965. The effect of transported stream sediments on survival of sockeye and pink salmon eggs and alevin. *Int. Pac. Salmon Fish. Comm. Bull.* 18.

Degerman E., Fogelgren, J.E., Tengelin, B., and Thörnelöf, E. 1986. Occurrence of salmonid parr and eel in relation to water quality in small streams on the west coast of Sweden*. Water, Air, and Soil Pollution*. 30:665–671.

Denton, K.P., Rich Jr, H.B. and Quinn, T.P. 2009. Diet, movement, and growth of dolly varden in response to sockeye salmon subsidies. *Trans. Am. Fish. Soc*. 138:1207-1219.

Deschenes, J. and Rodriguez, M.A. 2007. Hierarchical analysis of relationships between brook trout (*Salvenlinus fontinalis*) density and stream habitat features. *Can. J. Fish. Aquat. Sci*. 64:777-785.

Dorazio, R.M., Jelks, H.L. and Jordan, F. 2005. Improving removal-based estimates of abundance by sampling a population of spatially distinct subpopulations. *Biometrics*, 61:1093–1101.

Elton, C. 1927. *Animal Ecology*. Sidgwick and Jackson, London.

English, K.K., Bocking, R.C. and Irvine, J.R. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. *Canadian Journal of Fisheries and Aquatic Sciences*. 49:1982-1989.

Field, R.D. and Reynolds, J.D. 2011. Sea to sky: impacts of residual salmon-derived nutrients on estuarine breeding bird communities. *Proc. Biol. Sci.* 278:3081-3088.

Finke, D.L. and Denno, R.F. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*. 8:1299-1306.

Foote, C.J. and Brown, G.S. 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.

Fukushima, M. 2001. Salmonid habitat-geomorphology relationships in low-gradient streams. *Ecology*. 82:1238-1246.

Fukushima, M. and Smoker, W. 1998. Spawning habitat segregation of sympatric sockeye and pink salmon. *Trans. Am. Fish. Soc*. 127:253-260.

Garcia, E.A., Bertness, M.D., Alberti, J. and Silliman, B.R. 2011. Crab regulation of cross-ecosystem resource transfer by marine foraging fire ants. *Oecologia.* 166:1111-1119.

Gende, S.M., Quinn, T.P., Hilborn, R., Hendry, A.P. and Dickerson, B. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos. 104:518-528.

Giannico, G.R. and Hinch, S.G. 2007. Juvenile coho salmon (Oncorhychus kisutch) responses to salmon carcasses and in-stream wood manipulations during winter and spring. *Can. J. Fish. Aquat. Sci*. 64:324-335.

Graham, M.D., Vinebrooke, R.D. and Turner, M. 2006. Coupling boreal forests and lakes: Effects of conifer pollen on littoral communities. *Limnology and Oceanography.* 51:1524-1529.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology*. 84:2809-2815.

Gravel, D., Guichard, F., Loreau, M., Mouguet, N. 2010. Source and sink dynamics in meta-ecosystems. *Ecology*. 91:2172-2184.

Gresh, T., Lichatowich, J. and Schoonmaker, P. 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*. 25:15-21.

Groot, C. and Margolis, L. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.

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

Grueber, C.E., Nakagawa, S., Laws, R.J. and Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology.* 24:699-711.

Guisan, A. and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Model*. 135:147-186.

Harding, J.N., Harding, J.M.S. and Reynolds, J.D. 2014. Movers and shakers: nutrient subsidies and benthic disturbance predict biofilm biomass and stable isotope signatures in coastal streams. *Freshwater Biology*. *59:1361-1377.*

Harding, J.N. and Reynolds, J.D. Opposing forces: Evaluating ecological roles of Pacific salmon (*Oncorhynchus* spp.) in coastal stream ecosystems. (in prep)

Hartman, G.F., Andersen, B.C. and Scrivener, J.C. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. *Canandian Journal of Fisheries and Aquatic Sciences*. 39:588-597.

Harvey, B.C. and Wilzbach, M.A. 2010. Carcass addition does not enhance juvenile salmonid biomass, growth or retention in six northwestern California streams. *North American Journal of Fisheries Management*. 30:1445-1451.

Hawkins, C. P., Murphy, M.L., Anderson, N.H., and Wilzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences.* 40:1173–1185.

Heintz, R.A., Nelson, B.D., Hudson, J., Larsen, M., Holland, L. and Wipfli, M.S. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. *Trans. Am. Fish. Soc.* 133:559-567.

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

Healey, M.C., Lake, R. and Hinch, S.G. 2003. Energy expenditures during reproduction by sockeye salmon (*Oncorhynchus nerka*). *Behav*. 140:161-182.

Hocking, M.D., Dulvy, N.K., Reynolds, J.D., Ring, R.A. and Reimchen, T.E. 2013. Salmon subsidize an escape from a size spectrum. *Proceedings of the Royal Society B*. 280. DOI: 10.1098/rspb.2012.2433.

Hocking, M.D. and Reimchen, T. E. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos*. 118:1307-1318.

Hocking, M. D. and Reynolds, J.D. 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.

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist.* 124:377–406.

Holt, R.D and Polis, G.A. 1997. A theoretical framework for intraguild predation. *American Naturalist*. 149:745-764.

Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. *Journal of the Fisheries Research Board of Canada*. 16:835-886.

Hubert, W. A., and Kozel, S.J. 1993. Quantitative relations of physical habitat features to channel slope and discharge in unaltered mountain streams. *Journal of Freshwater Ecology*. 8:177-183.

Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. *Journal of the Fisheries Research Board of Canada*. 16:835-886.

Huey, R.B. 1991. Physiological consequences of habitat selection. *Am. Nat*. 137: S91–S115.

Huxel, G.R. and McCann, K. 1998. Food web stability: the influence of trohpic flows across habitats. *American Naturalist*. 152:460-469.

Inoue, M., Nakano, S. and Nakamura, F. 1997. Juvenile masu salmon (*Oncorhychus masou*) abundance and stream habitat relationships in Northern Japan. *Can. J. Fish. Aquat. Sci*. 54:1331-1341.

Janetski, D.J., Chaloner, D.T., Tiegs, S.D. and Lamberti, G.A. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*. DOI 10.1007/s00442-008-1249-x

Kershner, J. L., and Snider, W.M. 1992. Importance of a habitat-level classification system to design instream flow studies. Pages 179–93 *in* P. J. Boon, P. Calow, and G. E. Petts, editors. *Conservation and Management.* John Wiley & Sons, Ltd., Chichester, England.

Kline T.C., Goering J.J., Mathisen O.A. & Poe P.H. (1990) Recycling of Elements Transported Upstream by Runs of Pacific Salmon: 1. 815N and 813C Evidence in Sashin Creek, Southeastern Alaska1. *Can. J. Fish. Aquat. Sci.* 47, 136–144.

Knight, T.M. *et al*. (2005) Trophic cascades across ecosystems. *Nature.* 437, 880-883

Lang, D.W., Reeves, G.H., Hall, J.D. and Wipfli, M.S. 2006. The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences.* 63:917-930.

Levi, T., Darimont, C.T., MacDuffee, M., Mangel, M., Paquet, P. and Wilmers, C.C. 2012. Using grizzly bears to assess harvest-ecosystem tradeoffs in salmon fisheries. *PLoS Biology*. 10(4): e1001303. doi: 10.1371/journal.pbio.1001303.

Levi, P.S., Tank, J.L., Tiegs, S.D., Ruegg, J., Chaloner, D.T. and Lamberti, G.A. 2011. Does timber harvest influence the dynamics of marine-derived nutrients in Southeast Alaska streams? *Canadian Journal of Fisheries and Aquatic Sciences.* 68: 1316-1329.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*. 73:1943-1967.

Marcarelli, A.M., Baxter, C.V., Mineau, M.M. and Hall Jr, R.O. 2011. Quanitity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*. 92:1215-1225.

Marczak, L.B. and Richardson, J.S. 2008. Timing of a resource subsidy alters growth and development rates in a riparian spider. *Oecologia.* 156: 249-258.

Mason, J.C. and Chapman, D.W. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. *Journal of the Fisheries Research Board of Canada*. 22:173-190.

May, C.L., Pryor, B., Lisle, T.E. and Lang, M. 2009. Coupling hydrodynamic modeling and empirical measures of bed mobility to predict the risk of scour and fill of salmon redds in a large regulated river. *Water Resources Research*. 45. W054402, doi:10.1029/2007/WR006498.

McArthur, R.H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Harper and Row, New York.

McGarigal, L.S., Cushman, S. and Stafford, S. 2000. *Multivariate statistics for wildlife and ecology research*. Springer-Verlag. New York, NY.

McPhail, J.D. 2007. *The freshwater fishes of British Columbia*. University of Alberta Press, Edmonton, AB.

Michael, J.H. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: Managing one resource to benefit another. *Northwest Science*. 69:228-233.

Moore, J.W., Hayes, S.A., Duffy, W., Gallagher, S., Michel, C.J. and Wright, D. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. *Canadian Journal of Fisheries and Aquatic Sciences*. 68:1161-1170.

Moore, J.W. and Schindler, D.E. 2004. Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences*. 61:1582-1589.

Moore, J.W. and Schindler, D.E. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology*. 77:275-284.

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

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

Murphy, M.L. and Hall, J.D. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the cascade mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*. 38:137-145.

Murphy M.L., Hawkins, C.P. and Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society.* 110:469-478.

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

Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Science*. 98:166-170.

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

Nelson, M.C. and Reynolds, J.D. 2014a. Time-delayed subsidies: Interspecies population effects in salmon. PLoS one. 9:6. e98951 .

Nelson, M.C. and Reynolds, J.D. 2014b. Effects of subsidies from spawning chum and pink salmon on juvenile coho salmon body size and age class proportion. Ecosphere. (*in press*).

Paine, R.T. 1966. Food web complexity and species diversity*. American Naturalist.* 100:65-75.

Peterson, N.P. and Foote, C.J. 2000. Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. *Transactions of the American Fisheries Society*. 129:924-934.

Pojar, J., Klinka, K. and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage*. 22:119-154.

Polis, G.A., Anderson, W.B. and Holt, R.D. 1996. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics.* 28:289-316.

Polis, G.A. and Holt, R.D. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution.* 7:151-154.

Polis, G.A., Holt, R.D., Menge, B.A. and Winemiller, K.O. 1995. Time, space, and life history: influences on food webs. 435-460 in G.A. Polis and K. Winemiller, Eds. *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York, NY.

Polis, G.A., Meyers, C.A. and Holt, R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual review of ecology and systematics*. 297-330.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R. and Maron, J. 2000. When is a trophic cascade a trophic cascade? *TREE.* 15:473-475.

Polis, G.A. and Strong, D.R. 1996. Food web complexity and community dynamics. *American Naturalist.* 147:813-846.

Power, M.E. 1990. Effects of fish in river food webs. *Science.* 250:811-814.

Povia-Scott, J. *et al*. (2011) Effects of experimental seaweed deposition on lizard and ant predation in an island food web. *Science.* 331:461-463

Quinn, T.P. and Peterson, N.P. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhychus kisutch*) in Big Beef Creek, Washington. *Can. J. Fish. Aquat. Sci*. 53:1555-1564.

Quinn, T.P., Wetzel, L., Bishop, S., Overberg, K., and Rogers, D.E. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Can. J. Zool.* 79: 1782-1793.

R Development Core Team. 2009. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. R 2.15.2 GUI.

Reisinger, A.J., Chaloner, D.T., Ruegg, J., Tiegs, S.D. and Lamberti, G.A. 2013. Effects of spawning Pacific salmon on the isotopic composition of biota differ among southeast Alaska streams. *Freshwater Biology*. 58:938-950.

Richardson, J.S., Zhang, Y., Marczak, L.B. 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications.* 26:55-66.

Rinella, D.J., Wiplfi, M.S., Walker, C.M., Stricker, C.A. and Heintz, R.A. Seasonal persistence of marine-derived nutrients in south-central Alaskan salmon streams. *Ecosphere.* 4:122. http://dx.doi.org/10.1890/ES13-00112.1

Roni, P. and Quinn, T.P. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. *Can. J. Fish. Aquat. Sci*. 58:282-292.

Rosenfeld, J., Porter, M., and Pakinson, E. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout and coho salmon. *Canadian Journal of Fisheries and Aquatic Sciences. 57: 766-774*

Roth, J.D. 2002. Temporal variability in arctic fox diets as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*. 133:70-77.

Ruckelshaus, M.H., Levin, P., Johnson, J.B. and Kareiva, P.M. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics*. 33:665-706.

Salisbury, E.J. 1926. The geographical distribution of plants in relation to climatic factors. *Geogr. J.* 57: 312–335.

Schaff, C.D. and Compton, J.E. 2009. Differential incorporation of natural spawners vs. artificially planted salmon carcasses in a stream food web: evidence from 15N of juvenile coho salmon. *Fisheries*. 34:62-72.

Scheu, S. 2001. Plants and generalist predators as links between the below-ground and above-ground system. *Bas. App. Ecol.* 2:3-13.

Scheuerell, M.D., Levin, P.S., Zabel, R.W., Williams, J.G. and Sanderson, B.L. 2005. A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*. 62:961-964.

Scheuerell, M.D., Moore, J.W., Schindler, D.E. and Harvey, C.J. 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., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B. and Palen, W.J. 2003. Pacific salmon and the ecology of coastal ecosystems. *Front. Ecol. Envrion*. 1:31-37.

Schnute, J. 1983. A new approach to estimating populations by the removal method. *Canadian Journal of Fisheries and Aquatic Sciences*. 40:2153-2169.

Sharma, R. and Hilborn, R. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. *Can. J. Fish. Aquat. Sci*. 58:1453-1463.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D. and Halpern, B.S. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters.* 5:785-791.

Spence, B.C. and Dick, E.J. 2013. Geographic variation in environmental factors regulating outmigration timing of coho salmon (*Oncorynchus kisutch*) smolts. *Can. J. Fish. Aquat. Sci*. 71:56-69.

Spiller, D.A., Piovia-Scott, J., Wright, A.N., Yang, L.H., Takimoto, G., Schoener, T.W. and Iwata, T. 2010. Marine subsidies have multiple effects on coastal food webs. *Ecol.* 91:1424-1434.

Stapp, P. and Polis, G.A. (2002) Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia* 134, 496-504

Swain, D.P. and Holtby, L.B. 1989. Differences in morphology and behavior between coho salmon (*Oncorhychus kisutch*) rearing in a lake and its tributary stream. *Canadian Journal of Fisheries and Aquatic Sciences*. 46:1406-1414.

Swain, N.S., Hocking, M.D., Harding, J.N., and Reynolds, J.D. 2014. Effects of salmon on the diet and condition of stream-resident sculpins. *Canadian Journal of Fisheries and Aquatic Sciences.* 71: 1-12.

Swain, N.S., and Reynolds, J.D. Effects of salmon-derived nutrient subsidies and habitat characteristics on population densities of stream-resident sculpins. *PLoS One.* (*in press).*

Tiegs, S.D., Chaloner, D.T., Levi, P., Ruegg, J., Tank, J.L. and Lamberti, G.A. 2008. Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecological Applications*. 18:4-11.

Tiegs, S.D., Levi, P.S., Ruegg, J., Chaloner, D.T., Tank, J.L. and Lamberti, G.A. 2011. Ecological effects of live salmon exceed those of carcasses during an annual spawning migration. *Ecosystems*. 14:598-614.

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

Verspoor, J.J., Braun, D. C. and Reynolds, J.D. 2010. Quantitative links between Pacific salmon and stream periphyton. *Ecosystems*. 13:1020-1034.

Verspoor, J.J., Braun, D.C., Stubbs, M.M. and Reynolds, J.D. 2011. Persistent ecological effects of a salmon-derived nutrients pulse on stream invertebrate communities. *Ecosphere*. 2(2):art18. DOI:10.1890/ES10-00011.1

Vincenzi, S., Hallowell Satterthwaite, W. and Mangel, M. 2012. Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics and management of stream-dwelling salmonid populations. *Rev. Fish. Biol. Fisheries*. 22:813-825.

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

Williams, K.L., Griffiths, S.W., Nislow, K.H., McKelvey, S. and Armstrong, J.D. 2009. Response of juvenile Atlantic salmon, Salmo salmar, to the introduction of salmon carcasses in upland streams. *Fish. Manage. Ecol*. 16:290-297.

Wilzbach, M.A., Harvey, B.C., White, J.L. and Nakamoto, R.J. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. *Can. J. Fish. Aquat. Sci*. 62:58-67.

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

Wipfli, M.S., Hudson, J.P. and Caouette, J. 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., Hudson, J.P., Chaloner, D.T. and Caouette, J.P. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Can. J. Fish. Aquat. Sci.* 56:1600-1611

Wipfli, M.S., Hudson, J.P., Caouette, J.P. and Chaloner, D.T. 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., Hudson, J.P., Caouette, J.P., Mitchell, N.L., Lessard, J.L., Heintz, R.A. and Chaloner, D.T. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: A test on multiple trophic levels in streamside experimental channels. *Trans. Am. Fish. Soc.* 139:824-839.

Wolman, M.G. 1954. A method of sampling coarse riverbed material. *Trans. Am. Geophys. Union*. 35:951-956.

Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics.* 25:443-466.

Wootton, R.J. 1998. *Ecology of teleost fishes*, 2nd Ed. Kluwer Academic, Dordrecht.

Young, H.S., McCauley, D.J. and Dirzo, R. 2011. Differential responses to guano fertilization among tropical tree species with varying functional traits. *Am. J. Bot.* 98:207-214.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics*. 12:163–189.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saleliev, A.A. and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York.

Zuur, A.F., Ieno, E.N. and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and evolution*. 1:3-14.

Appendix A. Supporting material for 4.0: Time-delayed subsidies: Interspecies population effects in salmon

Table A.1. Component loadings of 17 habitat variables for the first three components, which collectively explain 64.8% of the total variance in the data

Variable	PC1	PC2	PC3
	39.10%	*14.30%*	*11.40%*
Catchment area	**0.388**	-0.017	0.0407
Stream length	**0.461**	0.108	0.177
Maximum stream depth	0.256	0.047	0.019
Stream width at bankfull	**0.412**	-0.088	0.073
Stream wetted width	**0.432**	-0.079	0.067
Percent undercut	-0.079	**0.341**	-0.037
Pool volume	0.184	0.127	-0.069
Pool to riffle ratio	0.018	-0.005	-0.067
Large wood volume	0.029	**-0.305**	-0.288
Gradient	-0.051	**-0.543**	0.009
Percent fines	-0.059	0.209	0.222
Canopy density	0.051	-0.218	0.236
Maximum temperature	-0.005	-0.232	**-0.564**
pH	0.012	**-0.523**	0.241
Dissolved nitrate	-0.094	-0.169	**0.472**
Dissolved ammonia	-0.18	-0.07	-0.154
Dissolved phosphorous	**-0.354**	-0.001	**0.367**

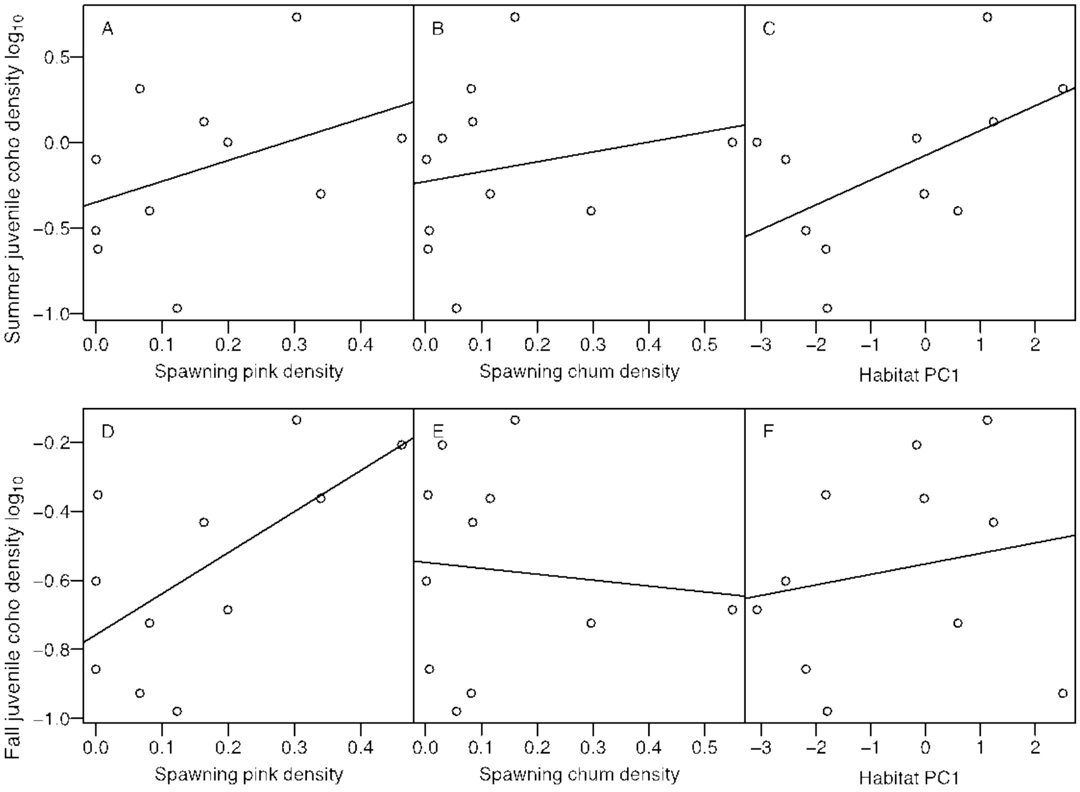


Figure A.1. Relationships between the densities of spawning pink and chum salmon and habitat principal components, and density of juvenile coho salmon in summer prior to spawning (A-C) and during spawning in fall (D-F). Large values of PC1 correspond to variables related to large watersheds.