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ECOLOGY OF JUVENILE SALMON IN LARGE FLOODPLAIN RIVERS: THE INFLUENCE OF HABITAT MODIFICATION BY BEAVERS (*Castor canadensis*) ON SALMON GROWTH AND PRODUCTION.

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Ecology of juvenile salmon in large floodplain rivers: the influence of habitat modification by beavers (*Castor canadensis*) on salmon growth and production.

Chairperson: Dr. Jack Stanford

ABSTRACT

I investigated the influence of beavers on aquatic floodplain habitats and determined how juvenile salmon habitat use, growth, survival, movement, and production varied by habitat type in a large alluvial floodplain of the Kwethluk River in western Alaska. I also compared juvenile salmon production at the floodplain scale in the Kwethluk River (with beavers), to a very similar salmon river in Kamchatka (the Kol) that has no beavers.

Beavers modified 87.5% of the aquatic off-channel habitat of the Kwethluk River, which was composed of three successional stages of beaver ponds (early-, mid-, and late-successional), and beaver-influenced spring brooks. Early-successional ponds were closer to and more connected to the main channel, while mid- and late-successional ponds were farther from the main channel with more dams and highly variable hydrology.

Juvenile salmon habitat use varied by habitat type. Total fish species and salmon species richness was 2-3x higher, the proportion of young-of-the-year salmon was over 50% compared to <5%, and densities of juvenile salmon were 5-7x higher in spring brooks and early-successional ponds compared to late-successional ponds. The growth of young-of-the-year coho and Chinook was almost 2x higher in early-successional ponds compared to both beaver-influenced and beaver-free spring brooks, but survival rates were consistently highest each month (46 to 80%) in beaver-free spring brooks. Within the parafluvial zone early-successional ponds produced a greater biomass of juvenile salmon than either type of spring brook (175 vs. 149 and 140kg) but only reared half the individuals as beaver-free spring brooks (24,100 vs. 41,400 salmon).

In contrast to the Kwethluk, there was no difference in species richness or density by habitat type within the Kol River, suggesting that juvenile salmon are able to rear in all parafluvial and orthofluvial habitats when beavers are not present.

I estimated that in the absence of beavers the entire Kwethluk floodplain could produce 2x the biomass (between June-August, 1174 vs. 667kg) and rear 3x the number of salmon (370,000 vs. 140,000). By damming off-channel habitats and blocking large amounts of orthofluvial habitats beavers could have a large effect on production of juvenile salmon in a large alluvial river floodplain.

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I would also like to thank all of those who came before me and conducted field work on the Kwethluk River, especially Tyler Tappenbeck and Jake Chaffin. Tyler and Jake pioneered the Kwethluk River for our research program and selected many of the original study sites on the floodplain. Zach Crete and Nathan Hoeme were also both instrumental in introducing my team to the Kwethluk River.

I am indebted to my husband, John Malison, who put his own plans on hold to support me in this degree. He worked with me every day for 3 long field seasons in the Alaskan bush. Without his support there is no way that I could have conducted such an extensive study in such a remote place. He acted as research assistant, camp manager, boat maintenance man, and logistical problem solver among other duties, and saved us from ending up on top of a log jam on more than one occasion.

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INTRODUCTION

BACKGROUND

Beavers as habitat engineers of streams

Large animals, especially herbivores like beavers, may directly alter the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994, Naiman and Rogers 1997). Beaver engineering of aquatic habitats can exert strong influences on physical and biological components of stream ecosystems by impounding water (Naiman et al. 1988). Most of our understanding of beaver effects on river processes and aquatic organisms comes from studies on low order systems, namely the types of habitats beavers are thought to prefer (Beier and Barrett 1987, Suzuki and McComb 1998, Pollock et al. 2004). In low order systems the presence of beaver dams results in lentic habitats with altered nutrient and carbon cycles (Francis et al. 1985, Naiman et al. 1991, Naiman et al. 1994), increased nutrient availability (Wilde et al. 1950, Naiman and Melillo 1984, Pinay and Naiman 1991), and altered fluxes of organic matter, sediment, and heat (Naiman et al. 1986, Naiman et al. 1994, Rosell et al. 2005).

The presence of beaver dams can also alter the hydrology of riparian zones, resulting in increased biocomplexity of low order streams (Naiman and Rogers 1997, Gurnell 1998, Wright et al. 2002, Rosell et al. 2005). Furthermore, by cutting trees and shrubs (Jenkins 1980) beavers alter the structure and productivity of the riparian zone and can change successional pathways of riparian vergetation (Naiman et al. 1988, Mouw et al. 2012). The combination of the effects of altering hydrology and riparian vegetation results in a mosaic of different vegetation types being present in beaver-impounded watersheds compared to beaver-free watersheds (Naiman et al. 1988).

Though most of our understanding of beaver effects on lotic processes comes from low order stream systems, beavers are also ubiquitous inhabitants of large North American rivers (Naiman et al. 1988).

Beavers in large alluvial floodplain rivers

The influence of beavers on large alluvial floodplains has not been examined in detail, though beavers are ubiquitous inhabitants of large North American rivers where they cut large amounts of riparian wood and construct dams lateral to the main channel (Naiman et al. 1988). Beavers have the potential to substantially impound and regulate the flow and exchange of surface and ground water in the low gradient flood channel networks of larger rivers (Gurnell 1998). Beavers could have large impacts on floodplain systems if they induce similar effects as seen on low order streams. For example, based on observations of beaver activity on the Bow River, in the Canadian Rocky Mountains, Rutten (1967) suggested that dams standing for decades in low gradient floodplains have the ability to confine the main channel, thus reducing floodplain complexity as sediments are deposited over time. Despite the generally observed substantial influence of beavers on large floodplain rivers, the extent and process of floodplain impoundment and water regulation by beavers has not been examined in detail, including influences on the distribution and abundance of aquatic organisms.

The influence of beavers on fish

The influence of beavers on stream fishes, including juvenile salmon, has been thoroughly studied in low order stream systems, resulting in both positive and negative effects (Collen and Gibson 2001, Kemp et al. 2011). The most commonly cited negative effect of beavers on fish include the impediment of fish movement because of dams

(Schlosser and Kallemeyn 2000, Mitchell and Cunjak 2007), declines in habitat characteristics that may influence fish habitat use and condition (e.g. low oxygen levels, Burchsted et al. 2010), and siltation of spawning grounds (Taylor et al. 2010). However, in most cases there is controversy over whether or not beaver impacts on fishes are actually negative. The movement and migration of fish that spawn in the autumn seem to be most strongly hindered by beaver dams (Cook 1940, Rupp 1955), however many studies show that both adult and juvenile fishes can move past dams at higher flows (Gard 1961, Bryant 1983, Murphy et al. 1989, Schlosser 1995). Similarly, the warming of stream temperature by beavers has been suggested to be detrimental to trout by some (Cook 1940, Rupp 1955), positive for production of trout by others (Huey and Wolfrum 1956), and other work has found no consistent relationship between downstream warming and size and number of beaver impoundments (McRae and Edwards 1994). Additionally, beavers are often thought to damage spawning areas by causing excessive siltation but even this potential impact is contentious and dams may be beneficial in streams with high silt loads by reducing the overall silt-carrying capacity of the stream (Macdonald et al. 1995).

A recent review of the effects of beavers on stream fish found that the benefits of beavers for stream fish are more often cited than negative impacts (Kemp et al. 2011). Beavers have been shown to positively influence salmon populations by improving habitat quality. For example, impounded habitats can provide good cover and increased production of invertebrate food resources (Hanson and Campbell 1963, Keast and Fox 1990). Impounded sections of small streams have also been found to be more productive in number and size of fish (Gard 1961, Hanson and Campbell 1963, Bryant 1983, Murphy et al. 1989, Leidholt Bruner et al. 1992, Schlosser 1995) and have had juvenile salmonids with higher survival rates (Bustard and Narver 1975, Quinn and Peterson 1996). Faster growth rates have also been suggested based on the presence of larger juvenile coho in ponds (Bustard and Narver 1975, Swales and Levings 1989). Lastly, ponds have also been shown to have increased production of coho (Nickelson et al. 1992, Layman and Smith 2001, Pollock et al. 2004).

Despite this body of research, little work has been done to understand how habitat modification by beavers may influence the ecology and production of juvenile salmon on expansive, multi-channel floodplains where habitat forming processes may be affected differently by beavers.

The importance of large alluvial river floodplains for juvenile salmon rearing habitat

Large alluvial rivers around the Pacific Rim have expansive floodplains which contribute habitat important for salmon production (Whited et al. 2013). In fact, forty-percent of all salmon produced in the world come from western Kamchatka rivers (Augerot 2005) and these rivers have complex floodplain habitats. Within floodplains of these rivers, off-channel spring brooks provide primary nursery grounds for juvenile salmon including *Oncorhynchus kisutch* (coho salmon), *O. tshawytscha* (Chinook salmon) and *O. nerka* (Eberle and Stanford 2010, Armstrong and Schindler 2013). Higher densities of juvenile salmonids (up to 4-10 fish m^{-2}) have been documented in spring brooks compared to main channel shallow shorelines and tributaries (Eberle and Stanford 2010). Shallow spring brooks are fed by effluent from the floodplain aquifer, have warm winter and cool summer temperature patterns, and have high ecological connectivity with riparian food webs; therefore enhanced growth and survival of juvenile salmon has been documented in these habitats (Sommer et al. 2001, Jeffres et al. 2008, Bellmore et al. 2013).

Beavers and juvenile salmon in large alluvial river floodplains

Off-channel spring brooks provide ideal habitats for beaver damming within floodplain networks of large rivers. As part of a project to compare physical features of salmon rivers around the North Pacific Rim (Luck et al. 2010, Whited et al. 2013), it was observed that in North American rivers native beavers routinely dam floodplain spring brooks creating massive pond complexes throughout the parafluvial (area of active scour near the main channel) and orthofluvial (area of deposition farther from the main channel) zones of many expansive floodplains. It is unknown how beaver ponds might differ in physical characteristics based on their location within the complex network of channels in expansive floodplain settings and how they might vary in connectivity to the main channel. Understanding how beaver modified habitats vary in characteristics and connectivity is important because the dynamics and connectivity of different types of ponds could strongly influence the ability of aquatic organisms to access and use riverine floodplain habitats. By modifying the habitat use and distribution of juvenile salmon beavers have the potential to influence the production of juvenile salmon from large alluvial floodplains. Chinook and coho salmon may be strongly influenced by beavers because they spend 2-3 years rearing in off-channel habitats. Moreover, they are preferred by subsistence fishers and are of great conservation concern.

STUDY SITE

I conducted the first study of habitat modification by beavers and the subsequent influence on the habitat use, growth and production of juvenile coho and Chinook salmon in an expansive alluvial floodplain river. My focal study site was the Kwethluk River, a 5th order tributary of the Kuskokwim River on the west coast of Alaska with a 3,787 km^2 catchment. The Kwethluk enters the Kuskokwim River just above the tidally influenced lower reach, approximately 15km upstream of Bethel, AK. I chose to work on the Kwethluk River because it was part of a larger suite of research on salmon rivers of the Pacific Rim. Moreover, beavers are prevalent on the floodplain and have coevolved with salmon for hundreds of years in this river. The river also has the characteristics of a natural undisturbed system, allowing me to test my hypotheses without the added complexities of modified hydrologic cycles. A long term record of spawner counts at a weir also exists and the Kwethluk is protected from development within the Yukon Delta National Wildlife Refuge. The Kwethluk Village people harvested beaver extensively in the river until lower prices for fur reduced incentive for trapping; very little or no harvest occurs today, so beavers are very abundant in the floodplain.

My study reach was an expansive anastomosing floodplain underlain by a shallow alluvial aquifer that is located between 37 and 64km (from Three-Step to Elbow Mountain) above the confluence of the Kwethluk with the Kuskokwim. The 27-km long reach is characterized by a laterally migrating main channel, coupled with anabranching avulsion events that create a complex network of flood and secondary channels and gravel bars. Many channels disconnect from the main river at upstream ends during base flow conditions. This process is mediated through sediment accretion or wood-jam levees. Channel beds that have been scoured low enough to intercept the shallow aquifer result in spring brooks that flow along the abandoned channels and into backwaters that connect to the main river. Spring channels that have been dammed by beavers are abundant in the study reach. The reach ends at Three-Step Mountain where the river switches to a torture meander as the river reaches base level influenced by the tidally induced backwater effects in the main Kuskokwim River.

I compared salmon metrics from the Kwethluk River with the Kol River, a 5th order river in southwestern Kamchatka without beavers (Russian Federation) (N53º49.506'E156º3.716'), to gain inference regarding how the presence of beaver-modified habitat might influence the production of juvenile salmon from an entire river floodplain. The Kol study reach was an expansive floodplain similar in features to the Kwethluk River, with a river formed of a complex network of anastomosing channels. Similar habitat forming processes occurred on the Kol as on the Kwethluk, with a laterally migrating main channel and anabranching avulsion events creating a complex network of flood and secondary channels. Spring channels are formed in a similar manner and are abundant throughout the entire floodplain (because no dams are present).

PURPOSE AND OVERARCHING QUESTION

The overarching goal of this dissertation was to determine how beavers influence aquatic habitats, thereby potentially modifying the production of juvenile salmon on a large alluvial river floodplain. As described above, the influence of beavers on fishes is well studied in small streams, as are the habitat forming processes of large alluvial floodplain rivers, allowing us to (1) ask questions about how beavers influence aquatic habitats, juvenile salmon habitat use, and juvenile salmon production in large river floodplains, and (2) compare our results for juvenile salmon in a beaver-dominated floodplain to one without beavers. The Kol floodplain served as an excellent comparison site for our study because it is a similarly complex floodplain located in Russia where beavers have never been present.

This study is important scientifically because most studies of beaver impacts on salmon have been on low order, tributary streams. However, some of the world's most important juvenile salmon producing habitats are in complex, large river floodplains. Despite the importance of these systems, no previous study has focused on the effects of beavers as a biotic driver of salmon productivity in a large alluvial river floodplain. Moreover, the study is a seminal investigation of beavers and salmon in a primary successional context (i.e., as the ponds age, does the habitat quality for salmon also change?).

Initial observations on the Kwethluk River indicated that beavers had the ability to exert strong influences on floodplain habitat structure by building extensive dam complexes. Because off-channel habitats are important for juvenile salmon, it was possible that by altering off-channel habitats beavers would have the ability to influence the habitat use and production of juvenile salmon. Therefore, I generated the working hypothesis that the presence of beaver ponds on floodplain spring brooks increases salmon production in the parafluvial zone of a large river floodplain because abundant lentic food and lower fish densities in ponds enhance growth in comparison to undammed spring brooks or spring brooks below beaver dams. Although I hypothesized that production would be positively influenced within the parafluvial zone, I also hypothesized that the influence of beavers on juvenile salmon production would be negative at the scale of the entire floodplain. Specifically, even if beavers stimulate the growth of fishes within beaver ponds of the parafluvial zone, they may still negatively impact production at the floodplain scale by blocking orthofluvial off-channel rearing habitats from use by juvenile salmon.

OVERVIEW OF CHAPTERS

This dissertation consists of three chapters which address the overarching hypothesis through comparative and experimental studies. Chapters are presented in manuscript format with co-author names omitted for the purpose of the dissertation. Chapter 1 presents the first analysis of beaver influences on an expansive floodplain of a large alluvial (gravel-bed) river. I quantified the distribution and abundance of aquatic habitat types, how different habitat types varied in physical characteristics, how the composition of macroinvertebrate forage items and fishes differed by habitat type, and finally, how different habitats varied in connectivity and if connectivity influenced the habitat use and movement of juvenile salmon. In this floodplain beavers predominantly dam off-channel spring brooks which are very important rearing habitats for juvenile salmon. Because of this I addressed these questions in spring brooks with and without dams and in different successional stages of beaver ponds. I found that 87.5% of the off-channel aquatic habitat of the expansive floodplain was altered by beavers damming spring brooks. Physical characteristics were similar among different types of beaver ponds and among different types of spring brooks, indicating that all habitat types were suitable habitat for juvenile salmon. However, beavers reduced habitat connectivity and added variability to macroinvertebrate assemblages within habitats by damming floodplain spring brooks. Early-successional ponds had high hydrologic synchrony values (closely tracking water fluctuations in the main channel), while mid- and late-successional ponds, being farther from the main channel with more dams blocking flow paths, had lower and highly variable synchrony values. Corresponding with these differences in connectivity, total species and salmon species richness was 2-3x higher, the proportion of fish captured in sites that were young-of-the-year was over 50% compared to <5%, and densities of juvenile salmon were 5-7x higher in spring brooks and early-successional beaver ponds compared to late-successional ponds. I also showed that though virtually no movement of juvenile salmon occurred past beaver dams at base flow, flooding mediated movement of juvenile salmon past beaver dams. Lastly, chapter 1 sets the stage for the following two chapters, which investigate the growth and production of juvenile salmon in the parafluvial zone of a beaver dominated riverscape and compare production in floodplains with and without beavers at the floodplain scale.

In chapter 2, I examine how the presence of beaver dams influences the production of juvenile salmon in the parafluvial zone of the floodplain study reach. I measured multiple factors that could influence the production of juvenile coho and Chinook salmon, including habitat, prey and diet characteristics. I conducted detailed habitat specific studies of the growth, survival, movement, and production of juvenile coho and Chinook in the parafluvial zone using a multistate robust closed capture design. Because beavers most strongly influence off-channel habitats by damming springbrooks (over 80% of the springbrooks in the entire floodplain were dammed, chapter 1) I focused study of juvenile salmon in 3 off-channel habitat types that serve as nurseries for the target species, specifically: a) early-successional beaver ponds, b) beaver-influenced springbrooks (i.e., the lotic reaches downstream from dams, connected downstream to the main channel network), and c) beaver-free springbrooks (i.e., free flowing from aquifer outflow to main channel confluence). I excluded study of older successional pond sites because they were largely devoid of juvenile salmon, apparently because dam complexes blocked immigration from parafluvial spawning sites (see Chapter 1). I assessed the influence of beavers by comparing salmon metrics in beaver-influenced and beaver-free habitats and by estimating potential production from the parafluvial zone if beavers were absent and all spring brooks were free flowing. I found that beavers stimulated the growth of young-of-the-year coho and Chinook in early-successional ponds compared to both beaver-influenced and beaver-free spring brooks (3.1 ± 0.1 vs. 1.83 ± 0.14 and 2.0 ± 0.3 %mass/day for coho and 1.8 ± 0.08 vs. 0.93 ± 0.16 and 1.35 ± 0.32 %mass/day for Chinook). Although growth rates were highest in early-successional beaver ponds, survival rates were consistently highest (46 to 80%) each month in beaver-free springbrooks where densities of juvenile coho and Chinook were highest. Ponds produced less juvenile coho and Chinook salmon biomass per unit area than beaver-free and beaver-influenced springbrooks (1.87 ± 0.57 vs. 2.98 ± 1.22 and 3.23 ± 0.73 g/m^2). However, due to the larger areal extent of early-successional pond habitat in the parafluvial zone, ponds produced a greater biomass of juvenile salmon than either type of spring brook habitat (175 vs. 149 and 140 kg). In contrast to biomass, early-successional beaver pond habitat reared about half the individuals that reared in beaver-free springbrooks (~24,100 salmon vs. ~41,400 salmon). I estimated that if beavers were not present, slightly less biomass would be produced but off-channel habitats in the parafluvial zone would be able to rear 1.5-2x more individuals, showing that beavers may be able to limit production on the floodplain.

In Chapter 3, I determine the influence of beavers on juvenile salmon production at the scale of the entire floodplain, by comparing two large alluvial rivers known for their production of salmon, one with beavers, the Kwethluk, and one without beavers, the Kol. My goal was to provide perspective on the likely influences of beavers on juvenile salmon habitat use and production by comparing two rivers with similar physical drivers but that differed due to the presence of beavers in one river. I compared species richness, densities, condition and growth of juvenile coho and Chinook salmon between parafluvial and orthofluvial habitats within both rivers, as well as between the rivers. Determining how parafluvial and orthofluvial habitat use compared in a beaver free river allowed me to infer how the orthofluvial zone might be used in the Kwethluk if beavers and dams were not present. These comparisons were necessary because experimental approaches to determine if beavers compromise salmon habitat and production at the scale of entire river floodplains are problematic because beavers would have to be removed over massive scales (hundreds of km^2), which is not feasible. Species richness was similar by habitat type in the Kol (without beavers). In contrast, in the Kwethluk (with beavers) parafluvial habitats had twice as many species as orthofluvial habitats. Salmon density was similar in all habitat types in the Kol, but in the Kwethluk coho densities were 8-12x higher in off-channel spring brooks vs. the main channel and Chinook densities were up to 2x higher in parafluvial spring brooks than other floodplain habitats. In the Kol there was no difference in coho condition by habitat type but Chinook condition was highest in orthofluvial spring brooks. Within the Kwethluk there was no difference in Chinook condition, but the condition of coho was lowest in main channel versus all other habitats (0.89 vs. 0.99 – 1.10). I found that the Kol produces an order of magnitude more salmon biomass and 40x the individuals than the Kwethluk. I estimated that in the absence of beavers the Kwethluk floodplain could produce 2x the biomass (between June-August, 1174 vs. 667kg) and 3x the number of salmon (370,000 vs. 140,000).

BROADER IMPACTS

Beavers are a dominant feature of North American salmon rivers and the findings of this study suggest that beavers can lower the production potential of large alluvial river floodplains by damming spring brooks and creating a mosaic of beaver ponds in the place of very productive salmon rearing habitat (i.e. spring brooks). Essentially, the presence of ponds near the main river resulted in decreased production potential because fewer individuals reared in them. Additionally, I found that the low connectivity between late-successional ponds (farther from the main channel) strongly limited the use of the entire outer portion of the river floodplain. In comparison, in a river in Russia with no beavers, juvenile salmon were able to utilize the entire floodplain. Thus, beavers have the potential to limit production on the floodplain if the availability of freshwater habitat is a limiting factor for the population.

For beavers to actually lower production of juvenile salmon on the floodplain, they would have to induce density dependent effects resulting in lower survival and growth of juvenile salmon. Beavers do not determine the number of eggs or the number of fry that emerge (unless spawning habitat is limited by beavers). These numbers are determined by the number of adults returning to the basin to spawn. It is possible that densities in ponds are highly variable and dependent on the number of returning adults. For example, more juveniles might rear in ponds when there are more of them on the floodplain. This was a short term study, whereas beavers and salmon have occupied the same river for centuries. It appears that beavers may negatively impact salmon populations by building dams and ponds that limit the use of portions of the floodplain and produce fewer individuals, but it is not clear how dynamic the use of different habitats might be over time. It would be very interesting to study density dependent effects in different habitats over different escapements to determine if beavers are actually limiting production through habitat modification.

The potentially negative influence of beavers on salmon production in large alluvial river floodplains is not currently part of the conversation regarding beaver reintroduction and management of salmon in large river basins. It is important to consider how the potentially negative impacts of beavers might balance the positive effects that have been documented (e.g. increased water storage, biodiversity, etc.), because beavers are regularly being reintroduced to salmon streams in the U.S. Furthermore, there is currently controversy over how reintroduction of Eurasian beavers might influence Atlantic salmon in Scotland and other European countries. Beaver introductions to South America (Tierra del fuego) show extreme habitat modification but no negative influences on introduced trout have been documented (Anderson et al. 2009, Moorman et al. 2009). Because of wide scale reintroductions, and cited positive effects of beavers on fishes (Kemp et al. 2011), it is important that the potentially negative influence of wide scale modification of low-gradient floodplain systems become part of the discussion regarding beaver reintroductions into large salmon rivers. Thus this work contributes to the science of salmon management and is potentially transformative of how we think about beavers influencing salmon in large basins with expansive floodplains.

Additionally, the question of how beavers influence salmon is an important topic regionally in western Alaska. Within western Alaska there is a cultural view that beavers are detrimental to salmon and many people view the decline in salmon stocks in western Alaska at least in part as being the result of beavers and their dams. Providing information on how beavers may influence juvenile salmon production in a large alluvial river floodplain is important for management of beavers and salmon in Alaskan rivers. It seems unlikely that recent declines in salmon returns (i.e. over the past decade) are due specifically to beavers because beavers have been present in Alaskan river systems over much longer time periods (since the early Holocene, see Robinson et al. 2007).

As a society, we view salmon as valuable for their cultural, economic, and ecological roles and thus the conservation of salmon populations is an important goal for many. Because some of the most important rearing habitat for salmon is located where there are strong impacts by beavers it is important to understand how the influence of beavers may influence salmon populations.

RELATION TO SYSTEMS ECOLOGY PROGRAM

The Systems Ecology program focuses on the "understanding of interactions of physical, chemical and biological factors affecting ecological systems across spatial and temporal scales and the factors affecting coupled natural and human systems." This dissertation fits into the Systems Ecology framework by describing and investigating a natural floodplain ecosystem in the context of both physical (river processes) and biological (ecosystem engineering by beavers) factors that influence the production of juvenile salmon across spatial scales spanning from individual rearing habitats to the entire floodplain.

River floodplains are ideal systems in which to study the processes that create and maintain environments and to quantify the effects of heterogeneous environments on the function of ecosystems and on biodiversity (Tockner et al. 2009). Floodplains are complex systems that exist where four major habitat zones and their associated communities (riparian vegetation, main channel, off-channel, and aquifer) are interconnected energetically by the flux of water, materials, and organisms. Physical processes maintain a shifting mosaic of floodplain habitats (Stanford et al. 2005) and a complex network of channels, and the composition and spatial arrangement of patches controls the movement of organisms and materials to other patches. Beavers have the ability to strongly alter floodplain systems spatially across the floodplain and temporally as dams built by beavers can last for centuries. In this dissertation I investigate how herbivory and dam building by beavers interacts with physical river processes to form the habitat mosaic that influences the distribution, growth and production of juvenile salmon.

Furthermore the Kwethluk River is a good example of a coupled natural/human system in that the floodplain produces salmon which provide subsistence fisheries that are extremely important for many people. Though the Kwethluk River is largely uninfluenced by humans in a physical habitat sense, the subsistence fisheries strongly influence escapement (the number of adults returning to spawn) which will in turn strongly influence how many salmon can be produced by the river. It is important that we understand the ecological interactions and factors associated with beavers in large alluvial river floodplains that may influence the production of salmon, especially since most large North American Rivers that produce salmon also have beavers.

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CHAPTER 1: BEAVERS (*Castor canadensis*) INFLUENCE HABITAT AVAILABITY AND USE BY MACROINVERTEBRATES AND JUVENILE SALMON IN A LARGE ALASKAN RIVER FLOODPLAIN.

SUMMARY

1. Our objective was to determine how beavers impact habitats and influence macroinvertebrates and juvenile salmon. This study on the Kwethluk River in western Alaska represents the first analysis of beaver influence on rearing habitat carried out on an expansive North American floodplain river known to be important for producing salmon.

2. Habitat modification by beavers was quantified using 3 years of satellite imagery to assess the amount and spatial distribution of potential juvenile rearing habitat. Macroinvertebrate composition and juvenile salmon abundances within identified juvenile salmon habitats (e.g. beaver ponds, spring brooks with and without upstream beaver dams, and main channel shorelines) were quantified to determine beaver influence. Presence of beaver dams and time-series measures of water levels were used to assess hydrologic connectivity and fish access between sites and the river as modified by beavers.

3. 87.5% of the off-channel aquatic habitat was altered by beavers damming spring brooks.

4. Physical characteristics were similar among different successional stages of beaver ponds and among different types of spring brooks (by NMDS ordination), indicating that all habitat types are suitable habitat for juvenile salmon.

5. Aquatic macroinvertebrate community composition differed between beaver ponds and spring brooks (by NMDS ordination) with differences driven by larval mayflies and stoneflies in spring brooks compared to cladocerans, snails, copepods, and freshwater clams in beaver ponds.

6. Chinook and coho salmon were predominant in all habitat types except late-successional ponds. Total fish species and salmon species richness was 2-3x higher, the proportion of young-of-the-year salmon was over 50% compared to <5%, and densities of juvenile salmon were 5-7x higher in spring brooks and early-successional ponds compared to late-successional ponds.

7. Early-successional ponds had high hydrologic synchrony values (closely tracking water fluctuations in the main channel), while mid- and late-successional ponds, being farther from the main channel with more dams blocking flow paths, had lower and highly variable synchrony values.

8. Almost no movement of juvenile salmon past dams occurred at base flow. However, summer and fall flooding mediated movement past dams, allowing individuals to “escape” ponds or enter ponds to rear overwinter.

9. Beavers reduced habitat connectivity and added variability to macroinvertebrate assemblages within habitats by damming floodplain spring brooks, which are extremely important rearing areas for juvenile salmon in rivers that do not have beavers. Nonetheless, juvenile salmon were able to effectively inhabit and move between early-successional ponds and spring brooks in the Kwethluk, though the presence of beaver dams strongly limited the use of late-successional ponds on the large alluvial river floodplain.

INTRODUCTION

Large animals, especially herbivores like moose, elk (Collins and Helm 1997, Beschta 2003, Butler and Kielland 2008) and beavers (*Castor canadensis*) have the ability to strongly modify habitats and influence the availability of resources for other organisms (Naiman 1988, Jones et al. 1994, Naiman and Rogers 1997). Beavers are well known to shape the physical environment by cutting vegetation and building dams that impound small streams and create ponds. In low order streams, beaver damming results in lentic habitats with altered nutrient and carbon cycles (Francis et al. 1985, Naiman et al. 1991, Naiman et al. 1994), increased nutrient availability (Wilde et al. 1950, Naiman and Melillo 1984, Pinay and Naiman 1991), altered fluxes of organic matter, sediment, and heat (Naiman et al. 1986, Naiman et al. 1994, Rosell et al. 2005) and increased overall biocomplexity (Naiman and Rogers 1997, Gurnell 1998, Wright et al. 2002, Rosell et al. 2005).

Most of our understanding of beaver effects on lotic processes and organisms comes from studies on low order streams that are generally considered preferred beaver habitats (Beier and Barrett 1987, Suzuki and McComb 1998, Pollock et al. 2004). However, beavers are also ubiquitous inhabitants of large North American rivers (Naiman et al. 1988). Beavers have the potential to substantially impound and regulate the flow and exchange of surface and ground water in the low gradient flood channel networks of larger rivers (Gurnell 1998). For example, based on observations of beaver activity on the Bow River, a floodplain river in the Canadian Rocky Mountains, Rutten (1967) suggested that dams standing for decades in low gradient floodplains have the ability to confine the main channel, thus reducing floodplain complexity as sediments are deposited over time. Despite the generally observed substantial influence of beavers on large floodplain rivers, the extent and process of floodplain impoundment and water regulation by beavers has not been examined in detail, including influences on the distribution and abundance of aquatic organisms.

Large alluvial river floodplains are characterized by a shifting habitat mosaic (SHM) (Stanford et al. 2005) that encompasses a catena of habitat types and rate of change which may be influenced by beavers. Off-channel habitats include an array of spring brooks, ponds and wetlands that occur at base flows within the network of abandoned flood channels (Bayley 1995, Brown 1997, Petry et al. 2003, Stanford et al. 2005). Because flood channels scour the bed and intercept the water table, spring brooks develop in abandoned channels making them ideal sites for construction of beaver dams creating ponds. As part of a project to compare physical features of salmon rivers around the North Pacific Rim (Luck et al. 2010, Whited et al. 2013), we observed that in North American rivers native beavers routinely dam floodplain spring brooks creating massive pond complexes throughout the parafluvial (area of active scour near the main channel) and orthofluvial (area of deposition farther from the main channel) zones of many expansive floodplains. Understanding how extensively beavers can modify large alluvial river floodplains and how the resulting suite of beaver ponds may differ in physical characteristics based on their location within the floodplain and successional stage (see

Mouw et al., 2012), is important because habitat quality is a critical controlling influence on the distribution and abundance of biota. In this study we were particularly interested in the influence of beaver ponding on the ecology of juvenile salmon.

The potentially strong influence of floodplain impoundment by beavers may be expected to strongly influence forage (macroinvertebrates) and consumer (salmon and other fishes) communities by creating lentic habitats in areas that would otherwise be lotic. Macroinvertebrate community composition, richness and diversity have been shown to be altered by beaver activities in low order stream systems (McDowell and Naiman 1986, Smith et al. 1989, Hammerson 1994). Impounded sections of low order streams have also been found to have greater numbers and sizes of fish (Hanson and Campbell 1963, Leidholt Bruner et al. 1992, Schlosser 1995), though in other cases reduced habitat quality has negatively impacted fish habitat use (e.g. low oxygen levels, Burchsted et al. 2010). How strongly the presence of beaver dams and ponds influences the composition and distribution of juvenile salmon and their food resources on an alluvial river floodplain should depend on the amount of habitat dammed and the degree to which habitat quality differs.

In addition to altering habitat quality, beavers may change the physical and hydrological connectivity of floodplain habitats, which in turn may strongly influence juvenile salmon movement and habitat use. In the absence of beavers, off-channel habitats, including spring brooks, have been shown to be very important rearing areas for juvenile salmon (Morley et al. 2005, Eberle and Stanford 2010). However, access to off-channel rearing habitats could be limited if beaver dams block fish movement and limit physical connectivity (Schlosser and Kallemeyn 2000, Mitchell and Cunjak 2007).

Despite the potential for limited movement, many studies have shown that movement of adult and juvenile fish does occur past beaver dams, especially at higher flows (Bryant 1983, Murphy et al. 1989, Schlosser 1995). Both the magnitude and patterns of flooding could determine when dammed habitats are inundated and accessible, and whether or not juvenile salmon can utilize these habitats for rearing and then leave the habitats in order to outmigrate to the ocean. Thus, understanding how beavers influence the hydrological dynamics of a floodplain system is critical in determining whether juvenile salmon distributions may be influenced by beavers.

Herein we present the first analysis of beaver influences on an expansive floodplain of a large alluvial (gravel-bed) river. Our study site was the Kwethluk River in western Alaska, a typical example of a North American floodplain river that is known to be an important salmon producer (Miller and Harper 2012). Specifically, we addressed the following questions:

1) What proportion of the floodplain is influenced by beavers, what types of habitats are present, and has the influence of beavers been relatively constant over the last decade?

2) How do different habitat types vary in physical characteristics and habitat qualities that may be important for salmon production?

3) How does the composition of macroinvertebrate forage items and fishes differ by habitat type?

4) Do different habitat types vary in physical and hydrological connectivity, and does this influence habitat use and movement of juvenile salmon?

METHODS

Study Area

The Kwethluk River is a 5th order tributary of the Kuskokwim on the west coast of Alaska with a 3,787 km^2 catchment. The Kwethluk enters the Kuskokwim River just above the tidally influenced lower reach, approximately 15 km upstream of Bethel, AK. It is protected from development and flow regulation by inclusion within the Yukon Delta National Wildlife Refuge. We choose to study the influence of beavers on this floodplain landscape because beavers are prevalent and their long term presence has resulted in altered successional pathways of riparian vegetation on the floodplain (Mouw et al. 2012).

The study reach is an expansive anastomosing floodplain that is located between 37 and 64km (from Three-Step to Elbow Mountain) above the confluence of the Kwethluk with the Kuskokwim (FIGURES

Figure 1.1). The floodplain is underlain by an extensive alluvial aquifer that maintains a robust riparian zone, in this case mainly composed of willow (*Salix spp.*), alder (*Alnus spp.*) and cottonwood (*Populus balsamifera*), with white spruce (*Picea glauca*) as the climax riparian species (Mouw et al. 2012). The floodplain has a laterally migrating main channel, that coupled with frequent occurrences of anabranching avulsions (mediated by gravel bar and drift wood deposition), creates a complex channel network of primary, secondary and tertiary channels that flow continuously (as described by Arscott et al. 2002 generally for gravel bed rivers). Flood channels disconnect from the main river during base flow conditions owing to levee formation from wood jamming and sediment accretion at upstream ends (Lorang and Hauer 2006). Spring brooks form in abandoned flood channels from upwelling groundwater during base flow and remain free-flowing (beaver-free spring brook) or are dammed by beavers. Dammed spring brooks form ponds that often have multiple dams and ponds in a downstream sequence to the main channel confluence or, alternatively, have one or two dams and ponds that feed a spring brook to the river confluence (beaver-influenced spring brook) (Figure 1.**2**).

Our floodplain reach ends at Three-Step Mountain where the river switches to torture meander morphology due to the tidally induced backwater effects in the main Kuskokwim River. The change in elevation from the top of the 27 km study reach to the bottom is ~ 68m, resulting in an overall floodplain slope of 0.0025. The floodplain is surrounded on both sides by permafrost tundra (~3m higher in elevation). The river generally experiences spring (from snowmelt) and fall (from rain events) flooding that can inundate the entire floodplain or at lower levels simply activate some portion of the flood channel network.

Field and Laboratory Methods

Spatial and Temporal Habitat Composition

To measure spatial modification of the floodplain by beavers we quantified the types, amount and distribution of aquatic habitats in the entire study reach from Quickbird satellite multispectral imagery for 2004, 2008, and 2011. Initially, pixels associated with water bodies were classified and delineated using Definiens Developer (version 8.6; Definiens, Westminster, Colorado; www.ecognition.com/) and Erdas Imagine (version 9.3; Intergraph, Norcross, GA; www.geosptail.intergraph.com) software. Following delineation, habitat patches (i.e., ponds, spring brooks, and main channel shallow shorelines) were manually demarcated using heads-up digitizing (manually drawing polygons around features) in Arc/Map (version 10; ESRI, Redlands, California, USA; www.esri.com) for each year, following similar methods used by Whited et al. (2013). We classified three types of beaver ponds (early-, mid-, and late-successional) based on the dominant vegetation surrounding ponds. Ponds were classified as early-successional if they were embedded in willow/alder (*Salix* and *Alnus spp.* – see Mouw et al. 2012). Ponds were classified as mid-successional if they were embedded in meadows and as late-successional if embedded in spruce forest (*P.* glauca).

Image classifications were validated from field observations of these habitats at specific study sites.

We analyzed temporal variation in floodplain habitats with three images, for a total of two time steps between 2004-2008 and 2008-2011. We calculated the amount of area in the following cover type classes for both time steps: restored spring brooks (following dam blow out, i.e. dam present in the first image but not in the second), recently dammed spring brooks (free flowing in first image, dammed in the second), new spring brooks with dams (spring brook not present in first image but present and dammed in second), and new free flowing spring brooks (present only in the second image and not dammed). Classifications were made by visual inspection of the imagery and confirmed for a portion of the 2011 image through a field survey.

Habitat Characteristics

We compared physical characteristics among different types of beaver ponds (early-, mid-, and late-successional) and among different types of spring brooks (beaver-free or beaver-influenced). We selected a subset of each habitat type identified in the satellite image for on the ground study and refer to individual study “sites.” We selected 6 early-, 4 mid-, and 3 late-successional beaver pond sites, as well as 3 beaver-free and 4 beaver-influenced spring brook sites along the length of the floodplain. We systematically selected representative sites based on the distribution and accessibility of habitat types. It is common for multiple ponds and a beaver-influenced spring brook to be present and connected in one area, which we call a “complex”. Four beaver-influenced spring brooks were located in the same complexes as 4 early-successional ponds, resulting in the 17 beaver-influenced sites being located within 13 complexes. Thus, we had a total of 20 study sites, located within 16 study areas on the floodplain (13 beaver complexes and 3 beaver-free spring brooks, FIGURES

Figure 1.**1**).

Site area and perimeter was measured from satellite imagery using Arc/Map and on the ground validation was completed by hiking the perimeter of the pond with a handheld Trimble GeoXM 2005 GPS (Trimble, Sunnyvale, California) for a subset of sites. Conductivity and pH were measured in ponds and spring brooks with an Oakton handheld meter (Waterproof pH/CON 10 Series, Oakton, Vernon Hills, IL; www.4oakton.com) because these metrics typically vary significantly between groundwater and surface water sources. Width and depth was measured on cross sectional transects every 10m along the length of each spring brook site. At 100 locations (every 1m) along each spring brook, a rock was randomly selected and its size and embeddedness was measured (Davis et al. 2001). We monitored water temperature hourly at each site year-round using HOBO and Vemco data loggers from 2006-2011 (Vemco, Halifax, Nova Scotia; www.vemco.com). Cumulative degree days were calculated by summing the mean daily temperatures for each site above 0 degrees. Mean diel change in temperature was calculated by subtracting the minimum temperature from the maximum temperature for each day and taking the average for the study period.

Multivariate techniques were used to test for differences in physical habitat characteristics by pond type and spring brook type. Site characteristics were analyzed using nonmetric multidimensional scaling (NMDS) (Kruskal and Wish 1978) because it does not require linear relationships between variables. Metrics used in the pond analysis included cumulative degree days, mean diel change in temperature, vegetation type, site area and perimeter, mean conductivity and mean pH. Metrics used in the spring brook analysis included cumulative degree days, mean substrate embeddedness and size, mean width and depth, and mean pH and conductivity. We used multiresponse permutation procedures (MRPP) to test for significant differences in variable composition by habitat type (Mielke and Berry 2001).

Macroinvertebrate and Fish Composition

Macroinvertebrates

We sampled study sites to determine if macroinvertebrate communities varied among habitat types on the floodplain. We collected samples of macroinvertebrates at a subset of the habitat sites including, 4 early-, 3 mid-, and 3late-successional beaver ponds as well as 4 beaver-influenced and 3 beaver-free spring brooks for a total of 17 sites. At each pond site we collected 3 replicate samples by sweeping a D-net (125 µm mesh) through vegetation, along logs and over the substrate for 1 minute. In spring brooks, 3 replicate samples were obtained from riffles selected systematically from each site by disturbing bed-sediments within a .25m^2 area for 1 minute (upstream of a 125 µm kick mesh net). All samples from ponds and spring brooks were sorted in the field for one hour or until no more specimens were visible; samples were preserved in ethanol until identified to order or family in the laboratory.

We also used NMDS (Kruskal and Wish 1978) to identify possible patterns in macroinvertebrate taxonomic composition among the 5 habitat types. We used relative abundance values for taxa for all NMDS ordinations because of high variation in raw values. We excluded rare taxa (relative values, <5%) from the data set to reduce skewness in the data. We used multi-response permutation procedures (MRPP) to test for significant differences in community composition by habitat type.

Fish Composition and Juvenile Salmon Density

The abundance and distribution of fish in the shallow water habitats of an expansive alluvial floodplain likely is determined by the availability and characteristics of different habitat types. In 2006 we conducted a preliminary study to determine the density of juvenile salmon in beaver-free spring brooks (n=5) and main channel shallow shorelines (n=5) by electrofishing, and in early- (n=4), mid- (n=4), and late-successional (n=3) ponds by depletion minnow trapping. Depletion sampling was conducted in known areas and population estimates made using a regression of catch to previous total catch (Zippin 1958). Between 2009-2011 we sampled to determine how fish species richness and composition, and the size distributions and condition of juvenile salmon varied by habitat type by sampling 16 beaver complexes and 3 beaver-free spring brooks. We sampled entire beaver complexes rather than just individual sites to increase our sample size and to allow for potential detection of fish movement (see below). The 16 beaver complex sites included the same sites sampled for habitat characteristics, as well as two additional early-successional and one late-successional beaver complex (FIGURES

Figure 1.**1**). Each habitat was sampled once a month during (June-September) using minnow traps placed throughout the habitat at ~5m intervals. To standardize trapping effort baited traps soaked for 2 hours and were removed in the order they were deployed. Captured fish were held in buckets with aerators. Fish were identified and measured and a subset was weighed. For each sampling date and site we calculated Fulton's condition factor, K (Ricker 1975), for each fish by dividing weight (g) by length (mm) cubed and multiplying by a scalar of 10^5.

The effect of habitat type on juvenile salmon density, total species richness, salmon richness, condition, and proportion of young of the year was analyzed using one-way analysis of variance (ANOVA)(PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). All data sets were tested for normality and, where necessary, 1og10 transformed to improve normality and homogeneity of variance prior to statistical analysis.

Connectivity and Movement

Physical Connectivity

Distance and the number of dams may influence the ability of juvenile salmon to move in to different habitat types. We measured physical connectivity among sites relative to the active channel network from the Quickbird satellite imagery (as described above) using five metrics: 1) upstream aquatic distance along the shortest flow path from the site to the main channel, 2) downstream distance of the shortest flow path, 3) perpendicular distance (closest straight line distance to the main channel), 4) number of upstream dams (along the shortest flow path), and 5) number of downstream dams (along the shortest flow path). Juvenile salmon could enter or leave rearing habitats by following aquatic flow paths upstream or downstream of the site (from the main channel), or if overland flooding occurred by moving perpendicularly to access a site.

The effect of pond type on physical connectivity metrics was analyzed using one-way analysis of variance (ANOVA)(PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). Data violating parametric assumptions were transformed or a non-parametric Kruskal Wallis test was performed. Because five comparisons of physical connectivity were made a Bonferroni correction factor was used to determine significance at $P<0.01$ (.05/5).

Hydrological Connectivity

The hydrological connectivity of habitats to the main channel may influence juvenile salmon movement because some habitats may constitute a sink or trap as the hydrology of the channel-floodplain system varies in relation to discharge. We monitored changes in site stage height relative to changes in the main channel with HOBO pressure transducer data loggers (Onset, Pocasset, Massachusetts; www.onsetcomp.com). Loggers were anchored on the bed in 13 of the study sites (2 main channel, 2 spring brook, 4 early-successional, 3 mid-successional, and 2 late-successional ponds). Year-round hourly changes in habitat stage height were determined from pressure data and accuracy was checked by coherence of logger data with visual measurements on staff gauges. Though water depth data spanned from 2006 to 2011, data were only available for every logger between 10/17/07-12/14/07 and 5/14/08-9/27/08 and these data were used for water fluctuation analyses.

Synchrony analysis was used to assess the seasonal patterns in beaver pond hydro-dynamics in relation to the river. Temporal coherence, or synchrony, measures the similarity between a pair of sampling sites (e.g., Soranno et al. 1999, Kling et al. 2000, Karaus et al. 2005, Patoine and Leavitt 2006). Synchrony was calculated as the Pearson product-moment correlation coefficient (r) between time series of data for each site paired with the main channel (sites responding similarly to the main channel will have high values, close to 1). To avoid bias from differences in ranges of water level fluctuations all time-series data were Z-transformed to standardize variances (Rusak et al. 1999). Plots of daily fluctuations and normalized depth plots were used to visually investigate patterns in water level fluctuations.

Juvenile Salmon Movement

We conducted an elastomer tagging study from 2009-2011to measure if juvenile salmon could move past beaver dams. Nine of the sixteen beaver complexes (described above) were sampled for the movement study because they contained at least 2 (and up to 6) adjacent habitats separated by dams (either multiple ponds, or early-successional pond/s and a beaver-influenced spring brook), for a total of 32 discrete sampling habitats. Salmon 55mm and larger were implanted with visual implant elastomer (VIE) tags (Northwest Marine Technology, Shaw Island, Washington; www.nmt.us) in the caudal and anal fins to allow recognition of tagged individuals moving between discrete habitat units each month. VIE tags have been applied to a wide variety of small fish without compromising their growth, survival or behavior (Bailey et al. 1998, Hale and Gray 1998, Garcia et al. 2004, Walsh and Winkelman 2004, Kano et al. 2006). Movement rates were calculated as a percentage (the number of fish that moved from one habitat to another/the total number tagged in the original habitat).

RESULTS

Spatial and Temporal Habitat Composition

Spatial Habitat Composition

Eighty-seven and a half percent of the entire off-channel aquatic habitat was comprised of ponds and beaver-influenced spring brooks in 2011 (FIGURES

Figure 1.**1**). Mid- and late-successional pond habitats made up the majority of off-channel habitats (38% and 27%, respectively), with early-successional ponds making up the next largest portion (15%, FIGURES

Figure 1.**1**). Spring brooks made up 11% of the total off-channel habitat but half of them were located downstream of beaver dams (i.e., beaver-influenced, FIGURES

Figure 1.**1**). The smallest portion included parafluvial ponds (0.9%, see Crete 2012) and backwaters (1.5%). Beaver-free and beaver-influenced spring brooks and early-successional beaver ponds were located in the parafluvial zone, while mid- and late-successional ponds were located farther from the main channel in the active and passive orthofluvial zones (

Figure 1.**3**).

Temporal Habitat Composition

Over almost a decade there was little temporal variation in the total amount of beaver modified habitat. The percent of off-channel habitat modified by beavers generally increased with 70.9% dammed in 2004, 81.7% in 2008, and 80.2% in 2011(**Error! Reference source not found.**). The total number of dams in the study reach was 369 in 2004, 414 in 2008, and 373 in 2011. However, some of these differences could be due to variation in imagery leaf cover or discharge between years (August 2004 vs. October 2008).

From 2004-2008 7.8% of all off-channel aquatic habitats changed (i.e. new spring brooks formed, new dams were built, spring brooks were restored, etc; Table 1.2.1). The damming of existing spring brooks (i.e. brooks free flowing in 2004, but dammed by 2008; 3.42 ha, 64%), followed by the formation of new spring brooks (1.4 ha, 25%) made up most of the change. Dammed spring brooks blowing out (0.3 ha, 6%) and newly formed spring brooks being dammed (0.2 ha, 5%) contributed much less to habitat change. From 2008-2011 slightly less of the total off-channel aquatic habitat changed (5.1%, Table 1.2.1). During this period the dominant habitat change (40%, 1.6ha) was caused by the restoration of dammed spring brooks (i.e. dams blew out); but, almost as much habitat change (1.2 ha) was composed of existing and newly formed spring brooks being dammed (0.6ha, 15% and 0.6ha, 14%, respectively). Despite these dynamics, there was little cumulative change in total amount of each habitat type over time. Between 2004 and 2011 channel avulsions occurred in the study reach altering the path of the main channel predominantly within the parafluvial zone, with little change occurring in the orthofluvial zone (see

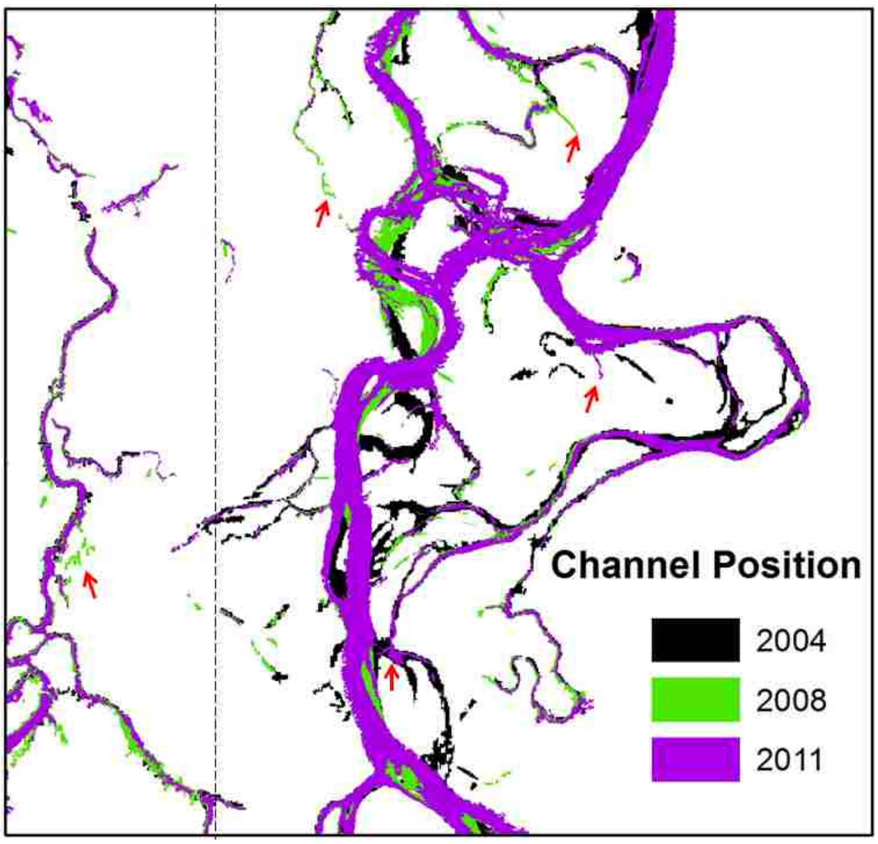


Figure 1.**4**).

Habitat Characteristics

Physical Characteristics

Habitat characteristics were similar among different stages of ponds, suggesting that all types of ponds should be equally suitable for juvenile salmon. The NMDS ordination of seven site characteristics yielded a solution that represented 98.5% of the total variation among sites on 2 axes, but ponds in different habitat categories (early-, mid-, and late-successional ponds) were not significantly separated in habitat space (MRPP, *A* = -0.0642, *P* = 0.7718). Habitat characteristics were also similar among the two types of spring brooks, with the NMDS yielding a solution that represented 93.9% of the total variation among sites on 1 axis and no separation of spring brook type in habitat space (MRPP, $A = -0.0096$, $P = 0.4666$).

Temperature

The presence of ponds and spring brooks provided a wide range of thermal habitats for aquatic organisms with temperatures between 4ºC and 15ºC available on the floodplain during a given day during the ice free period. Over the course of one year there was a marginally significant difference in degree days between successional stages of beaver ponds, with early-successional ponds generally being warmer than mid- and late-successional ponds (734 ± 56 vs. 581 ± 141 and 607 ± 153 DD, respectively; $F_{2,12} = 3.233$, $P = 0.0753$). However, there was no difference in growing degree days by spring brook type for a portion of the year (274 ± 36 vs. 304 ± 57 DD, respectively; $t = 2.776$, $P = 0.4860$).

Macroinvertebrate and Fish Composition

Macroinvertebrates

Assemblage composition of macroinvertebrates differed across habitat types (Figure 1.5). The NMDS ordination, based on the relative abundances of 35 taxa groups, yielded a solution that represented 90.4% of the total variation among sites on 2 axes (Figure 1.5). Sites in different habitat categories were significantly separated in community ordination space (MRPP, $A = 0.231$, $P = 0.0005$), with beaver ponds being significantly different than spring brooks ($P < 0.029$). There was no significant difference among types of beaver ponds ($P > 0.217$) or among types of spring brooks ($P = 0.347$), though there was some separation in species space by spring brook type (see

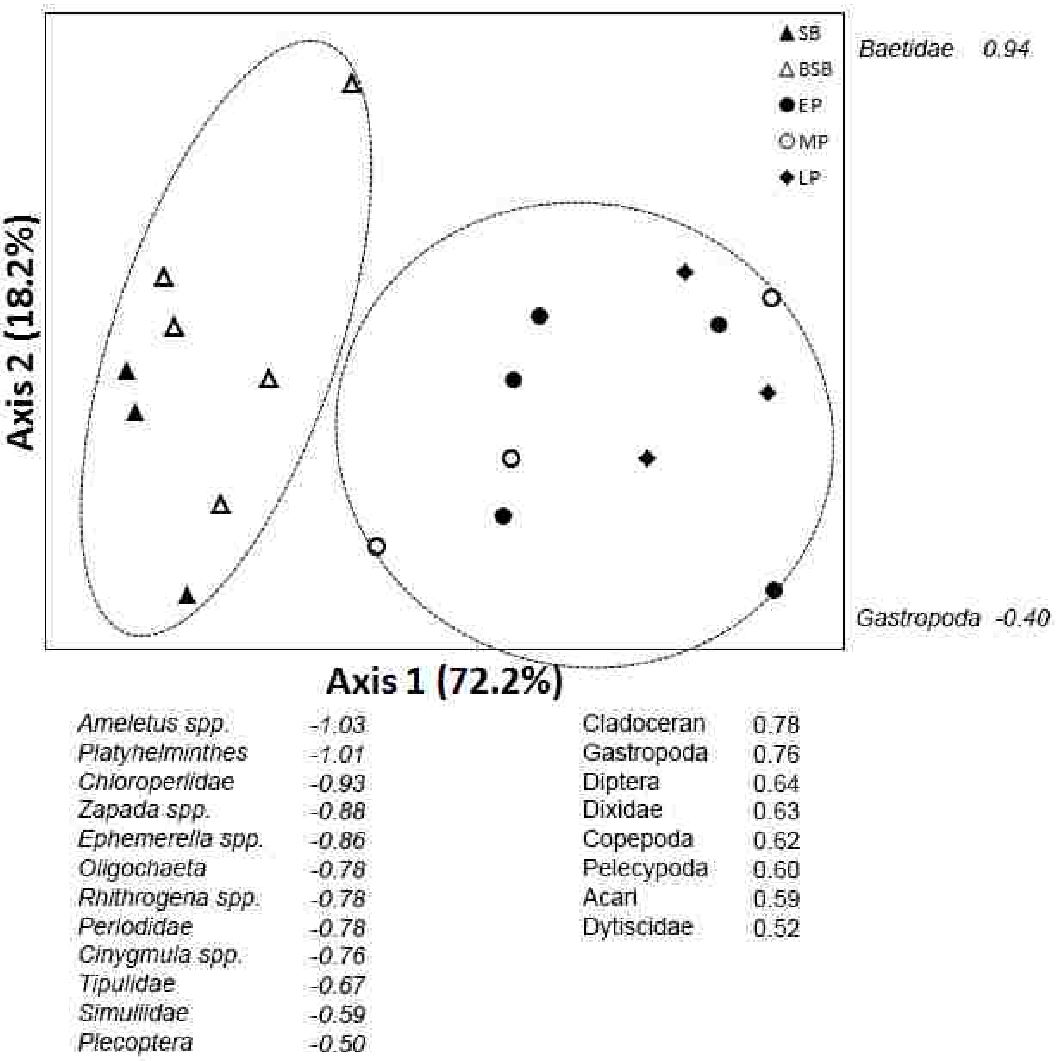
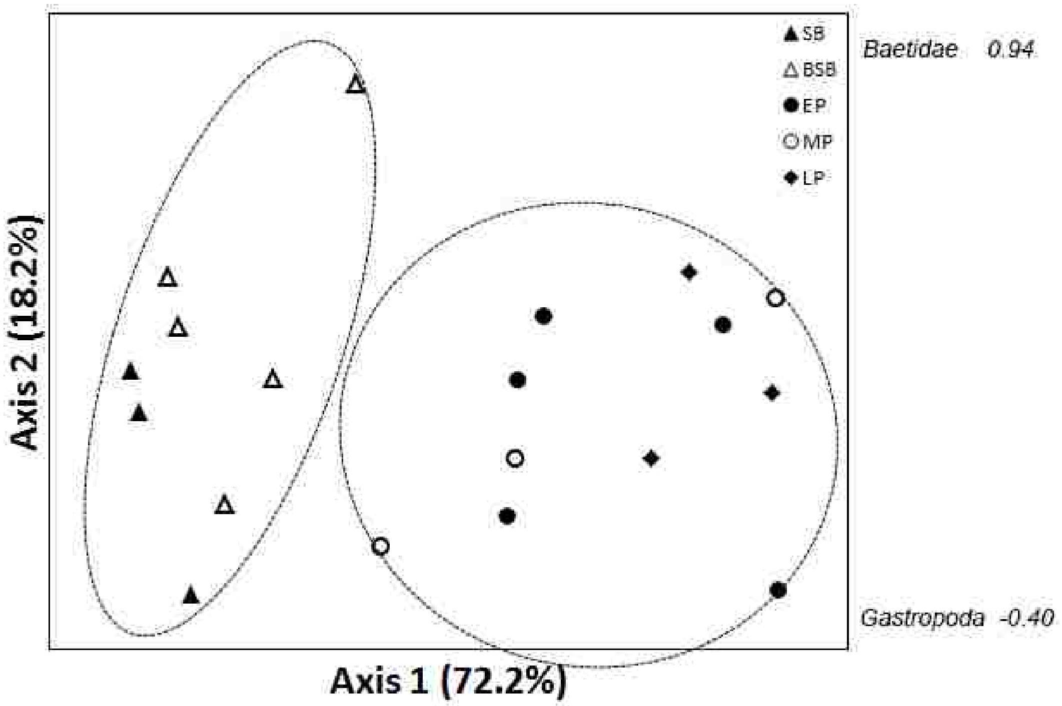


Figure 1.5). Habitat types most strongly separated along Axis 1, which explained 72.2% of the variation in assemblage structure. Larval stoneflies and mayflies, *Platyhelminthes*, *Oligochaeta, Tipulidae,* and *Simuliidae* (see



Ameletus spp.	-1.03
Platyhelminthes	-1.01
Chloroperlidae	-0.93
Zapada spp.	-0.88
Ephemerella spp.	-0.86
Oligochaeta	-0.78
Rhithrogena spp.	-0.78
Perlodidae	-0.78
Cinygmula spp.	-0.76
Tipulidae	-0.67
Simuliidae	-0.59
Plecoptera	-0.50

Cladoceran	0.78
Gastropoda	0.76
Diptera	0.64
Dixidae	0.63
Copepoda	0.62
Pelecypoda	0.60
Acari	0.59
Dytiscidae	0.52

Figure 1.5 for correlation values) were more predominant in spring brook habitats than in beaver ponds. Small crustaceans, *Gastropods*, *Diptera*, *Pelecypoda*, *Acari*, and *Dytiscidae* had higher relative abundances in beaver ponds than in spring brooks.

Fish

Fish species composition varied by habitat type (

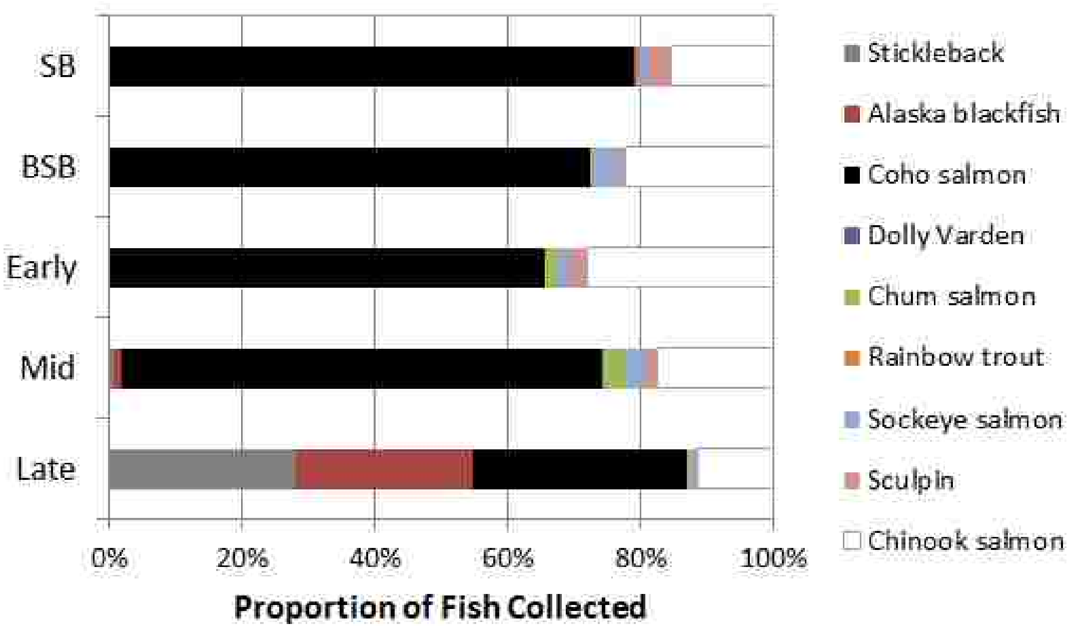


Figure 1.**6**). Coho (*O. kisutch*) salmon were dominant in both types of spring brooks and early- and mid-successional ponds (65-79%), while Chinook (*O. tshawytscha*) salmon were found in the greatest proportions in early-successional ponds (28%), followed by beaver-influenced spring brooks (22%). Late-successional ponds had greater proportions of Alaska blackfish (*Dallia pectoralis*, 27%) and Ninespine stickleback (*Pungitius pungitius*, 28%) compared to all other habitats (0-1%). Total species richness and salmon richness varied significantly by habitat type ($F_{[4,26]} = 5.11$, $P = 0.0036$ and $F_{[4,26]} = 6.99$, $P = 0.0006$). Both types of spring brooks and early-successional ponds had 2x the total fish species as late-successional ponds (7 ± 0, 6.4 ± 1.7, 6.3 ± 1.6 vs. 3 ± 1.2;

Tukey's HSD, *P* < 0.0339). Spring brooks, early-, and mid-successional ponds had significantly more salmon species then late-successional ponds (4.3 ± 0.6, 4.1 ± 1.0, 3.9 ± 1.0, 3.3 ± 1.0 vs. 1.3 ± 1.5; Tukey's HSD, *P* < 0.0035).

Densities of juvenile salmon varied strongly by habitat type ($F_{[4,17]} = 15.23$, *P* < 0.0001;

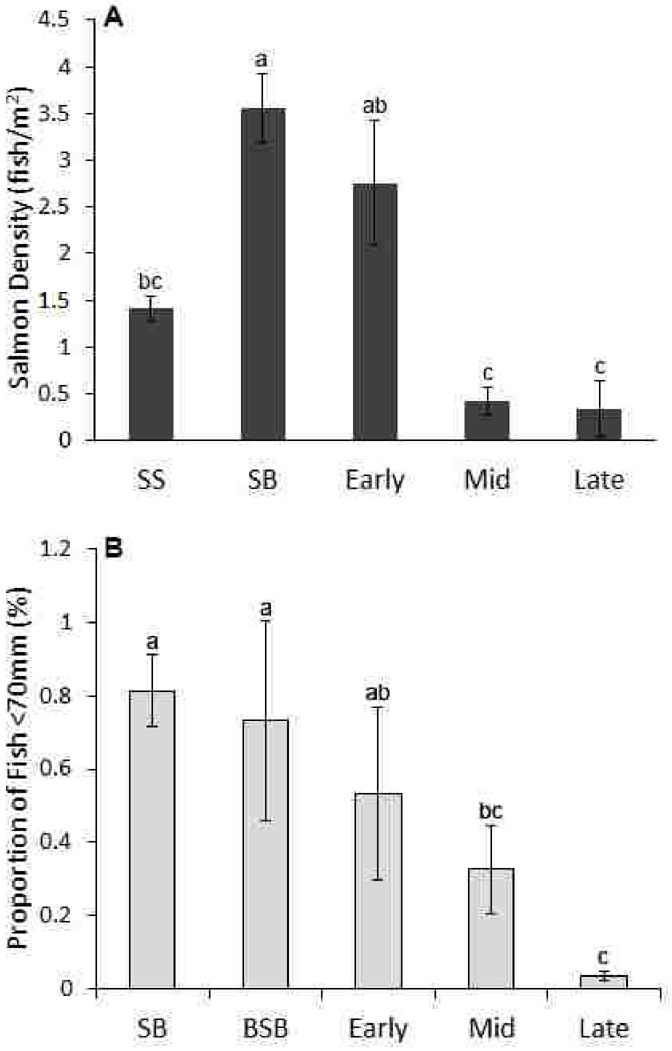


Figure 1.7A). Spring brooks and early-successional ponds had higher juvenile salmon densities than mid- and late-successional ponds (Tukey's HSD, $P < 0.0044$). Spring brooks had significantly higher densities and early-successional ponds had marginally higher densities than main channel habitats (Tukey's HSD, $P = 0.0015$ and $P = 0.0794$, respectively). The percentage of young-of-the-year (YOY, fish less than 70mm) also varied by habitat type (

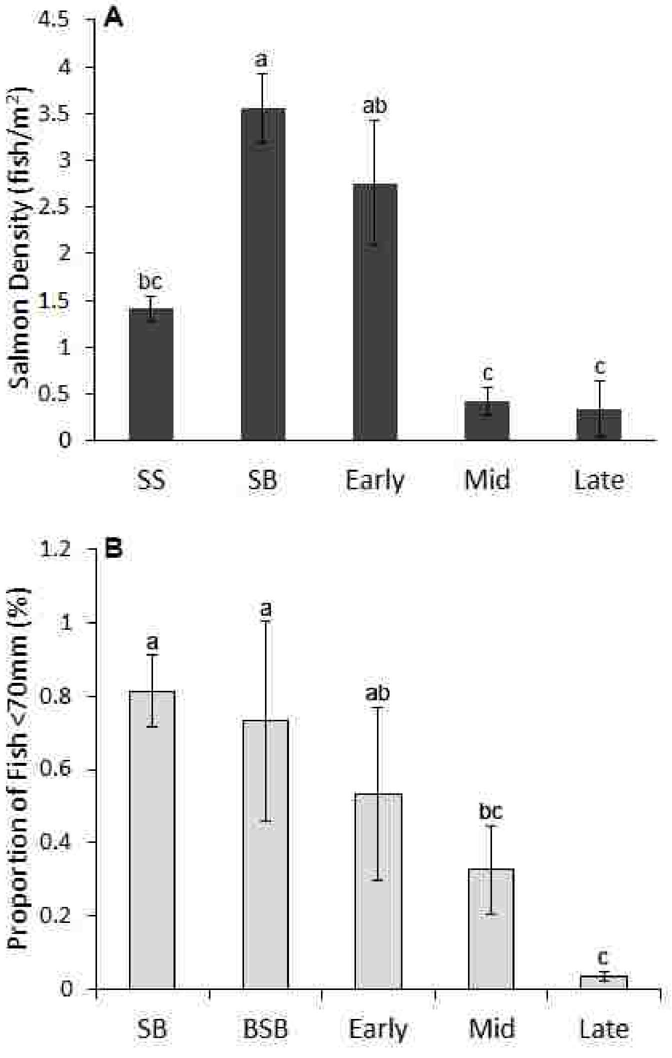
A
Salmon Density (fish/m²)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
bc
a
ab
c
c
SS
SB
Early
Mid
Late
B
Proportion of Fish <70mm (%)
1.2
1
0.8
0.6
0.4
0.2
0
a
a
ab
bc
c
SB
BSB
Early
Mid
Late

Figure 1.7B; $F_{[4,23]} = 11.56$, $P < 0.0001$). Spring brooks had higher proportions than mid- and late-successional ponds (Tukey's HSD, $P \leq 0.0224$) and early-successional ponds had higher proportions than late-successional ponds (Tukey's HSD, $P = 0.0006$).

The condition of juvenile coho and Chinook was highly variable by habitat type and over time, but there was no significant difference in mean condition of coho or Chinook by habitat type for the entire season ($F < 0.8395$, $P > 0.5171$). However, coho in late-successional ponds and spring brooks did exhibit the largest drop in condition by September.

Connectivity and Movement

Physical Connectivity

The length of pathways that juvenile salmon could follow to enter and rear in sites varied significantly by habitat type ($F_{[2,14]} > 11.04$, $P < 0.0013$). Both mid- and late-successional ponds were marginally farther from the main channel in the upstream direction than early-successional ponds (Tukey's HSD, $P < 0.0362$). Late-successional ponds were significantly farther from the main channel than both early- and mid-successional ponds in the downstream direction (Tukey's HSD, $P < 0.0109$). There was also a significant difference in the number of dams present between sites and main channel in the downstream direction ($\chi^2_{[2, N = 14]}$, $P = 0.0041$) and a marginally significant difference in the number of dams between sites and the main channel in the upstream direction ($\chi^2_{[2, N = 14]}$, $P = 0.0219$).

Hydrological Connectivity

Synchrony values varied by habitat type and with distance of the site from the main channel (

Figure 1.8). Spring brooks and early-successional ponds consistently had higher synchrony values (0.53 ± 0.13 and 0.54 ± 0.14), compared to mid- and late-successional ponds which exhibited high variation (0.17 ± 0.57 and 0.21 ± 0.72). For spring brooks and early-successional ponds, synchrony values generally declined with increasing distance (along the shortest upstream aquatic flow path) to the main channel; mid- and late-successional sites were more variable (

Figure 1.8).

Differences in synchrony were reflected in daily water level fluctuations (

Figure 1.**9**). Spring brook depth tracked fluctuations in the main channel most closely, except for two peak events which may have been caused by avulsions or the formation of debris jams (

Figure 1.**9**A). In comparison, all beaver ponds exhibited multiple depth changes that were greater in magnitude than changes in the main channel (

Figure 1.**9**B-D). These fluctuations were likely due to water retention by the dams during flood events and subsequent dam repair and building activities by beavers. Cumulative water-level change (sum of the absolute values of depth changes recorded each hour) ranged from 8.6 to 12.6m for pond habitats and from 12.8 to 12.9m for spring brooks, as

compared to 18.2m for the main channel of the river (Figure 1.10), showing that beaver dams in flood channels buffered flow dynamics compared to the main channel.

Normalized depth plots illustrate differences in flood pulse response by habitat type and floodplain position (Figure 1.11). Main channel sites exhibited fast inclines and declines in depth as flood waters pulsed through the system and were closely tracked by rising and falling limbs in spring brook habitats (MS, SS, BS in blue, Figure 1.11A&B). In contrast, the ponding behind beaver dams prolonged the flood pulse (Figure 1.11C&D). Early-successional ponds responded faster and more strongly to the flood pulse than mid- and late-successional ponds, illustrating a greater degree of connectivity to the main channel. Additionally, floodplain position influences flood response. Note in particular in Figure 1.11A that the flood wave passing through the upstream main river site (KC) lagged 1-2 days behind the flood wave for the downstream most site (WK). This illustrates a fact common to alluvial floodplains but one that is infrequently documented: downstream areas of the floodplain flood before upstream areas. This apparently occurs because the expansive alluvial aquifers are typically losing channels at the upstream end and gaining channels on the downstream end, hence the floodplain subsurface has to fill to capacity before overland flooding can occur (except perhaps in very sudden spates, see Helton et al. 2012). This phenomenon is enhanced on the Kwethluk owing to the beaver ponds that impound nearly all of the flood channels.

Movement

The only movement of juvenile salmon past dams was detected in early-successional pond complexes. No tagged salmon were detected moving past dams in mid-successional pond complexes and too few salmon were present in late-successional ponds to tag. Within the early-successional complexes we documented almost no movements past beaver dams when the river remained near base flow. Only 3 out of 8229 (0.04%) elastomer tagged individuals moved between ponds and spring brooks and this was detected following the one minor flood event. Very low movement rates of individuals between separate beaver ponds within the same complexes occurred at the same time (i.e. past dams, 0.12%, from 8 coho and 2 Chinook). During this time we did detect slightly higher movement rates between unique spring brooks within a complex where no dams blocked potential movements (0.4%, 39/1020 coho and Chinook). During baseflow ponds were discrete units (the white boundary in

Figure 1.12) but at high flows there were many potential paths for fish to leave or enter ponds (arrows in

Figure 1.12). During a season with multiple flood events we detected higher movement rates, suggesting that flooding mediates movement in and out of beaver ponds.

Prior to large floods we documented 25 out of 1762 marked individuals moving (1.4%; 15 fish from ponds into spring brooks and 10 from spring brooks into ponds). Following flooding we documented an additional 95 fish (of 5102, 1.9%) move between habitat types. Fish “escaped” beaver ponds (49), but a surprising number of fish (46) moved in the opposite direction, upstream from spring brooks into ponds. It is likely that movement rates were even higher (we couldn’t sample every pathway). Despite the ability of salmon to leave beaver ponds during flooding many fish stayed in the ponds to overwinter. Recapture rates during the flood ranged between 16-35% in August and remained as high as 22% (range: 1-22%) in beaver ponds in September.

DISCUSSION

By modifying the physical connectivity and hydrological dynamics of floodplain habitats beavers have the potential to strongly influence juvenile salmon populations. Beaver ponds are characteristically different habitats than lotic streams and spring brooks (Naiman et al. 1988) and the presence of ponds introduces a fundamentally different habitat type for use by juvenile salmon. Beaver modified habitats occupied eighty-seven percent of all aquatic off-channel area on the Kwethluk River floodplain. Modified habitat included beaver-influenced spring brooks, and early-, mid-, and late-successional beaver ponds. Despite the presence of different types of ponds, habitat characteristics of all ponds were very comparable; suggesting all provided similar quality rearing habitats. However, different successional stages of ponds varied from each other and from spring brooks in their hydrological and physical connectivity to the main channel. Reduced connectivity to late-successional pond habitat resulted in a large portion of the floodplain having very low densities of juvenile salmon (and often no salmon at all). By reducing connectivity to a large portion of the off-channel floodplain habitat, the presence of beaver ponds and dams strongly influenced the habitat use and distribution of juvenile salmon.

We documented little temporal change in the total amount of habitat influenced by beavers, but the location of individual spring brooks and ponds did shift, especially in the parafluvial zone. Hence beavers are influencing shift component of the SHM (sensu Stanford et al. 2005). Approximately 6% of the parafluvial zone actively shifted in spring brook location due to flood driven processes that blew out beaver dams and created new spring brooks for beavers to dam. However, little change occurred in the orthofluvial zone (see

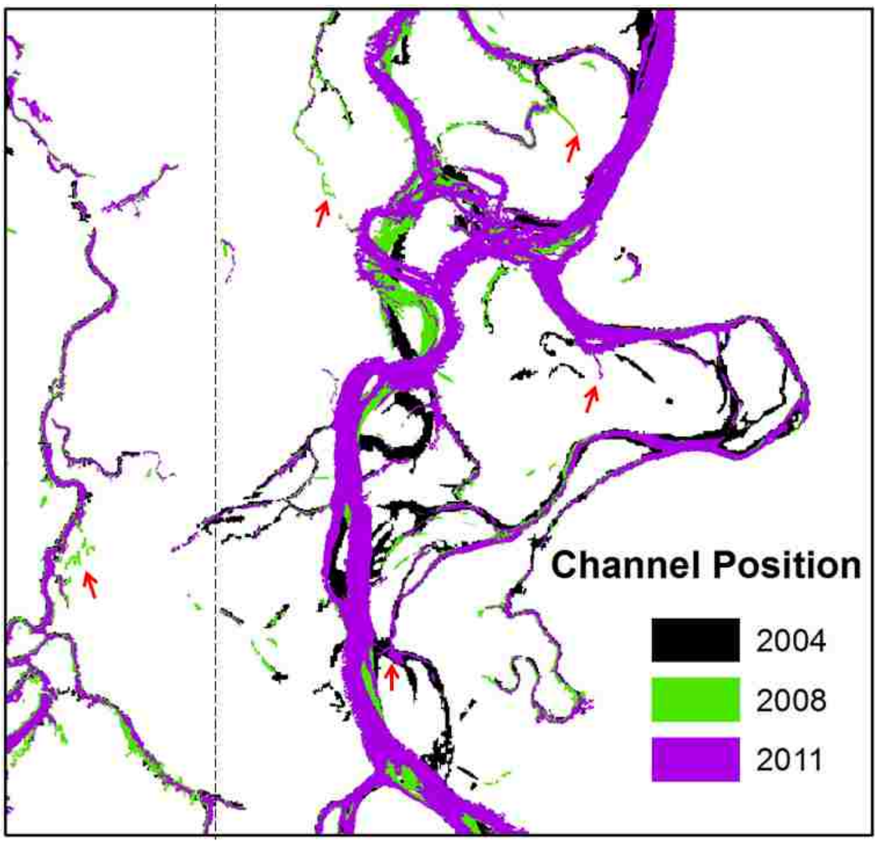


Figure 1.**4**), compared to the documented channel avulsions in the main channel and parafluvial zone. If beavers act to confine the main channel over time as suggested by Rutten (1967), then the levee effect of extensive dam complexes would decrease lateral connectivity in large floodplains and potentially increase channel incisement. This effect could reduce the power of flood waters across the floodplain and potentially confine the erosive power of the main channel network within the parafluvial zone. Reducing the river's ability to avulse and cut through new sections of the floodplain could be a positive feedback mechanism promoting additional development of late-successional beaver complexes and late successional species like *P. glauca*. Indeed, Mouw et al. (2012) found that ~65% of the Kwethluk floodplain area was comprised of *P. balsamifera* galleries and *P. glauca* forest. Due to long-term beaver habitat modification, the Kwethluk floodplain

is dramatically changed from what we would predict it would look like just based on the SHM, with beaver ponds making up a majority of the off-channel habitat (

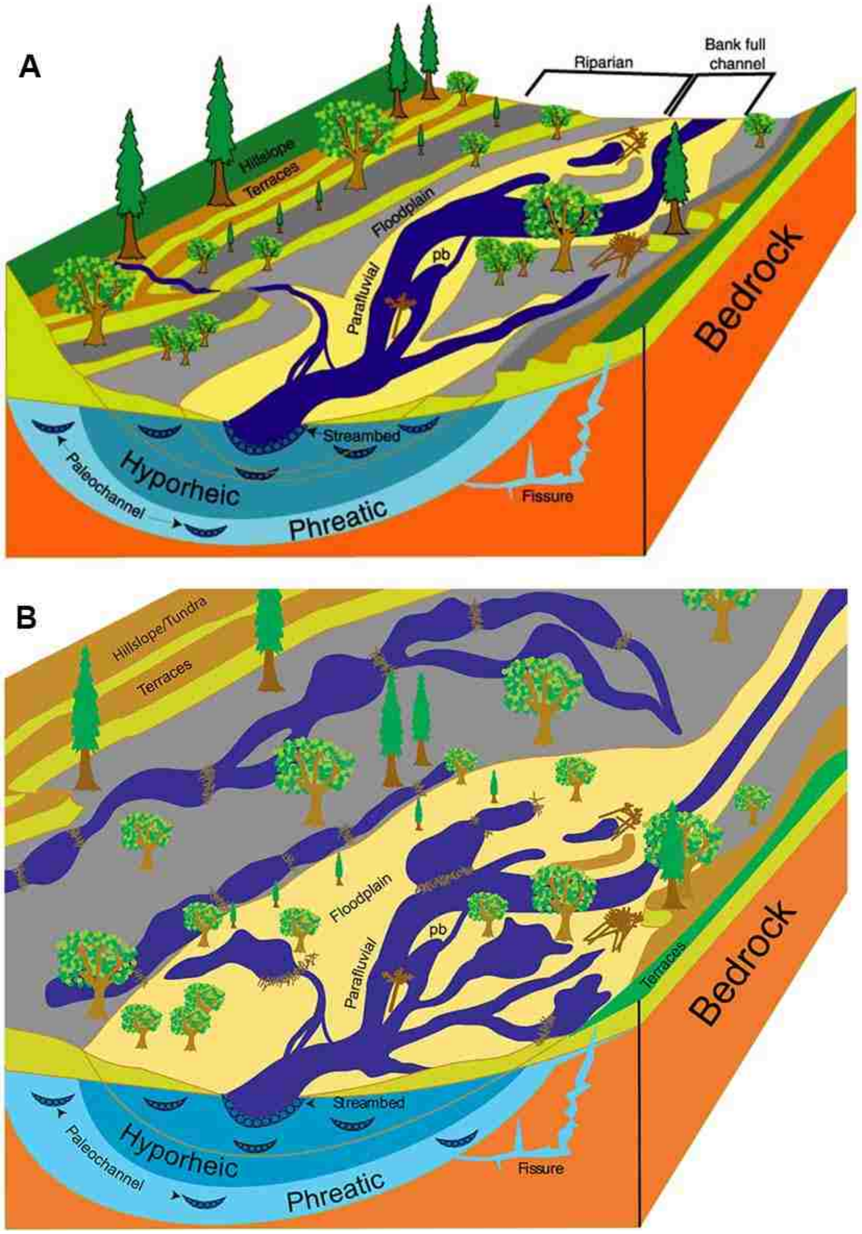


Figure 1.**13**A&B).

By changing the types and availability of freshwater rearing habitats, beavers have the ability to strongly influence the distribution of juvenile salmon on the floodplain. Both total fish and salmonid species richness was lower in mid- and late-successional ponds as compared to early-successional ponds and spring brooks.

Furthermore, densities of juvenile salmon were lowest in late-successional ponds in the passive orthofluvial zone, illustrating the fact that habitat connectivity influences juvenile salmon distributions. In addition to altering juvenile salmon distributions in general, we also observed differences in the distribution of individual salmon species. As expected, higher proportions of coho occurred in early-successional ponds and spring brooks. Coho fry are typically found in pools and off-channel habitats, including beaver ponds (Sedell et al. 1984, Murphy et al. 1989, Swales and Levings 1989, Leidholt Bruner et al. 1992). More surprisingly, we also found higher proportions of Chinook salmon in some beaver ponds, including age 1+ Chinook (up to 107mm, *R.M. personal observation*), despite the fact that Chinook generally occupy different habitat types than Coho (i.e. river vs. off-channel habitats, Stein et al. 1972, Murphy et al. 1989). The presence of ponds may be influencing the life history of Chinook, resulting in some Chinook rearing in freshwater for longer than the typical 0-1 summers (Quinn 2005).

Altered physical connectivity of off-channel habitats is a likely mechanism explaining juvenile salmon distributions on the floodplain. Beavers can be detrimental to fish populations by blocking fish movements (Schlosser and Kallemeyn 2000, Mitchell and Cunjak 2007). It is clear from our work that while some habitats behind dams are not utilized (late-successional ponds), others are strongly used by juvenile salmon (early-successional ponds). The early-successional complexes, where juvenile salmon densities were higher, were located within the parafluvial zone and only had one to a few dams present between the sites and main channel. In contrast, the mid- and late-successional ponds in which we detected lower densities (or no salmon) were typically located farther away from the main channel behind multiple dams. Understanding whether or not juvenile salmon can move in and out of different off-channel floodplain habitats is important for three reasons: 1) Inaccessible habitats may be effectively removed from salmon production, 2) If juvenile salmon aren't able to leave ponds after accessing them, they will never contribute to the population, and 3) When conducting studies, if juvenile salmon move between habitats too much, then measured responses may not be habitat specific. It is clear that juvenile salmon can pass beaver dams to enter early-successional ponds and rear (because adult salmon do not spawn in the ponds), but late-successional ponds may have too many dams blocking fish passage for these habitats to be used for rearing.

Variation in the hydrological connectivity of different habitats will determine if juvenile salmon are able to pass over dams and rear in different portions of the floodplain. Spring brooks and early-successional ponds exhibited higher synchrony with the main channel compared to mid- and late-successional ponds which were much more variable. This reflects the fact that spring brooks and early-successional ponds were more strongly connected to the main channel, quickly becoming inundated during flooding. We expected that synchrony would be lower for mid- and late-successional ponds because of their location in the orthofluvial zone. However, these sites exhibited both high and low synchrony values, which was likely due to variation in site position relative to the main channel and beaver activity. For example, the mid-successional site with the highest synchrony value (CB, 0.76,

Figure 1.8) was located below a bend of the main river, while the mid-successional site with a negative synchrony value (TC, -0.40) was located downstream of a tundra tributary and had a very active beaver (that was observed repairing and rebuilding the dam on multiple occasions). By repairing and building dams beavers are able to raise pond levels even as the main channel drops and these activities seem to be reflected in patterns of daily water level fluctuations and normalized depth plots for the ponds (

Figure 1.**9** and Figure 1.11). Beaver dams also hold back and slowly release water following the time when the river and spring brooks have already receded (see

Figure 1.**9** and Figure 1.11) which may increase viability as potential juvenile salmon rearing habitat over spring brooks that would dry up without the ponds and pond maintenance by the beavers. Water storage varied with pond type and location, creating a dynamic template of water levels that could influence the amount of habitat available for juvenile salmon rearing and site accessibility (for example when ponds are inundated upstream pathways are present for fish movement, see

Figure 1.12). The storage of more water in the floodplain through summer and in to the winter could also have important consequences for over-winter habitat for aquatic organisms (Malison 2013).

The movement of juvenile salmon past dams varied based on habitat type and was mediated by flooding. Reflecting their higher connectivity with the main channel, early-successional ponds tended to fill even during small flood events, providing more opportunities for juvenile salmon to move into these habitats (

Figure 1.12). We expect that it would take much larger flood events to inundate the floodplain sufficiently for juvenile salmon to utilize late-successional pond habitat. Such large floods might connect late successional ponds, but would have devastating effects on early-successional ponds, most likely removing them entirely from the floodplain. In the case of such a large flood event, late-successional ponds might become survival refuges for both beavers and salmon. Despite the ability of juvenile salmon to enter and rear in early-successional beaver ponds, the movement rates past dams separating early-successional beaver ponds from beaver-influenced spring brooks was extremely low at base flow. We documented the movement of more individuals between ponds and spring brooks in both directions during flood events (when multiple flow paths were possible,

Figure 1.12), which suggests that salmon are not trapped once they enter the ponds (also see Malison 2013), as long as natural flow regimes (including flood events) occur.

By damming significant amounts of off-channel floodplain habitats beavers may impact the production of juvenile salmon. Spring brooks have been shown to be among the most important rearing habitats for juvenile salmon (Eberle and Stanford 2010). In large alluvial rivers, like the Krutogorova (Kamchatka, Russia) that have no beavers, floodplains are very complex with dynamic channels and alluvial spring brooks are full (up to 5 fish per m^2 often including 3 or more salmonid species) of juvenile salmonids throughout the parafluvial and orthofluvial zones (Stanford et al. 2002). In contrast to the Krutogorova, over 80% of the spring brooks in the Kwethluk have been dammed on the floodplain, which may result in portions of off-channel habitat generally being lost to use by juvenile salmon. Though we have shown that juvenile salmon can and do use pond habitats, especially early-successional ponds, it remains unclear as to how this modified landscape might influence the growth, survival and overall production of juvenile salmon on a large alluvial river floodplain. If early-successional ponds stimulate the growth and production of juvenile salmon by reducing competition in larger rearing areas, then the overall impact of beavers on juvenile salmon could be positive. However, if substantial habitat is lost from use in the orthofluvial zone, that would otherwise be full of juvenile salmon (as is the case in the Krutogorova), then the overall influence of beavers on juvenile salmon could be negative (see Malison 2013).

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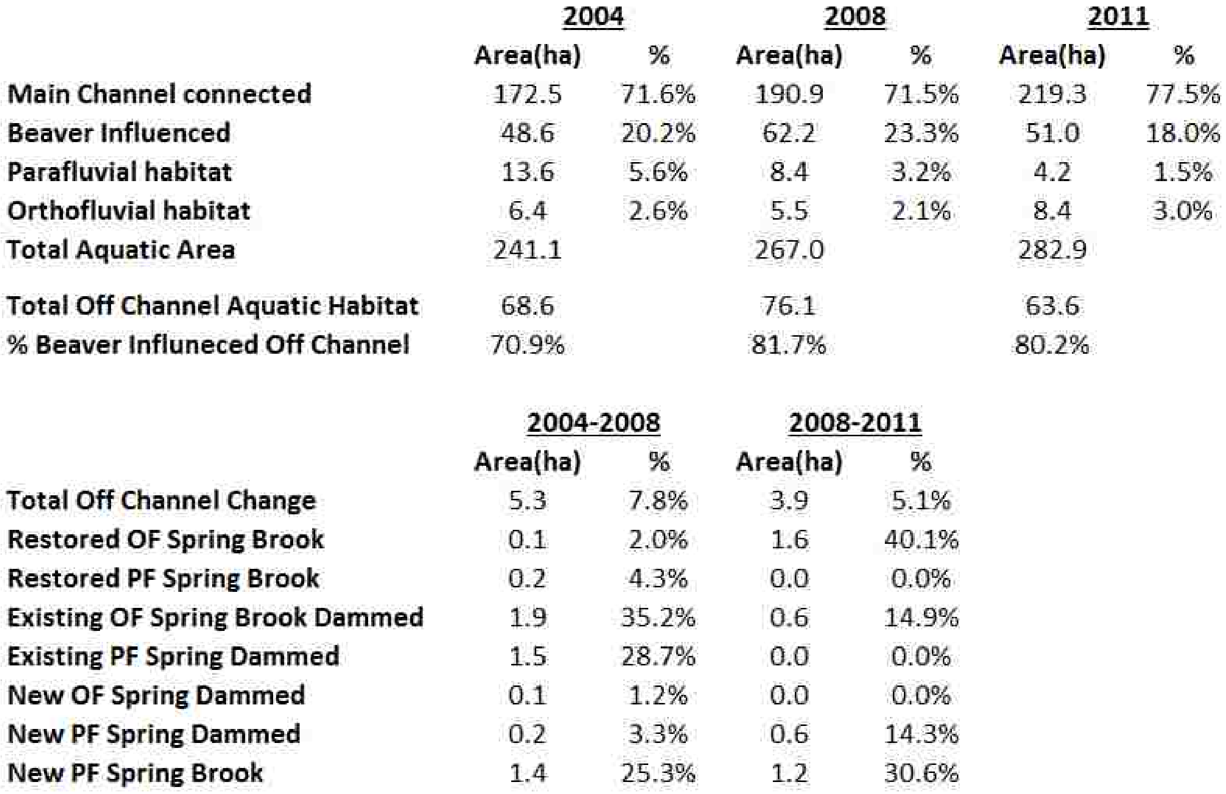
Table 1.2. Area and percent of total for habitats influenced by beavers on the Kwethluk floodplain and analyzed for temporal change based upon classification of multispectral imagery from the Quickbird satellite obtained in August 2004, October 2008, and September 2011.



	2004		2008		2011	
	Area(ha)	%	Area(ha)	%	Area(ha)	%
Main Channel connected	172.5	71.6%	190.9	71.5%	219.3	77.5%
Beaver Influenced	48.6	20.2%	62.2	23.3%	51.0	18.0%
Parafluvial habitat	13.6	5.6%	8.4	3.2%	4.2	1.5%
Orthofluvial habitat	6.4	2.6%	5.5	2.1%	8.4	3.0%
Total Aquatic Area	241.1		267.0		282.9	
Total Off Channel Aquatic Habitat	68.6		76.1		63.6	
% Beaver Influneced Off Channel	70.9%		81.7%		80.2%	

	2004-2008		2008-2011	
	Area(ha)	%	Area(ha)	%
Total Off Channel Change	5.3	7.8%	3.9	5.1%
Restored OF Spring Brook	0.1	2.0%	1.6	40.1%
Restored PF Spring Brook	0.2	4.3%	0.0	0.0%
Existing OF Spring Brook Dammed	1.9	35.2%	0.6	14.9%
Existing PF Spring Dammed	1.5	28.7%	0.0	0.0%
New OF Spring Dammed	0.1	1.2%	0.0	0.0%
New PF Spring Dammed	0.2	3.3%	0.6	14.3%
New PF Spring Brook	1.4	25.3%	1.2	30.6%

FIGURES

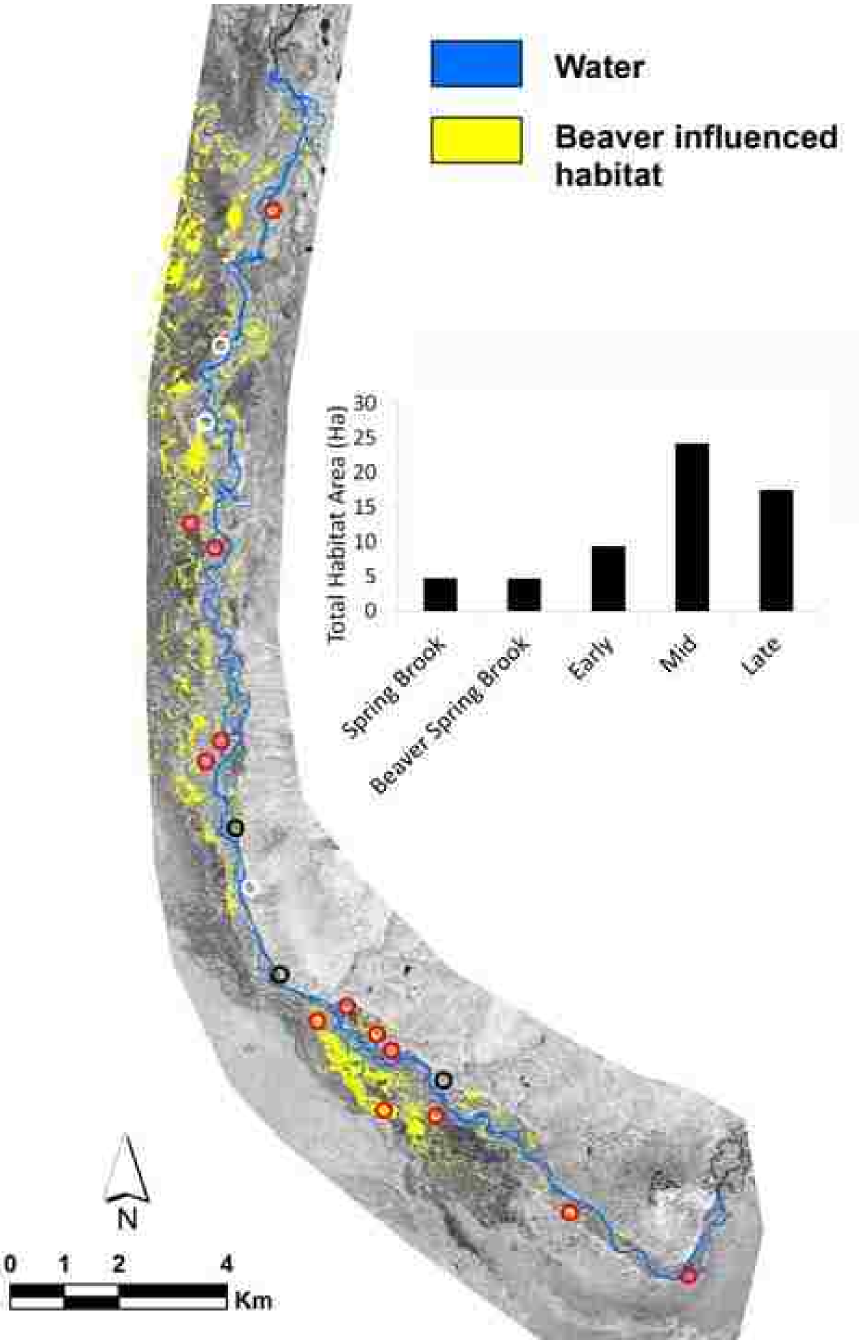


Figure 1.1. The lower floodplain of the Kwethluk River extends approximately 27 km (by air). Beaver modified habitat is highlighted in yellow and the main (base flow) channel network is highlighted in blue. Red circles show location of 13 beaver pond complexes where individual sites (including ponds of 3 successional stages and beaver-influenced spring brooks) described in text were sampled. Black circles show the location of beaver-free spring brooks and white circles show the location of the additional 3 beaver complexes sampled for fish. Inset gives total habitat area (ha) of the 5 primary habitat types in 2011.

Figure 1.2. (A) Aerial view showing the main river (top) and dammed (circled) off-channel habitats. Beaver-free spring brooks (B), beaver-influenced spring brooks (C, with upstream dam), early-successional beaver ponds (D, embedded in willow and alder), mid-successional beaver ponds (E, embedded in meadow), and late-successional beaver ponds (F, embedded in spruce forest) are present on the floodplain. White dots in some pictures are floats attached to minnow traps.

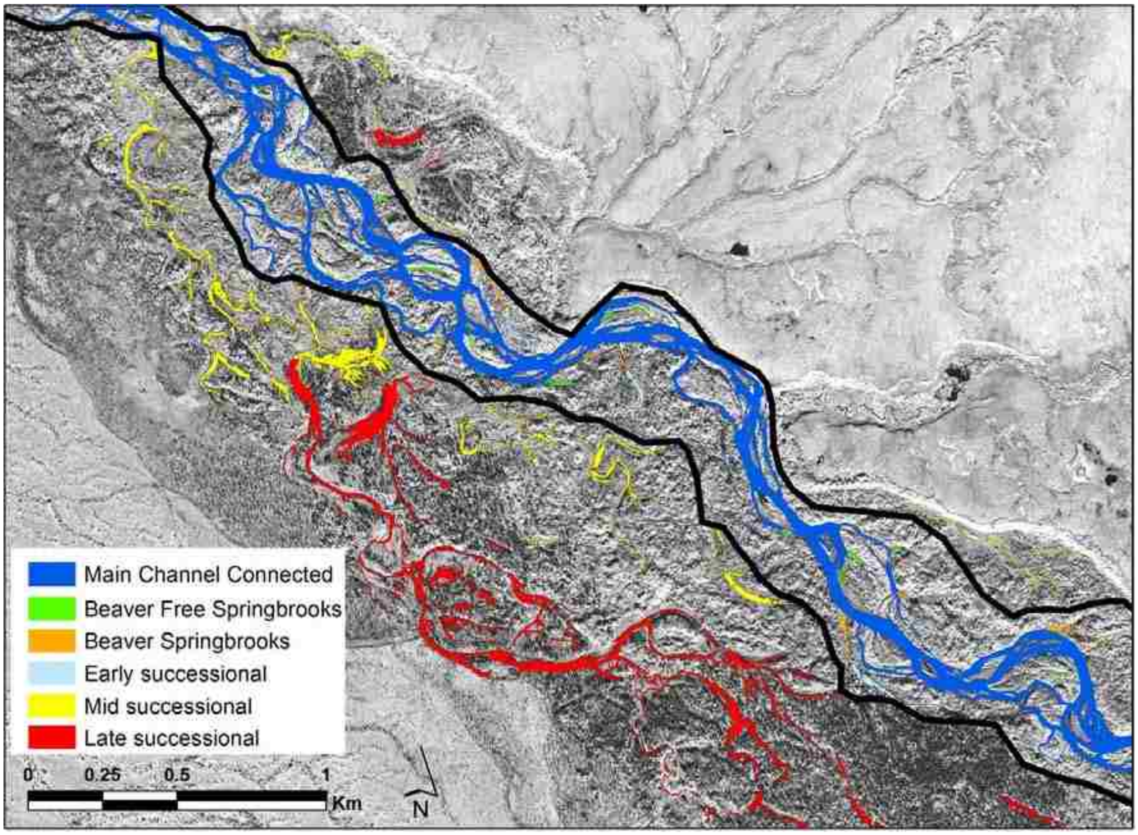


Figure 1.3. Distribution of the predominant off-channel habitats on the Kwethluk River floodplain.

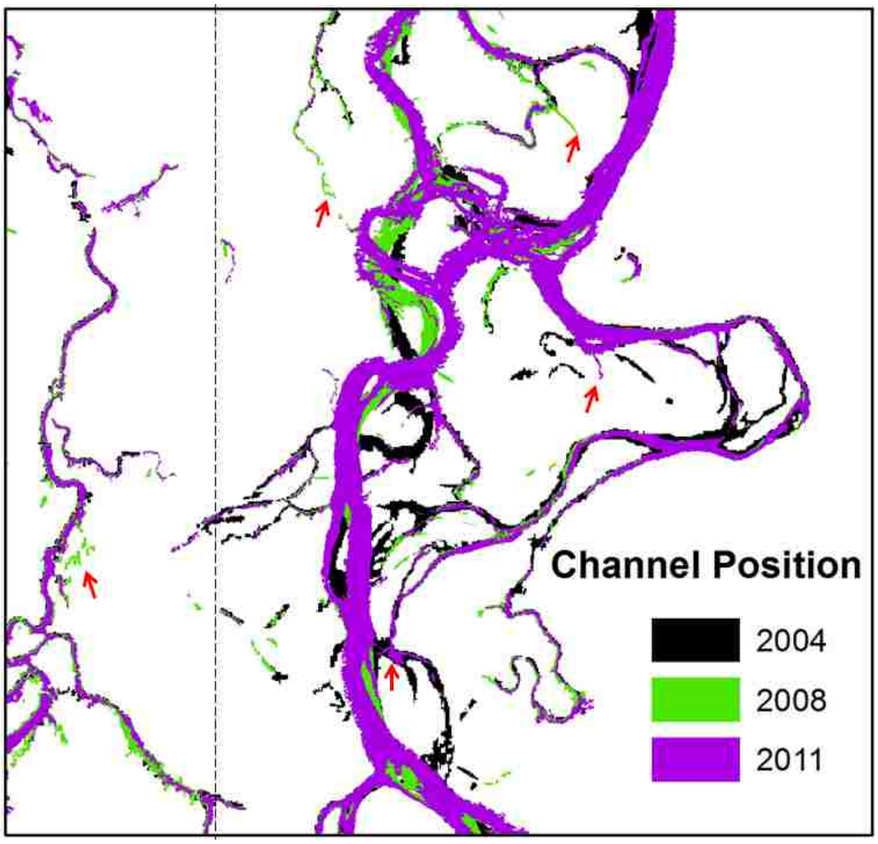


Figure 1.4. Time series of the position of main channel network at base flow, illustrating channel avulsions in the parafluvial zone (right side of dotted line) and formation of new spring brooks at arrows. Only very minor changes occurred in the orthofluvial zone (left side of the dotted line).

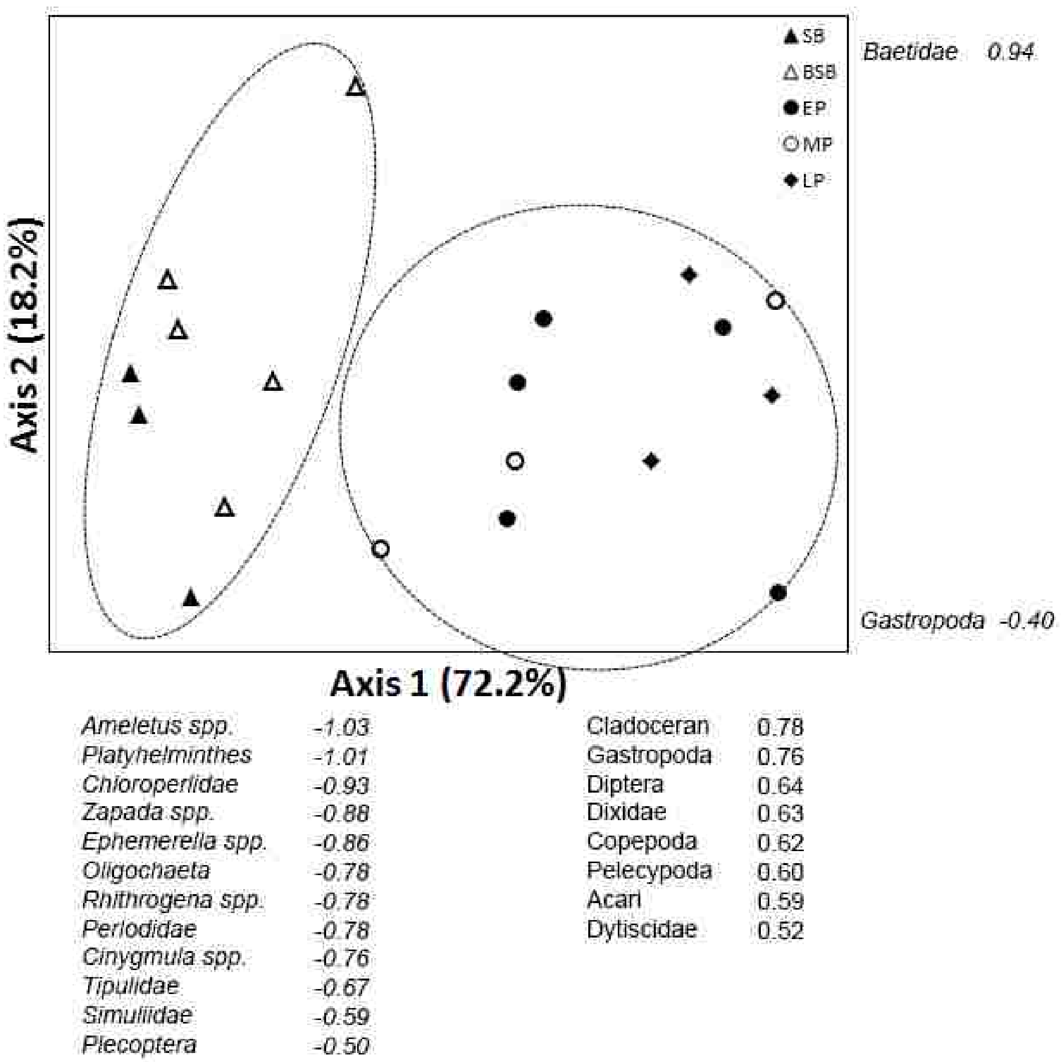


Figure 1.5. Nonmetric multidimensional scaling (NMDS) ordination plot of relative abundance of macroinvertebrates (beaver-free spring brooks: SB, beaver-influenced spring brooks: BSB, early-successional beaver ponds: EP, mid-successional beaver ponds: MP, late-successional beaver ponds: LP). Site position in species ordination space is shown relative to Axis 1 and 2. Circles enclose groups of sites that were significantly different based on multi-response permutation procedure analysis by habitat type: spring brooks and ponds segregated nicely. Data in the plot are mean abundances by site and percent of total variation explained by each axis is given in parentheses. Pearson's correlation coefficients between taxa and the axes are given. Taxa with highest correlation values most strongly drive differences in sites with community space.

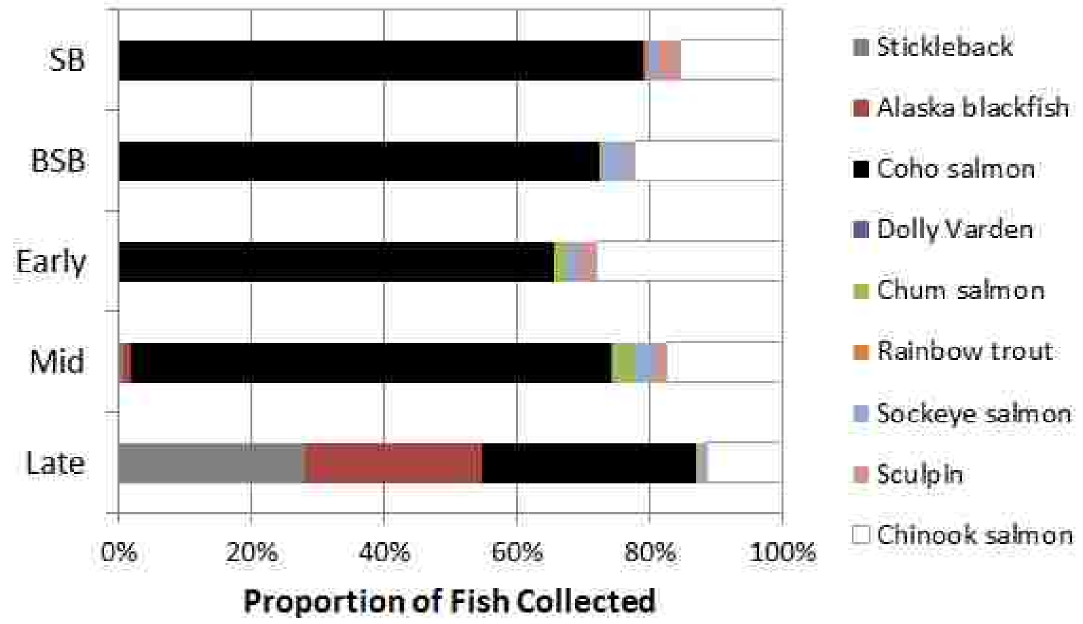


Figure 1.6. Fish species composition by habitat type (SB = beaver-free spring brooks, BSB = beaver-influenced spring brooks and Early, Mid and Late representing successional stage of the beaver ponds sampled). Species included Stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*), Coho salmon *(Oncorhynchus kisutch*), Dolly Varden (*Salvelinus malma*), Chum salmon (*O. keta*), Rainbow trout (*O. mykiss*), Sockeye salmon (*O. nerka*), Slimy sculpin (*Cottus cognatus*), and Chinook salmon *(O. tshawytscha*).

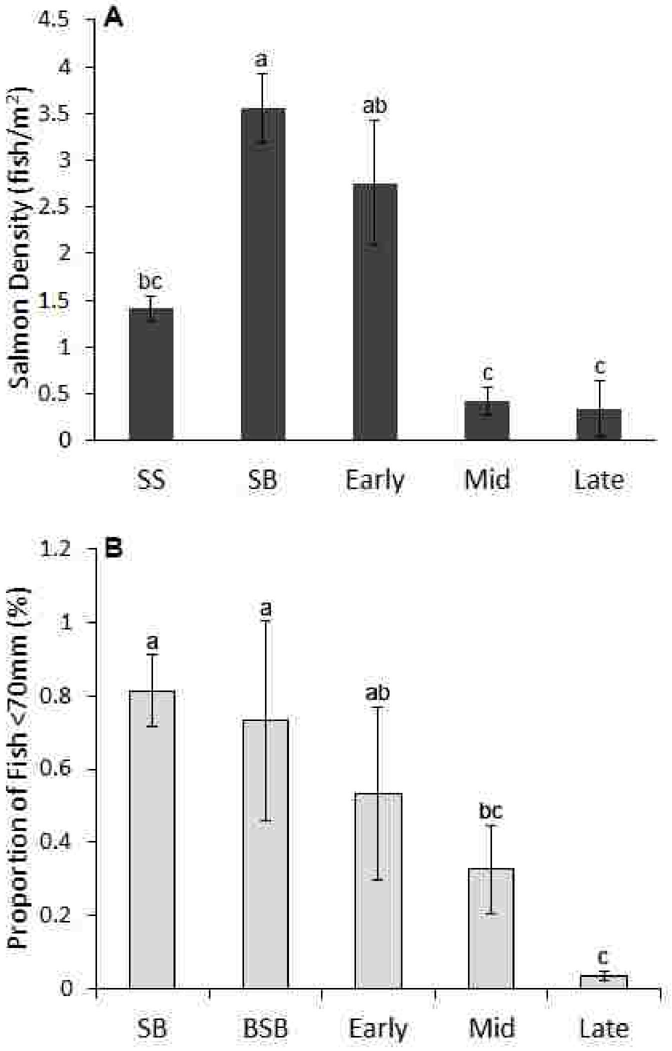


Figure 1.7A&B. A) Mean (±1 SE) juvenile salmon density and B) Proportion coho and Chinook salmon that were young of the year (out of total including all young of the year and age 1+ or 2+) among primary habitat type (SS = main channel shallow shore, SB = beaver-free spring brooks, BSB = beaver-influenced spring brooks and Early, Mid and Late represent successional stage of the beaver ponds sampled). Differences among were determined by one-way analysis of variance and pairwise comparisons using Tukey's honestly significant difference (HSD).

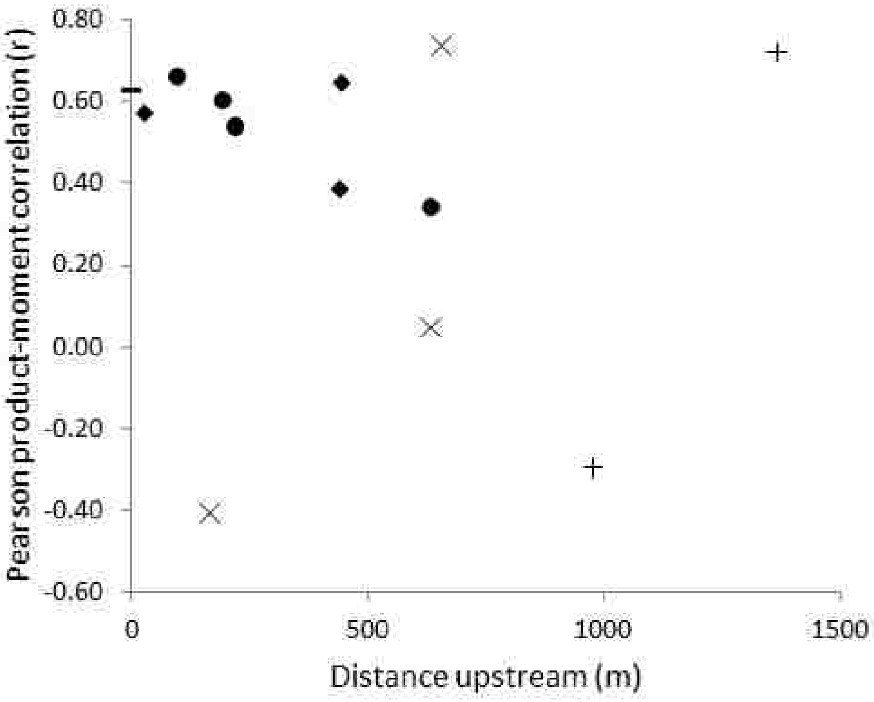


Figure 1.8. Synchrony values (correlation of water level relative to the main channel) for each site plotted against nearest upstream distance along the shortest flow path. Symbols represent synchrony values between the main channel and different habitat types: Dash = another main channel site, diamonds = spring channels, circles = early-successional ponds, x's = mid-successional ponds, and pluses = late-successional ponds.

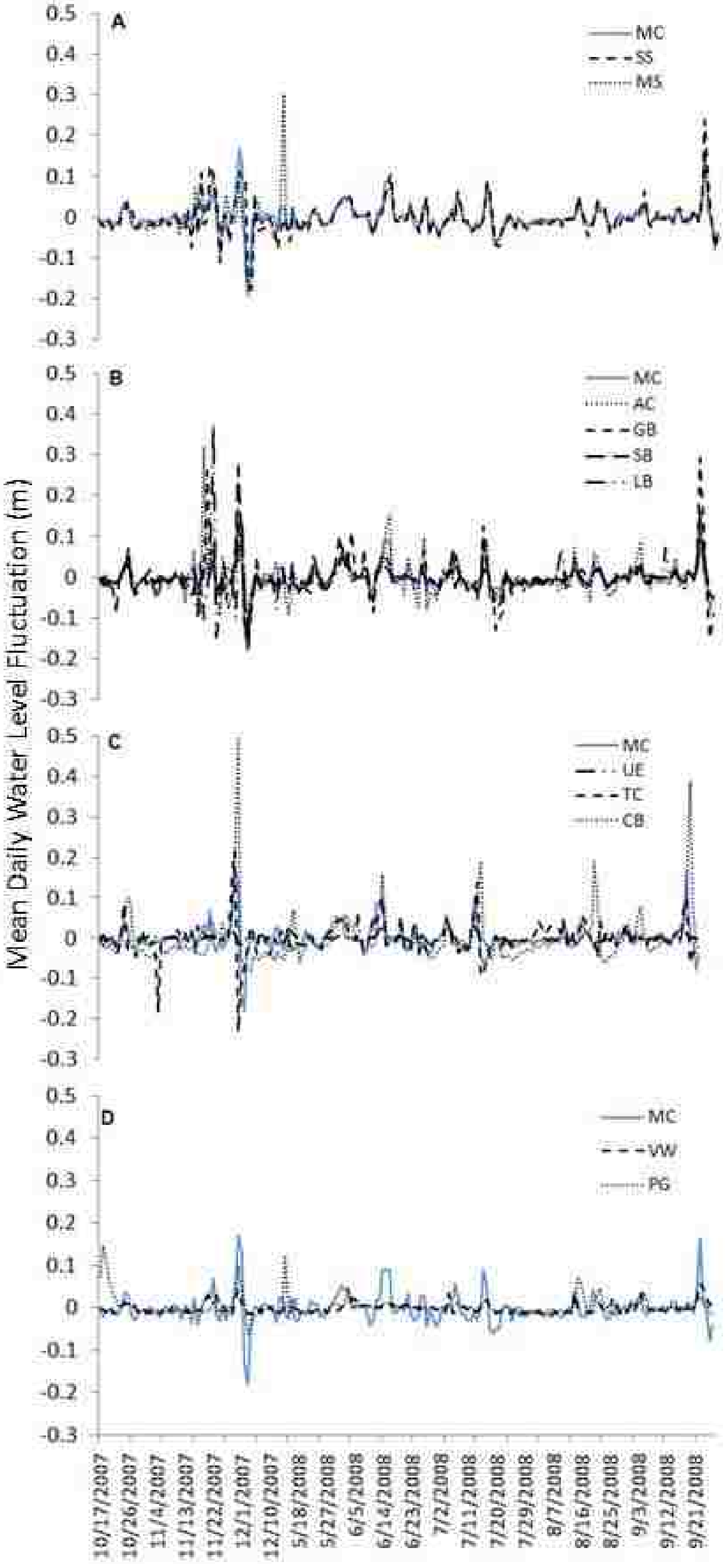


Figure 1.9. Daily water-level changes of A) spring channels, B) early-successional beaver ponds, C) mid-successional beaver ponds, and D) late-successional beaver ponds relative to water level changes for the main channel (MC blue line in all panels).

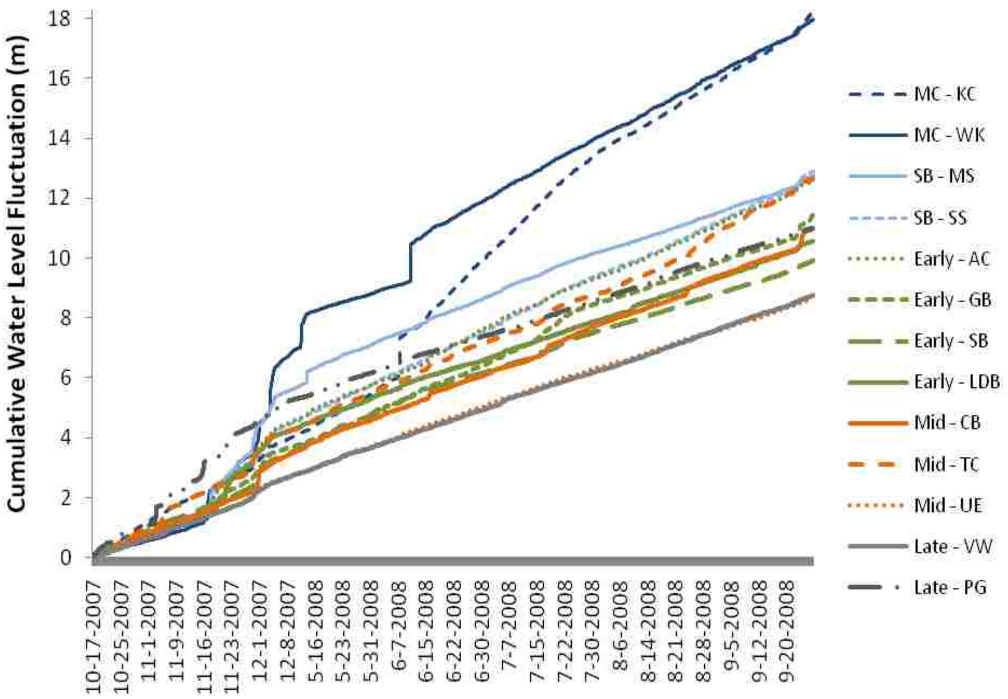


Figure 1.10. Cumulative water level change over the study period for each habitat type. Cumulative change calculated as the sum of the absolute values of depth changes measured each hour. Main channel habitats shown in dark blue, beaver-free spring channels in light blue, early-, mid-, and late-successional ponds in green, orange, and gray respectively.

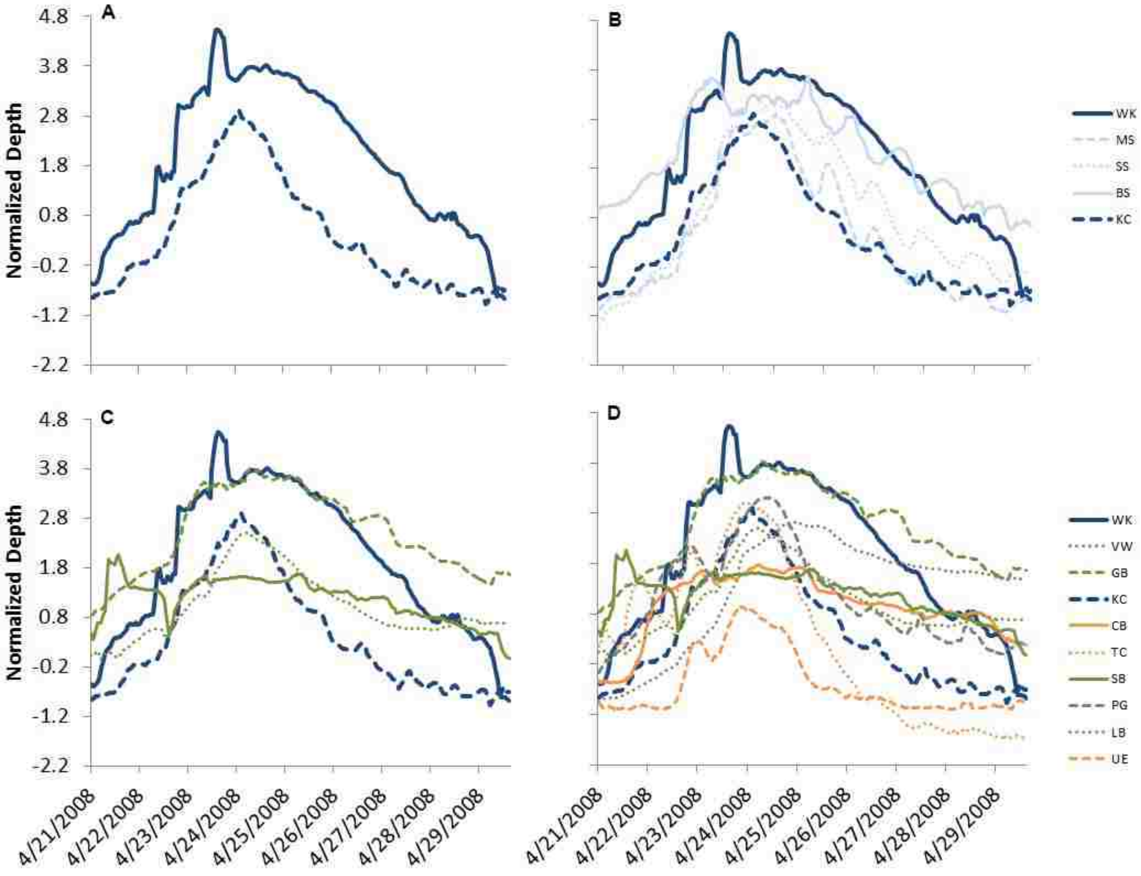


Figure 1.11. Normalized depth plots for one week in April 2008. A) represents two main channel sites in differenct floodplain positions (dark blue lines, WK = downstream site, KC = upstream site), B) represents the close tracking of main channel flucations by spring brook sites (light blue), C) represents differences in water level fluctuations between early-successional beaver pond sites (green) compared to the main channel sites, and D) shows differences in stage height between all successional stages of beaver ponds and the main channel (early-successional = green, mid-successional = orange, and late-successional = grey).

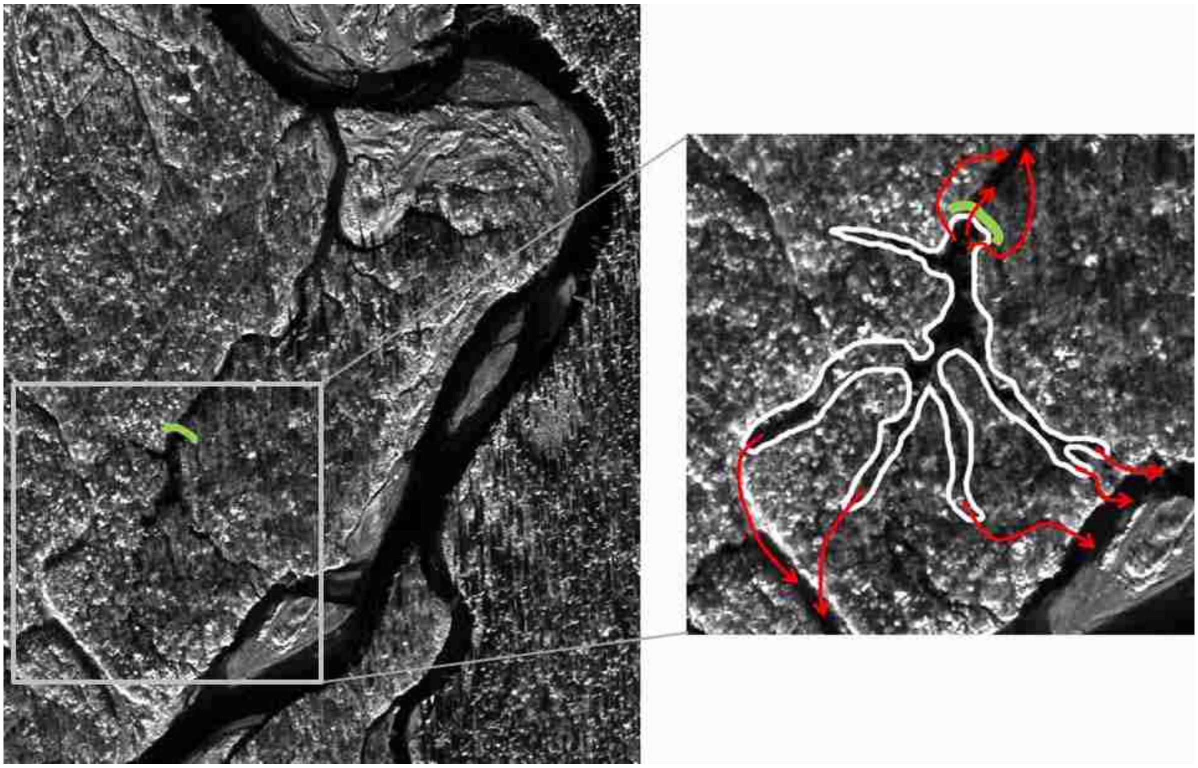


Figure 1.12. A section of the study reach illustrating a beaver complex with an early-successional beaver pond and beaver-influenced spring brook below (between the pond and the main channel). At low flow movement between the pond and spring brook was limited (i.e. fish stayed within the white pond boundary), but at high flow fish were able to move between the two habitats. The brown shape shows the location of the beaver dam and arrows indicate potential pathways of connectivity for juvenile salmon at high flows.

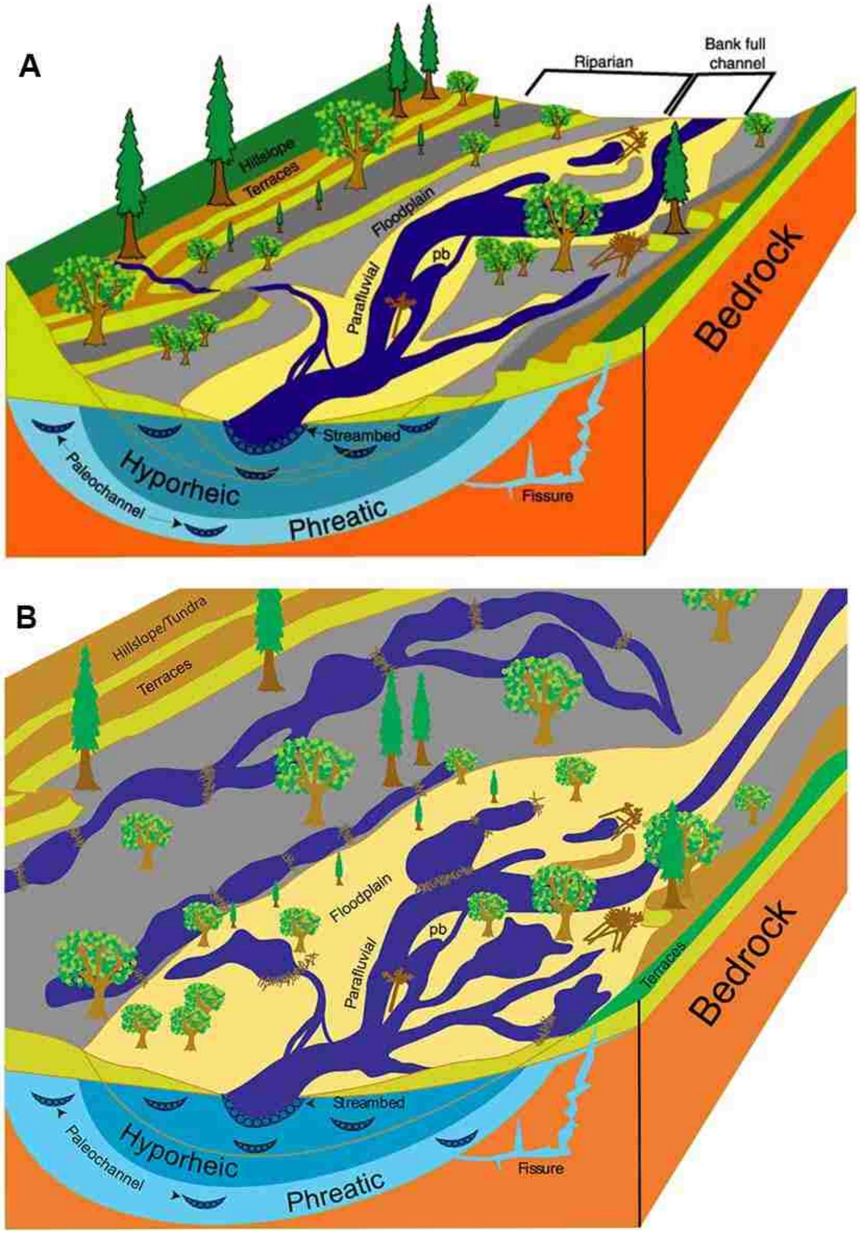


Figure 1.13. (A) The 3-D structure of alluvial floodplains without beavers, emphasizing dynamic longitudinal, lateral, and vertical dimensions and recruitment of wood debris. (B) Beavers influence the shifting habitat mosaic, creating a variety of beaver influenced habitats that modify the structure of alluvial floodplains. Beaver habitat modification results in the presence of additional aquatic habitat types on the floodplain including beaver influenced spring brooks, and early-, mid-, and late-successional beaver ponds (modified from Stanford et al. 2005, illustrated by Joe Giersch).

CHAPTER 2: JUVENILE SALMONID GROWTH, SURVIVAL, AND PRODUCTION IN A LARGE RIVER FLOODPLAIN MODIFIED BY BEAVERS (*Castor canadensis*).

ABSTRACT

By damming floodplain springbrooks that provide primary rearing areas, beavers may influence the production of juvenile salmon. We hypothesized that the presence of beaver modified habitat on a large alluvial floodplain would increase juvenile salmon production in the parafluvial zone because ponds provide more favorable habitat that increase growth rates. We studied three habitats important for rearing salmon in the Kwethluk River, Alaska: free-flowing and beaver-influenced springbrooks, and early-successional beaver ponds. We focused on early-successional ponds in the parafluvial zone of the river, because fish presence in later successional ponds on springbrooks in the orthofluvial zone is vastly reduced owing to lack of access past multiple dams. We measured multiple factors that could influence the production of juvenile coho and Chinook salmon, including habitat, prey and diet characteristics. We conducted a multistate robust design capture-mark-recapture study that allowed us to measure juvenile salmon growth, movement, survival and densities by habitat type. Though beaver ponds cover substantially more area than spring brooks, other habitat characteristics and the biomass of prey in diets was similar for all habitats. Beavers increased the growth of young-of-the-year coho and Chinook in early-successional ponds compared to beaver-influenced and beaver-free springbrooks (3.1 ± 0.1 vs. 1.83 ± 0.14 and 2.0 ± 0.3 %mass/day for coho and 1.8 ± 0.08 vs. 0.93 ± 0.16 and 1.35 ± 0.32 %mass/day for Chinook). Nonetheless, survival rates were consistently highest (46 to 80%) each month in beaver-free springbrooks even though densities of juvenile coho and Chinook were highest in the same habitat. Survival rates varied more for beaver ponds and beaver-influenced springbrooks (6 to 73%). Ponds produced less juvenile coho and Chinook salmon biomass per unit area than beaver-free and beaver-influenced springbrooks (1.87 ± 0.57 vs. 2.98 ± 1.22 and 3.23 ± 0.73 g/m^2). However, due to the larger areal extent of early-successional pond habitat in the parafluvial zone, ponds produced a greater biomass of juvenile salmon than either type of spring brook habitat (175 vs. 149 and 140 kg). In contrast to biomass, ponds reared about half the individuals that reared in beaver-free springbrooks (~24,100 salmon vs. ~41,400 salmon). If beavers were not present and all springbrooks were free flowing, we calculated that slightly less biomass would be produced from the parafluvial zone of the floodplain but 1.5-2x more individuals would be reared, showing that beavers may be able to limit production on the floodplain. The difference would be much greater if orthofluvial springbrooks on the floodplain were accessible to young of the year salmon.

Key words: coho salmon, Chinook salmon, beavers (*Castor Canadensis*), river, floodplain, winter ecology, growth, survival, production, food web, Kwethluk River, Kuskokwim River

INTRODUCTION

Large alluvial rivers of the North Pacific Rim have expansive floodplains that provide abundant spawning and rearing habitat for wild salmonid fishes (Whited et al. 2013). In fact, forty-percent of all wild Pacific salmon are produced in the expansive floodplain rivers of Kamchatka, Russia, and the large floodplain river and lake systems of Alaska and British Columbia make up most of the balance (Augerot 2005). These floodplains are characterized by a shifting habitat mosaic (SHM) for aquatic and riparian organisms that is created by cut and fill alluviation, channel avulsion, riparian plant succession, ground- and surfacewater exchanges and erosion and deposition of live and dead wood (Stanford et al. 2005). The floodplain SHM encompasses a complex network of channels, ponds and wetlands with attendant riparian vegetation and alluvial aquifers fed by the river. In addition to the main channel, many off-channel floodplain aquatic habitats (located lateral to the main channel and inundated during flooding) provide important habitats for a variety of aquatic organisms. In fact, floodplain springbrooks have protective and productive qualities (Morley et al. 2005, Eberle and Stanford 2010) that often result in high densities of juvenile salmonids being present in these habitats (up to 4-10 fish m^{-2}) compared to main channel shallow shorelines and tributaries (Eberle and Stanford 2010). Enhanced growth and survival of juvenile salmon has also been documented (Sommer et al. 2001, Jeffres et al. 2008). Floodplain springbrooks provide critical nursery grounds for juvenile salmon including *Oncorhynchus kisutch* (coho salmon) and *O. tshawytscha* (Chinook salmon). Coho salmon fry rear in freshwater 1-2 years prior to seaward migration as smolts, whereas ocean-type Chinook salmon emigrate following emergence, and stream-type Chinook generally rear in freshwater for 1 year and emigrate to the ocean the following spring (Quinn 2005).

Rearing space and food for juvenile salmon controls the size and production of smolts (Quinn 2005). Thus, modification of important nursery habitats may influence salmon productivity. Beavers have the ability to strongly influence aquatic environments by cutting vegetation and building dams, thereby creating lentic habitats that would otherwise be free flowing (Naiman et al. 1988). Malison et al. (In review) found that 80% of the springbrooks of an expansive floodplain in western Alaska were impounded by beavers, which strongly influenced hydrologic connectivity and juvenile salmon densities. Juvenile salmon densities were 5-7 times higher near the main channel in springbrooks and early-successional beaver ponds, than in mid- and late-successional ponds that were more disconnected from the active channel network by complexes of beaver dams and ponds.

By modifying floodplain rearing habitats beavers may influence the survival, density and production of juvenile salmon from expansive alluvial floodplains. In studies of small, low-order streams, beaver dams have been shown to impede movement (Schlosser and Kallemeyn 2000, Mitchell and Cunjak 2007), cause siltation of spawning sites (Taylor et al. 2010), and cause hypoxia and elevated temperatures above thresholds conducive to salmonid growth and survival (Burchsted et al. 2010). Beaver damming of springbrooks in floodplain settings could have similar effects. On the other hand, a recent review of the effects of beavers on stream fish found that the benefits of beavers are more often cited than negative impacts (Kemp et al. 2011), especially related to the growth and production of fish. For example, beavers can have positive impacts because their ponds often provide good cover and increased production of invertebrate food resources (Hanson and Campbell 1963, Keast and Fox 1990). Impounded sections of low order streams have also been found to be more productive in number and size of fish (Gard 1961, Hanson and Campbell 1963, Bryant 1983, Murphy et al. 1989, Leidholt Bruner et al. 1992, Schlosser 1995) and can have higher survival rates for juvenile salmonids (Bustard and Narver 1975, Quinn and Peterson 1996). Faster growth rates have been suggested based on the presence of larger juvenile coho in ponds (Bustard and Narver 1975, Swales and Levings 1989) and ponds have also been shown to have increased production of coho (Nickelson et al. 1992, Layman and Smith 2001, Pollock et al. 2004). These tradeoffs have never been examined in expansive floodplain rivers of North America (beavers do not exist in Kamchatka and the Asian Far East), in spite of the acknowledged importance of these rivers to overall productivity of Pacific salmon and the predominance of beavers in many large floodplain rivers.

The presence of beavers may affect juvenile salmon production in large alluvial rivers if impounded habitats have different habitat characteristics than lotic habitats. Some possible mechanisms behind differences in fish growth and survival include variation in temperature, habitat area and subsequently lower densities, prey availability, and overwintering conditions. Temperature influences juvenile salmon growth and survival (Brett 1952, 1971, Thomas et al. 1986). The impoundment of water by beaver dams results in greater habitat area (Naiman et al. 1988), which may correspond with lower fish densities, thereby enhancing growth rates. Impoundment of streams and surrounding riparia may also influence the composition and quantity of aquatic and terrestrial prey for juvenile salmon (McDowell and Naiman 1986, Naiman et al. 1988, Smith et al. 1989). All of these factors may influence juvenile salmon survival and growth rates, thus influencing production. Furthermore, larger individuals have also been shown to have higher overwinter and marine survival rates (Holtby et al. 1990, Zabel and Achord 2004), which may also influence production. Lastly, ponds that freeze solid or experience winter de-oxygenation may substantially reduce survival of coho and Chinook juveniles whose life cycles are keyed to at least one over-winter period before emigration to the ocean.

In this study we investigated how beavers influence the production of juvenile coho and Chinook salmon on an expansive floodplain of a 5th order river in Western Alaska. We hypothesized that the presence beaver ponds on floodplain springbrooks increases salmon production in the parafluvial zone of a large river floodplain because abundant lentic food and lower fish densities in the ponds substantially enhance growth in comparison to undammed springbrooks or springbrooks below beaver dams. Thus we expected that the production potential of the parafluvial zone of the floodplain is higher than it would be if beavers were not present. From our working hypothesis we made the following predictions: 1) Habitat quality (including physical characteristics and prey availability) will be greater in beaver ponds compared to springbrooks, but juvenile salmon might not survive overwinter in ponds due to harsh winter conditions; 2) The growth and condition of juvenile salmon will be higher in beaver ponds than in springbrooks; 3) Movement rates of juvenile salmon will be higher in spring brooks than in ponds because springbrooks are more accessible; and 4) Survival rates will be higher in ponds. Thus, we expected the cumulative production from early-successional ponds will be higher than production from all springbrooks in the entire parafluvial zone due to increased fish growth rates and the large area covered by early-successional beaver ponds.

METHODS

Study Floodplain and Sampling Sites

The study was conducted on the lower floodplain of the Kwethluk River, a tributary of the Kuskokwim River in western Alaska (Figure 2.14 and Figure 2.15). The Kwethluk is in the Yukon Delta National Wildlife Refuge and enters the Kuskokwim River approximately 15 km upstream of Bethel, AK. We choose to study the influence of beavers on juvenile salmon production on this unregulated and productive salmon river (Miller and Harper 2012) because beavers are prevalent throughout the floodplain reaches of the Kwethluk. Beaver ponds varied in age from brand new in recently-formed flood channels that cut through early successional vegetation (*Salix spp.* and *Alnus spp.*) in the parafluvial zone of the river, to 100+ year old ponds persisting in old growth riparia (*Populus balsamifera* and *Picea glauca*) in the orthofluvial zone (Mouw et al. 2012). Moreover, the habitat is mostly unaltered by humans (though it is an important subsistence fishing area) and the floodplain experiences naturally occurring flood-pulse cycles.

The study reach is an expansive anastomosing floodplain that is located between 37 and 64km above the confluence of the Kwethluk with the Kuskokwim. The 27-km long reach is gravel-cobble bedded and characterized by a laterally migrating main channel, coupled with anabranching avulsion events that create an intricate network of flood and secondary channels and gravel bars (as described by Arscott et al. 2002 generally for gravel bed rivers). Springbrooks occur in the parafluvial (annually scoured) and orthofluvial (mainly depositional) zones of the floodplain (after Stanford et al. 2005) and are located lateral to the main channel network in areas inundated by direct connection to the main channel only during flooding. During base-flow periods, springbrooks are maintained as aquatic systems by outflows from the alluvial aquifers that exist in the bed sediments of all alluvial floodplains. Flood channels throughout the floodplain that are scoured deep enough to intercept the shallow aquifer contain springbrooks that flow along the abandoned channels and into backwaters that connect to the main river. Springbrooks may be free flowing from the source of upwelling to the main channel network at base flow (beaver-free springbrooks), or they may be impounded by one or more beaver dams upstream of a flowing section (beaver-influenced springbrooks). We selected study sites on beaver-free spring brooks, beaver-influenced spring brooks, and early-successional beaver ponds in the parafluvial zone of the floodplain (

Figure 2.**16**). We focused study on parafluvial springbrooks and ponds because Malison et al. (In review) showed that all orthofluvial springbrooks were so impounded by beavers that flooding rarely overtopped the dams and as many as 10 to 25 dams were present on single springbrooks. These later successional ponds contained very few juvenile salmon because access was substantially blocked by lack of flooding over multiple dams or because overwinter survival was problematic.

All five species of Pacific salmon are present in the Kwethluk River: Chinook, coho, sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*). Other fish species include rainbow trout (*O. mykiss*), Dolly Varden (*Salvelinus malma*), stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*), and slimy sculpin (*Cottus cognatus*). Round whitefish (*Prosopium cylindraceum*) and pike (*Esox lucius*) are also present but were not found in springbrooks or beaver ponds (Malison et al. In review). We focused on Chinook and coho salmon because they are abundant and spend 2-3 years rearing in floodplain habitats and thereby may be strongly influenced by beavers. Moreover, they are preferred by subsistence fishers and are of great conservation concern. Adult Chinook salmon spawn in the main channel network primarily in tailouts whereas coho spawn in a nearly all habitats in the main and distributary channels and even springbrooks if they are deep enough.

Study Design

Our goal was to determine the influence of beavers on the production of juvenile coho and Chinook salmon from the parafluvial zone of the expansive lower floodplain of the Kwethluk River. We selected sampling sites to encompass the 3 habitat types that serve as floodplain nurseries for coho and Chinook salmon, specifically: a) early-successional beaver ponds, b) beaver-influenced springbrooks (i.e., the lotic reaches downstream from dams, connected downstream to the main channel network), and c) beaver-free springbrooks (i.e., free flowing from aquifer outflow to main channel confluence). Representative sites were selected systematically along the length of the study reach. For routine analyses we selected 3 beaver-free springbrooks, and 4 beaver-influenced springbrooks, each with an early-successional beaver pond upstream, as study sites (7 springbrooks and 4 ponds) within the parafluvial zone of the floodplain (Figure 2.2 and 2.3). All beaver ponds were early-successional and exhibited patterns in hydrology that were highly synchronous with the main channel (Malison et al. In review). Again, we emphasize that we excluded study of later successional pond sites because they were largely devoid of juvenile salmon apparently because dam complexes blocked immigration from parafluvial spawning sites (Malison et al. In review).

At each of the 11 sampling sites we measured key biophysical factors that most likely influenced production of juvenile coho and Chinook salmon (Figure 2.17, detailed methods below). We then scaled-up the data to the entire parafluvial zone of the floodplain using habitat area data from satellite imagery (methods below) to estimate overall floodplain production from the parafluvial zone. Finally, the influence of beavers was assessed in two ways. First, we compared distribution, abundance and growth of the two salmon species in beaver-influenced habitats in relation to data from beaver-free spring brooks. Second, we compared floodplain-scale production of the parafluvial zone to an estimate of potential production that likely would occur if beavers were not present and all parafluvial springbrooks were free flowing.

Habitat Characteristics

At each of the 11 sampling sites we measured key physical variables that likely influence juvenile salmon population dynamics and production. We monitored water temperature every hour year-round using HOBO pressure transducer data loggers (Onset, Pocasset, Massachusetts; www.onsetcomp.com) and Vemco data loggers (Vemco, Halifax, Nova Scotia; www.vemco.com) from 2009 to 2011. Growing degree days was calculated using the following equation (Elliott 1994, McMaster and Wilhelm 1997): Cumulative Degree Days (DD) = ∑[(Maximum Daily Temperature + Minimum Daily Temperature)/2]-4, for the time period between June and August. Dissolved oxygen was measured with an Oakton handheld meter (Waterproof DO 300, Oakton, Vernon Hills, IL; www.4oakton.com) during each mark-recapture visit. Although concentrations of DO change seasonally and daily in response to temperature and degree of photosynthesis and respiration (Elliott 1994), measuring DO allowed us to determine if the sites had sufficient oxygen to avoid fish stress. Conductivity and pH were measured in ponds and spring brooks with an Oakton handheld meter (Waterproof pH/CON 10 Series, Oakton, Vernon Hills, IL; www.4oakton.com). Site area was measured from satellite imagery collected in 2011 using Arc/Map (for detailed methods see Malison et al. In review) and on the ground validation was completed with a handheld Trimble GeoXM 2005 GPS (Trimble, Sunnyvale, California) at a subset of sites.

The effect of habitat type (beaver-free springbrook, beaver-influenced springbrook, or early-successional beaver pond) on temperature, dissolved oxygen, pH, conductivity, and site area was analyzed using one-way analysis of variance (ANOVA; PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). All data sets were tested for normality and, where necessary, 1og10 transformed to improve normality and homogeneity of variance prior to statistical analysis. All statistical tests were analyzed in SAS 9.3 and were considered significant where $P<0.05$.

Prey Availability

We sampled allochthonous and autochthonous prey resources at each site to investigate potential differences in prey availability because both the amount and composition of available food could influence the caloric content of fish diets and growth rates (Probst et al. 1984, Pope et al. 2001). We used floating pan traps (at each site four, 0.348 m^2, opaque pans) to measure the flux ($mg/day/m^2$) of allochthonous inputs once each month into each site (June-September) for period of 2-5 days (concurrent with mark-recapture sampling). Samples were sorted in the field and preserved in ethanol for later identification and drying in the laboratory. Invertebrates were identified to family and dried at 60℃ to obtain measures of biomass. Total site input (g/day) was calculated by extrapolating flux values to the entire habitat (pond or springbrook) by multiplying by total site area. Site area (instead of perimeter) was used to calculate total input because of the prevalence of overhanging vegetation and emergent vegetation within the aquatic habitats that could contribute fluxes of invertebrates. The effect of habitat type on fluxes of invertebrates was analyzed using one-way analysis of variance (ANOVA; PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). Invertebrates were also classified as either terrestrial or aquatic (flying adults of aquatic taxa) to determine whether there were more terrestrial prey in beaver ponds. The caloric value and nutrient content of prey taxa are highly variable (Brodmann and Reyer 1999, James et al. 2012), suggesting that differences in prey composition may result in differences in prey quality. We analyzed the relative abundance of taxa at each site with nonmetric multidimensional scaling (NMDS) (Kruskal and Wish 1978) to evaluate differences among habitat types. We excluded rare taxa (relative values, <5%) from the data set to reduce skewness in the data. We used multiresponse permutation procedures (MRPP) to test for significant differences in community composition by habitat category.

To compare biomass of benthic and drifting macroinvertebrates between beaver-free and beaver-influenced springbrooks, we sampled once a month using a kick net (125 μm, $0.25m^2$ metal frame). Replicate samples were collected from 3 riffles selected from each springbrook reach by disturbing the bed-sediments for 1 minute. Each sample was then sorted in the field for one hour, or until no more specimens were visible. Most samples were completely sorted, with a similar effort exerted for each sample and both large and small individuals were collected (as small as zooplankton). We sampled drifting prey in springbrooks using three drift nets (0.10m diameter opening, 125 μm mesh) which were deployed overnight once each month (June-September) at each site. Drift nets were placed in riffles distributed along the length of each springbrook and velocity at the net opening was measured to calculate volume of water sampled in each net. All samples were picked at the stream side for up to one hour, or until no more macroinvertebrates were visible and then preserved in ethanol until identification in the lab. In the laboratory the samples were identified, dried, weighed, and recorded as dry mass per taxon. The effect of habitat type on benthic and drift biomass was analyzed using t-tests.

To determine composition of prey in ponds 3 replicate sweep net samples were collected once a month during the study period. For each replicate a D-net was swept through vegetation and along logs in the pond for 1 minute. Each sample was sorted in the field for one hour, or until no more specimens were visible and samples were preserved in ethanol until identified, dried and weighed in the lab.

Fish Diets

To determine how diets related to prey availability and if fish were food limited we examined the amount of food consumed (biomass of fish diets) and the composition of prey in diets three times per site in 2010 (for four paired beaver pond and springbrooks) and four times per site in 2011 (for three beaver-free springbrooks). We collected diet samples from a subset of the fish collected during mark-recapture sampling events each month (see below). Twenty coho (CO) and Chinook (TW) were sampled per site in 2010 (CO: 59-117mm and TW: 61-87mm) and 20 coho (58-114mm) were sampled per site in 2011 in the evening at each site. Nonlethal stomach-content samples were collected via lavage (stomach-flushing). Gut contents for each site were pooled into a composite sample and preserved in ethanol. In the laboratory we identified individuals to Order or family. Identified samples were then dried at 60 °and weighed for biomass (g). Taxa were categorized as either terrestrial or aquatic, with aerial stages of aquatic insects categorized as aquatic to differentiate prey by origin and percent composition by number and biomass were calculated.

The effect of habitat type on fish diet biomass was analyzed using one-way analysis of variance (ANOVA; PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). We used a nonmetric multidimensional scaling analysis (NMDS) (Kruskal and Wish 1978) to evaluate differences among habitat types in the composition of fish diets. We used relative abundance values for taxa because of high variation in raw values and excluded rare taxa (relative values, <5%) from the data set to reduce skewness in the data. We used multiresponse permutation procedures (MRPP) to test for significant differences in diet composition by habitat category.

Fish Growth and Condition

To measure growth rates and calculate fish condition we individually tagged fish as part of a capture-mark-recapture study at the eleven sampling sites in 2010 and 2011, using Pollock's robust design of both closed and open sampling periods (Pollock 1982). We routinely sampled each site during 3 consecutive days in June, July, August and September of the respective year. Fish were sampled using minnow traps baited with salmon roe placed in film canisters with small holes (to have an attraction scent but ensure eggs were unavailable for consumption) and soaked for two hours (standardizing effort) during each sampling session to collect juveniles. Traps were placed throughout each entire site at approximately 5m intervals. During each sampling event all fish were measured and weighed after being anesthetized with MS-222. Juvenile coho and Chinook greater than 58mm were implanted with 12mm HDX or FDX PIT-tags into the abdominal cavity (ORFID, Portland, Oregon; www.oregonrfid.biz). Each PIT-tagged fish was given a secondary mark with visual implant elastomer (VIE) on the caudal fin (Northwest Marine Technology, Shaw Island, Washington; www.nmt.us). We implanted up to 300 individuals at each site each day with PIT-tags, the exact number depending on tag availability and number of individuals captured. We sampled each site for 3 days each month to recover marked fish and PIT-tag a proportion of new unmarked fish. Any coho and Chinook 58mm or larger that did not receive a PIT-tag (because we did not have enough tags for every fish) was implanted with a site specific elastomer mark. By measuring biomass of fish repeatedly captured in successive sampling events, we estimated growth rates. Growth rates were calculated for individual coho and Chinook salmon for each age class (age 0 and age 1+) for each sample time period and presented as % daily growth in both length and mass. For each sampling date and site we calculated Fulton's condition factor, K (Ricker 1975), for each fish by dividing weight (g) by length (mm) cubed and multiplying by a scalar of 10^5.

The effect of habitat type on %daily growth rates was analyzed using one-way analysis of variance (ANOVA; PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD).

Population Dynamics

Our overall objective was to compare habitat specific production, which required measuring dynamics of movement (Ψ), survival (ϕ), and population sizes and linking site specific population data to growth estimates. We estimated survival, movement and population sizes for each of the seven habitat complexes (4 paired beaver-influenced spring brooks and ponds and 3 beaver-free spring brooks) using the software Program Mark using a Multistate Robust Closed Capture model (White and Burnham 1999). Complexes were either composed of three states including a paired beaver pond (a) and beaver-influenced springbrook (b) with the main channel (c) network (n=4) or two states including a beaver-free springbrook (a) and the main channel (b) network (n=3, for a total of 7). The main channel network (i.e. "the river") was included specifically because fish needed to be assigned to a state when they left the complex and could no longer be recaptured. We used a Multistate Robust Closed Capture model because low movement rates occurred between states (<5%, i.e. between ponds and springbrooks and between springbrooks and the river). Within a complex each fish had a capture history representing its location during each sampling event. Even though fish size can influence capture probability, size was not included as a covariate because of the small range in fish sizes (60-100mm). We confirmed that recapture rates did not vary by fish size by comparing recapture rates for coho across four size classes for each site (50-59mm, 60-69mm, 70-79mm, and 80+ mm). Recapture rates were similar among all fish size classes for all habitat types each month ($F_{[2,8]} < 3.76$, $P > 0.0871$). Fish were detected in beaver ponds or springbrooks by minnow trapping during sampling events. Fish were detected moving into the river using PIT-tag antennae HDX readers (model LF HDX RFID, ORFID, Portland, Oregon) placed at the mouth of two beaver-influenced springbrooks in 2010 and two beaver-free springbrooks in 2011. The antenna systems were installed in June and ran until September and the portions of the springbrooks not encompassed by the antenna were blocked with mesh panels. Antennae ran continuously when functioning but they were inoperable for 23 days in 2010 due to flooding (Figure 2.18). Though flooding also occurred in 2011, the antennae remained operable.

Individual habitat complexes were analyzed separately in Program Mark. For a beaver complex the most “saturated” model with unique combinations of ϕ, Ψ, p, and c, and N by group and time contained 99 parameters. We held certain parameters constant based on study design and little detected movement between certain states. Survival and recapture probability within the river was fixed at zero because we did not tag or capture fish in the main channel network (Φ: C:C = 0; c of C:C = 0). Of course we recognized that coho and Chinook also rear in shallow shoreline areas of the main channel network (Malison et al. In review), but our intent here was to demonstrate the influence of beavers in the floodplain environment. Because we did not detect movement of tagged fish returning from the river into ponds or springbrook states (i.e. once fish left a complex they did not come back) these movement rates were fixed at zero (Ψ C to A and Ψ C to B = 0). Ponds were discrete units for most of the study period and if movement from the pond directly to the river did occur we could not estimate it, so movement from the ponds directly to the river was fixed at zero (Ψ A to C = 0). We followed the strategy of Zabel and Achord (2004) by analyzing the detection and recapture probabilities before modeling survival and movement rates. By doing so, we first set the structure of "nuisance" parameters and then focused on investigating which models with biologically relevant ϕ and Ψ parameters ranked the highest. For each complex, we began with the null model; designated as $\phi(.),\Psi(.),p(.),c(.),N(gt)$, with the previously described parameters fixed at 0. Then we tested models with different combinations of p and c varying over group or sampling session. To examine the contribution of different combinations of parameters to model fit, we compared alternative models comprising various combinations of variables using Akaike's Information Criterion (AIC). We selected the best model and if the top models did not vary more than 2 ΔAIC values then we took the average of the model estimates, or reported the best model if results were very similar. After the structure of p and c parameters was set, we developed alternative models comprising of various combinations of ϕ and Ψ parameters. In general we compared models of the parameters varying over state (pond vs. springbrook) or by session (so that parameters varied over time during open sessions but were constant during the closed period). Again, we selected the best model using the criteria listed above (see Table 2.1 and 2.2 for models).

We calculated monthly population estimates for each site in Program Mark. However, Program Mark estimated population sizes using only data from PIT-tagged individuals. Because we had a limited number of PIT-tags a large percentage (40-80%) of the juvenile coho and Chinook were only batch marked with elastomer even though they would have ideally been pit-tagged at each site. This may have resulted in Program Mark underestimating population sizes which would be a problem because then production estimates would be biased low; though no habitat or site should have been biased over another (i.e. all habitats had extra fish that weren’t PIT-tagged). We compared Program Mark population estimates to population estimates made using all large fish captured at each site. To do so we calculated population estimates using all captured fish (PIT-tagged and batch marked individuals combined) for each mark-recapture site using a Schnabel estimate. To incorporate survival rates into the Schnabel estimate we assumed that PIT-tagged and batch marked juvenile coho and Chinook in the same site had similar survival rates. Then we used the site specific survival rates calculated in Program Mark to modify the number of previously marked fish available at the beginning of each month that went in to the Schnabel estimate. Using a Schnabel estimate without any associated mortality would overestimate population sizes. We then compared our population estimates using all captured fish to those made in Program Mark using only PIT-tagged fish. We calculated site specific densities by dividing population estimates by site area.

Floodplain Production by Habitat Type

We estimated the amount of biomass produced in each site from June-August. We calculated the mean biomass accumulated per individual (g) by taking the mean of the biomass accumulated for individuals tagged in June and recaptured in August for each site. We then multiplied mean accumulated biomass by August population estimates for each site to calculate site specific production in kg. To extrapolate production estimates to the entire parafluvial zone of the floodplain we multiplied mean biomass produced per unit area for each habitat type by the total area of early successional beaver ponds, beaver-influenced springbrooks, and beaver-free springbrooks in the parafluvial zone (quantified from satellite imagery, see Malison et al. In review).

In addition to the biomass produced per habitat type, an understanding of the number of individuals that reared in each habitat type is important. Due to differences in accessibility (i.e. ponds are more difficult to enter than free-flowing springbrooks) the importance of higher growth rates in ponds may be negligible if few fish rear in pond habitats. To determine the abundance of individuals rearing in the entire parafluvial zone we used September densities (from each site, multiplied by site area) to determine the abundance of juvenile salmon by habitat type for the entire parafluvial zone. We used September densities because the population in the fall represents the number of individuals that will overwinter. We viewed the abundance of individuals as an important proxy for floodplain production because it is possible that patterns in biomass accumulation may be substantially different than the number of individuals produced.

Overwinter Survival

To determine if juvenile salmon could survive overwinter in our study ponds, we conducted winter field work in April 2011. We drilled holes in our four study ponds at deep pools and obtained dissolved oxygen profiles with a Hydrolab ds5 sonde (www.hachhydromet.com, Hach Hydromet, Loveland, CO, USA). Where possible, we placed two minnow traps baited with salmon roe overnight. We identified, measured and weighed all fish and checked for tags. Presence of healthy juveniles under the ice (especially marked individuals that we measured in the same habitats in the previous fall) was used to indicate overwinter survival. We calculated Fulton's condition factor, K (Ricker 1975), for each fish by dividing weight (g) by length (mm) cubed and multiplying by a scalar of 10^5.

RESULTS

Habitat Characteristics

Overall, all habitats exhibited similar temperatures, dissolved oxygen, pH and conductivity, and none of these variables were deemed limiting to salmon growth and survival. Indeed, all mark-recapture sites exhibited optimal temperatures for growth during the summer months (ranging between 6-12 ºC, Brett 1952), but ponds generally had the highest temperatures (8-12 ºC vs. 7-10 ºC for beaver-free spring brooks). Degree days varied for mark-recapture sites between June and August (though not significantly, $F_{[2,7]} = 3.37$, $P = 0.0945$), with beaver ponds being 1.3x warmer than beaver-free springbrooks (Tukey's HSD, $P = 0.0851$). Dissolved oxygen, pH and conductivity were similar for all habitat types ($F_{[2,6]} < 3.30$, $P > 0.1078$). However, habitat area was significantly variable among habitat types ($F_{[2,8]} = 7.57$, $P = 0.0143$), with beaver ponds having 8.4x the area as beaver-free springbrooks (Tukey's HSD, $P = 0.0144$) and 2.5x the area as beaver-influenced springbrooks (Tukey's HSD, $P = 0.0607$).

Prey Availability

Aerial food resources were similar in the different habitat types on a unit area basis. Pan traps in beaver-free springbrooks received 1.4-1.8x higher fluxes (mg/m^2/day) of invertebrates than traps in beaver-influenced habitats but no statistically significant difference occurred in any month (Figure 2.19A; $F_{[2,8]} \leq 2.97$, $P \geq 0.1082$). In contrast, after extrapolating to the area of complete habitat units (i.e. entire ponds or springbrooks), beaver ponds had 2.4-7x higher total inputs (mg/day) of invertebrates than spring brooks though differences were only significant for one month (Figure 2.19B; August: $F_{[2,6]} = 13.1$, $P = 0.0065$; June, July and September: $F_{[2,8]} \leq 3.91$, $P \geq 0.0653$). Aerial inputs were dominated by adult Diptera (true flies, both aquatic and terrestrial), collembolan (springtails), adult Trichoptera (caddisflies), adult Tipulidae (crane flies), Hemipterans (true bugs) and Coleoptera (beetles). Inputs into beaver-free springbrooks were comprised of 1.2-1.3x higher proportions of aquatically derived invertebrates than beaver-influenced springbrooks and beaver ponds, though the only significant difference by habitat type occurred in July ($F_{[2,8]} = 5.34$, $P = 0.0336$; June, August and September ($F_{[2,8]} \leq 3.94$, $P \geq 0.0645$). The composition of aerial inputs were similar for all habitat types (NMDS ordination; $A = 0.017$, $P > 0.129$).

Overall mean total biomass of benthic prey was similar between beaver-free and beaver-influenced springbrooks (t = -2.05, $P = 0.1692$), though beaver-free springbrooks had on average 2.8x greater biomass (but sample variance was high). Some qualitative differences occurred in the community structure of benthic prey between the two springbrook types, with some mayflies and stoneflies being more predominant in beaver-free springbrooks (see Malison et al. In review for NMDS results). Benthic samples were generally dominated by Chironomidae, Platyhelminthes and Oligochaeta. The biomass of drifting prey was low in all samples and similar in beaver-free vs. beaver-influenced springbrooks (0.028 ± 0.033 vs. 0.025 ± 0.025 mg/m^3; Z = -0.5303, $P = 0.5959$). Drift samples contained organisms from both the falling inputs and benthic samples but the predominant taxa were all aquatic including larval Chironomidae and larval Trichoptera, cladocerans, Oligochaeta (worms) and Ostracoda.

Sweep net samples collected from within ponds contained on average 96% (± 0.02) aquatic organisms (i.e. taxa entering ponds from aerial inputs were underrepresented in sweep samples), and had different species compositions compared to both types of springbrooks (also see Malison et al. In review for NMDS results). Dominant invertebrate taxa within the ponds included Chironomidae (nonbiting midges), cladocerans and copepods (small crustaceans), and gastropoda (snails), with Ostracoda (small crustacean) and Trichoptera making up slightly less of the samples. A few adult aquatic dipterans including Ceratopogonidae (biting midges), Chironomidae, Culicidae (mosquitos) and Simiuliidae (black flies) made up 1-6% of the sweep samples, and a small number of terrestrial organisms including Araneae (spiders), Collembolan, terrestrial Diptera, and Hemipterans made up 1-4% of the sweep samples.

Fish Diets

Diet samples from juvenile coho and Chinook in all habitat types had a similar biomass of prey in all months ($F_{[2,8]} < 4.16$, $P > 0.0644$). The occurrence of empty fish stomachs was rare in all sampling sites. Though the mean total biomass of diets was similar, strong differences in the origin (aquatic vs. terrestrial) and composition of diets by habitat type may have contributed to differences in growth rates. Terrestrially derived taxa made up a greater proportion of diets in beaver ponds and aquatically derived taxa made up greater proportions of beaver-free springbrook diets (Figure 2.20). Sixty-percent of diet items of pond fish were aquatically derived each month compared to eighty-four and ninety-two percent of prey items being from aquatic sources in beaver-influenced and beaver-free springbrooks. The composition of prey in fish diets also differed by habitat type. The NMDS ordination of mean relative abundance of 41 taxa groups found in diets yielded a solution that represented 87.8% of the total variation among sites on 2 axes (Figure 2.21). Diets from sites in different habitat categories were significantly separated in community ordination space (MRPP, $A = 0.335$, $P = 0.0006$). Beaver pond diet composition was different than beaver-influenced springbrook diet composition ($P = 0.024$), but diets from these two habitat types were still more similar to each other than to beaver-free springbrook diets ($P < 0.010$). Habitats were most strongly separated in diet composition space along Axis 1, which explained 63.7% of the variation. Larval Chironomidae were predominant in beaver-free springbrook diets, while Coleoptera, Simuliidae, Heptageniidae, Phoridae, Oligochaeta, Ceratopogonidae, Nematoda, Empididae, Trichoptera, and Tipulidae were associated more strongly with beaver pond and beaver-influenced springbrook diets (see Figure 2.21 for correlation values). Corixidae and Coleoptera most strongly drove separation in diet space along Axis 2, which represented 24.2% of the variation.

Fish Growth and Condition

In total, slightly over 8100 juvenile coho and Chinook were PIT-tagged at the 11 sites. Growth rates were calculated from individuals tagged at each site originally in June and recaptured in August (spring brooks, n=136, beaver-influenced spring brooks, n=140, ponds, n=176). Habitat type had a significant effect on % daily growth rates (in length and mass) for young-of-the-year (YOY) coho growing between June and August (

Figure 2.**22**A&B; $F_{[2,8]} = 11.68$, $P = 0.0042$ and $F_{[2,8]} = 16.89$, $P = 0.0013$, respectively). The greatest difference in YOY coho growth rates in % daily length was

between beaver ponds and beaver-influenced springbrooks (1.6x higher in beaver ponds, Tukey's HSD, $P = 0.0034$), and though not significant, rates were 1.3x faster in beaver ponds than in beaver-free springbrooks (Tukey's HSD, $P = 0.0605$). For % daily mass, YOY coho in beaver ponds grew faster than YOY coho in both beaver-influenced and beaver-free springbrooks (Tukey's HSD, $P \leq 0.0069$). Percent daily growth rates were similar in length and weight for Age 1+ coho by habitat type, largely due to high variance in growth rates in beaver-free springbrooks (

Figure 2.**22**A&B; $F_{[2,8]} \leq 2.86$, $P \geq 0.1371$). A key finding concerning growth was that young of the year coho were the same size in June but grew faster in beaver ponds resulting in September sizes of fish being 10-15mm longer in beaver ponds than both types of spring brooks (Figure 2.23; $F_{[2,8]} = 19.68$, $P = 0.0008$).

Growth of YOY Chinook followed patterns similar to coho although young of the year Chinook were not large enough to tag until July, so data are only presented for July-August. Growth rates (% daily, in length and mass) differed significantly for young of the year Chinook from July to August (

Figure 2.**22**A&B; Length: $F_{[2,3.74]} = 20.18$, $P = 0.0099$ and Mass: $F_{[2,8]} = 6.49$, $P = 0.0212$), with Chinook in beaver ponds growing significantly faster than those in beaver-influenced springbrooks (Tukey's HSD, $P = 0.0134$ and 0.0171, length and weight respectively).

The size and condition of fish going into winter is important because it influences the decision of when to smoltify for coho (at age 1+ or 2+) and may influence the survival of both species. By the end of the growing season (just before winter), the condition of coho was not significantly different among sites ($F_{[2,8]} = 3.14$, $P = 0.0983$), but coho in ponds had 2-3% higher condition factors than coho in both types of springbrooks. The condition of Chinook was similar for all habitat types in September ($F_{[2,8]} = 0.28$, $P = 0.7656$).

Population Dynamics

Model selection results are presented for the 4 beaver complexes (Table 2.1) and 3 beaver-free springbrooks (Table 2.2). The best models selected and used to estimate movement, survival, and population sizes are shown in bold with asterisks. We used Program Mark to model movement rates (Ψ, psi) from beaver ponds to springbrooks and from springbrooks to beaver ponds within beaver complexes, as well as movement rates out of one beaver-free and one beaver-influenced springbrook. Movement rates varied by complex, but were similar from ponds to springbrooks and from springbrooks to ponds ($t = -0.66$, $P = 0.5367$, Figure 2.24A&B). We were able to model emigration over time for the beaver-free springbrook and found that emigration was very low early in the season and increased to a level similar to that estimated for beaver-influenced springbrooks by the end of the season (Figure 2.24). Unfortunately the best models for the beaver complex with double antennae could not estimate movement varying over time (see Table 2.1), so the same value represented emigration each month (see Figure 2.24). Despite, the difficulty modeling emigration over time for the beaver-influenced springbrook, we did observe more individuals emigrating through the pit-tag antennae over the course of the sampling season (similar to what we saw for beaver-free springbrooks).

Survival rates were similar among habitat types from June to July, declined for both beaver ponds and beaver-influenced springbrooks from July to August, and were similar among all habitat types from August-September, except for two beaver ponds (

Figure 2.**25**). Even though we documented emigration at some sites with antennae, it is possible that sites without antennae had higher emigration rates which may have confounded survival estimates (resulting in exceptionally lower rates for two sites;

Figure 2.**25**). Additionally, the decreased survival for both beaver ponds and beaver-influenced springbrooks from July to August could have been confounded by missed emigration when pit-tag antennae arrays were not functioning.

Population estimates were divided by habitat area and data presented as densities to compare different habitat types. The density of PIT-tagged juvenile coho and Chinook varied by habitat type and over time (Figure 2.26A). However, the densities calculated using only PIT-tagged individuals in Program Mark underestimated densities by 3-14x compared to densities calculated using all PIT-tagged and elastomer tagged individuals (Figure 2.26B). The density of all tagged coho and Chinook (PIT and elastomer tags) differed significantly by habitat type ($F_{[2,8]} = 9.09$, $P = 0.0087$), with higher densities present in beaver-free springbrooks than in early-successional beaver ponds (Tukey's HSD, $P = 0.0074$; Figure 2.26B).

Floodplain Production by Habitat Type

Accumulation of juvenile coho and Chinook biomass per sq. meter was generally higher for beaver-free springbrooks and beaver-influenced springbrooks compared to beaver ponds, although the difference was not statistically significant ($F = 0.857$, $P = 0.4601$, Figure 2.27A). By extrapolating habitat specific biomass accumulation to the entire parafluvial zone of the floodplain, the total production of juvenile coho and Chinook biomass (kg) was highest in beaver ponds (175 kg) compared to either type of springbrook habitat (beaver-free, 140kg, or beaver-influenced, 149 kg), due higher growth rates and the greater areal extent of the ponds. However, the combined areas of both spring brook types produced a greater total biomass of juvenile salmon compared to the ponds. In total, we estimated that the three habitat types produced 463 kg of juvenile salmon biomass, or ~ 7.7kg/day, between June and August.

Without beavers, all floodplain habitats accessible to juvenile salmon would be free flowing springbrooks, totally usable as natal habitat. To make a rough estimate of what production might be like without beavers, we estimated that approximately 45% of early-successional pond area would remain as free flowing springbrooks (because less area is inundated without dams). If that was the case the total production of juvenile coho and Chinook biomass would be 13% lower (403 vs. 463 kg) in the parafluvial zone of the floodplain. Without beavers a large amount of rearing area and associated high growth rates would be lost, corresponding with the decrease in biomass produced.

In contrast to biomass, juvenile coho and Chinook salmon were most abundant in beaver-free springbrook habitat, were least abundant in early-successional beaver pond habitat, and beaver-influenced springbrook habitat fell intermediate (Figure 2.27B). Juvenile coho and Chinook salmon were almost 2x more abundant in beaver-free springbrook habitat (~41,400) than in beaver ponds (~24,100) and almost 1.5x more abundant in beaver-free compared to beaver-influenced springbrook habitat (~20,500). If beavers were absent on the floodplain we estimate that almost 1.5x more individuals would be able to rear in parafluvial habitats (~119,300 vs. 93,800), because densities were 1.5-3.5x higher in beaver-free springbrooks than in beaver-influenced springbrooks and beaver ponds. These numbers increase substantially (119,300 to 370,000) if orthofluvial springbrooks were also available as natal habitat (see chapter 3).

Overwinter Survival

In April 2011 all ponds and spring brooks were covered in ice. Ice on beaver ponds was 0.65 to 0.90m thick and half of them were frozen solid in the locations where we drilled (though this does not indicate that ponds were frozen throughout their entire area), but the others had fish surviving overwinter. In the two ponds where we found water, depth varied between 0.42 and 0.83m and mean dissolved oxygen concentrations indicated that oxygenated water was upwelling under the ice (56.2% ±9.1 and 7.3 mg/L ±1.2 and 77.4% ±1.5 and 10.0 mg/L ±0.3 for the two sites). We documented juvenile salmon overwinter survival in the two beaver ponds where we drilled to water. We captured a total of 27 coho, 42 Chinook, and 3 sockeye salmon. Of the 27 coho, 7 were tagged at the same sites in the summer/fall of 2010. Of the 42 Chinook, 9 were tagged in 2010. Fish condition was lower for juvenile coho and Chinook captured during the winter compared to fish sampled at the same sites during the summer and fall of 2010 (0.93 ± 0.02 vs. 1.10 ± 0.02 for coho and 0.95 ± 0.03 vs. 1.10 ± 0.05 for Chinook), but all juveniles were healthy.

DISCUSSION

We hypothesized that production would be increased by the presence of beaver ponds because ponds would stimulate the growth of juvenile salmon. Indeed, growth rates for young-of-the-year coho and Chinook were higher in early-successional beaver ponds than in springbrooks and similar patterns were seen for age 1+ coho. Additionally, the ponds provided the same quantity of rearing habitat as both types of springbrooks (beaver-free and beaver-influenced) combined. Increased growth rates and the large habitat area of ponds corresponded with a slightly higher biomass of juvenile salmon being produced with beavers in the parafluvial zone than if beavers were absent. However, in spite of higher growth rates in the ponds, the number of juveniles rearing in ponds was limited, resulting in pond densities being 3x lower than spring brook densities. It seems likely that densities were lower in ponds both due to the larger area of the ponds and limited accessibility compared to spring brooks. Surprisingly, high survival rates did not correspond with low densities and were actually similar among all habitat types, with the lowest rates observed between August and September in two of the beaver ponds. We did document individuals surviving in ponds under the ice during the winter in two of our study ponds, suggesting that ponds are not sinks for salmon production. In the ponds that were frozen solid where we drilled, it is likely that we missed pockets of open water in which juvenile salmon may have been overwintering.

The differences that we observed in growth rates by habitat type could have a variety of mechanistic explanations. Reduced competition and decreased energy expenditure has resulted in increased growth rates for Atlantic salmon in both lake and beaver pond habitats (Hutchings 1986, Sigourney et al. 2006). Like Atlantic salmon, coho and Chinook display territorial behavior and similar mechanisms may be driving the observed differences in growth rates (Chapman 1966). Juvenile salmon densities were lower in ponds vs. springbrooks which could have stimulated growth rates due to decreased competition. In fact, Malison (2013 chapter 3) found that growth rates were the same in early-successional ponds and spring brooks when densities were held at the same level in enclosures. Lower densities likely occurred in ponds because of two reasons: 1) fewer young of the year were able to find pathways into ponds and 2) habitat area of ponds is large. Indeed we found that in total a similar number of age-1+ coho were captured from springbrooks and ponds (3,142 vs. 3,258), but over three-fold more age-0 coho were caught in springbrooks than in beaver ponds (10,009 vs. 2,971). The marginally warmer temperatures in beaver ponds could also have contributed to increasing fish metabolic rates and consequently growth rates. It is likely that a combination of the above mechanisms, as well as the lower maintenance costs of lentic environments contributed to the increased growth rates in ponds (Enders et al. 2003).

Fewer fish combined with generally greater inputs of food resources could have resulted in less competition in the ponds which would promote higher growth rates, especially for young-of-the-year which had 1.5-3.5x higher densities in springbrooks.

Other studies have found that increased prey resources promote increased growth of juvenile salmon in beaver ponds (Peterson 1982). Ponds received up to 2.4-7x as much allochthonous prey inputs as spring brooks per unit area, though the composition was similar for all habitat types. Furthermore, benthic prey was on average 2.8x greater in beaver-free vs. beaver-influenced springbrooks. Though the biomass of diet samples was similar by habitat type it is possible that variation in the time of sample collection and the composite sampling technique introduced error that masked any differences. Variation in the quality of prey in different habitat types could be important because we did find differences in the composition of diets by habitat type. Diets of beaver-free spring brook fish, which exhibited intermediate growth rates, were dominated by Chironomidae, while multiple prey taxa dominated diets of beaver pond fish, which grew the fastest. Furthermore, aquatically derived taxa made up greater proportions of beaver-free springbrook diets while terrestrial taxa were more important in pond diets.

By the end of the summer the size of young of the year coho in beaver ponds was 10-15mm higher than in both types of springbrooks, which could have important implications for survival. Larger parr and smolts have been shown to have higher overwinter (Zabel and Achord 2004) and higher marine (Holtby et al. 1990) survival rates. Survival during the time that smolts first enter the ocean is an important determinant of subsequent adult populations (Zabel and Achord 2004, Quinn 2005). If ponds produce more robust individuals then these individuals may have higher survival rates. If this is the case, then a greater proportion of the salmon produced in ponds may return to spawn than those produced in springbrooks. Consequently, the greater number of smolts that reared in springbrooks may not be as important as the larger individuals produced in the ponds. Nonetheless, larger smolts do not always have consistently higher survival rates (Holtby et al. 1990) and it is questionable whether higher survival rates for beaver pond fish would make up the difference for the greater number of individuals rearing in springbrooks. Tracking the return of adult salmon tagged as juveniles in known freshwater habitats would provide the necessary information to determine if any differences in marine survival occurred in relation to freshwater rearing habitat.

The survival and movement of fish strongly influenced habitat specific population sizes and densities. We expected that patterns in survival rates would be similar to growth rates and higher in ponds, but this was not the case. Some ponds did exhibit similar survival rates to beaver-free springbrooks between June-July and from August-September, but the consistently highest survival rates were exhibited by beaver-free springbrooks over the entire course of the study period. In general, survival rates in ponds had greater variation and survival rates were reduced for both beaver ponds and beaver-influenced springbrooks from July-August. However, it seems likely that the estimated rates for beaver influenced habitats from July-August were biased low because of untracked emigration when PIT-tag antennae were incapacitated. Similarly, the extremely low survival rates for two ponds from August-September (54 and 88% lower than all other sites) may be underestimates if these sites (that did not have antennae) had higher emigration rates than the site with the double antennae.

We found that salmon densities varied with habitat type, though growth rates did not always follow the expected pattern. Using population estimates from all juvenile coho and Chinook large enough to tag (>58mm, both elastomer and pit-tags) we found that densities were highest in beaver-free springbrooks, intermediate in beaver-influenced springbrooks, and lowest in early-successional beaver ponds. If small young-of-the-year (too small to tag) were also included in the estimate this relationship may change and would result in densities being the highest in beaver-influenced springbrooks. The influence of small young-of-the-year could help explain why even though the highest growth rates corresponded with lowest densities in beaver ponds, the same relationship did not hold for densities and growth in the two types of springbrooks. Beaver-free springbrooks had higher growth rates and higher densities than beaver-influenced springbrooks when only fish large enough to tag were considered, but if young-of-the-year were included then higher densities in beaver-influenced springbrooks could help explain why growth rates were lower in this habitat type if competition between age classes occurred.

We determined that beavers may increase production from the parafluvial zone in terms of biomass by increasing growth rates, but may limit the total number of individuals that may rear in the parafluvial zone. We estimated that if ponds and beaver-influenced springbrooks were present as beaver-free springbrooks these habitats would rear 1.5-2x more individuals. However, in order to make a more robust estimate of what production might be like without beavers we need to have a much better understanding of how rearing habitat availability would change if beavers weren't present (i.e. exactly how much area would be covered by spring brooks if dams were absent). Additionally, we need a better understanding of whether or not rearing habitat availability is actually a limiting factor for juvenile salmon production on the floodplain. The presence of ponds (that rear lower densities of juveniles) may not limit production if juvenile salmon densities are not at carrying capacity. It seems unlikely that rearing habitats are saturated at the current level of escapement for both coho and Chinook on the Kwethluk River because escapement levels have declined by 12-15x over the past 9 years (Miller and Harper 2012). Additionally, we observed lower (Eberle and Stanford 2010) or similar densities of juvenile salmon than have been observed in other salmon rivers (Murphy et al. 1986, Murphy et al. 1989), suggesting that perhaps density dependent factors are not be playing a large role. Studying how habitat specific densities change over different escapement levels would shed more light on how limiting the conversion of springbrooks to beaver ponds may actually be for the system.

We determined the presence of beavers and ponds results in a tradeoff, ponds grow larger fish, but fish are more abundant in spring brooks. If all spring brooks in the parafluvial zone were free flowing at the floodplain scale then production would potentially exceed the existing beaver-influenced system because greater numbers can rear in spring brooks. Even stronger differences in production may exist when the entire floodplain, with both parafluvial and orthofluvial zones included, is considered. In beaver-free floodplains, like the Kol and Krutogorova Rivers in Russia, juvenile salmon are able to rear in springbrooks spanning the floodplain from the parafluvial zone out in to the orthofluvial zone (Stanford et al. 2002). The springbrooks in beaver-free systems are extremely important spawning habitats and rearing areas because they tend to be quite large with dependable flows and good access to riparian food resources (Eberle and Stanford 2010). Whereas, in a beaver dominated floodplain like the Kwethluk, late-successional beaver complexes in the orthofluvial zone seem disconnected physically and ecologically (Malison et al. In review). Thus, overall beavers could reduce juvenile salmon production at the floodplain scale (including both parafluvial and orthofluvial zones) even more so than illustrated for the parafluvial zone if they block significant amounts of orthofluvial rearing habitat. In fact, Malison (2013 chapter 3) estimates that in the absence of beavers the entire Kwethluk floodplain could produce 2x the biomass (1174 vs. 667kg) and 3x the number of salmon (370,000 vs. 140,000).

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TABLES

Table 2.1. Models used to estimate survival, movement and population sizes are compared and results given for the 4 beaver complexes. Bold text and an asterisk indicate the best model for each paired beaver pond and beaver influenced spring brook complex. A model result highlighted in grey indicates that at least some of the parameters could not be estimated so that model was rejected. Bold text indicates the null model with the best p and c parameters that were then used to run different combinations of survival (S) and movement (Ψ, psi) parameters. Hash marks indicate certain models weren't for some complexes (because they contained the wrong selection of p and c parameters).

	Complex 1 (BU)	**Complex 2 (SB)**	**Complex 3 (LB)**	**Complex 4 (A)**
Model	AIC_c	AIC_c	AIC_c	AIC_c
S(null)psi(gt)p(g,se)c(g,se)N(gt)	-	-	-6726.5	-
S(null)psi(g)p(g,se)c(g,se)N(gt)	-	-	-6729.3	-
S(null)psi(gt)p(g)c(g,se)N(gt)	-	-9770.4	-	-10153.9
S(null)psi(g)p(g)c(g,se)N(gt)	-	-9770.3	-	-10124.5
S(null)psi(gt)p(g)c(se)N(gt)	-6972.1	-	-	-
S(null)psi(g)p(g)c(se)N(gt)	-6949.9	-	-	-
S(gt)psi(gt)p(g,se)c(g,se)N(gt)	-	-	-6780.9	-
S(gt)psi(gt)p(g)c(g,se)N(gt)	-	-9777.1	-	-10296.2
S(gt)psi(gt)p(g)c(se)N(gt)	-7020.3	-	-	-
S(gt)psi(g)p(g,se)c(g,se)N(gt)	-	-	-6784.5	-
S(gt)psi(g)p(g)c(g,se)N(gt)	-	***-9776.6**	-	***-10266.4178**
S(gt)psi(g)p(g)c(se)N(gt)	***-6999.3**	-	-	-
S(g)psi(gt)p(g,se)c(g,se)N(gt)	-	-	-6749.6	-
S(g)psi(gt)p(g)c(g,se)N(gt)	-	-9768.8	-	-10181.0
S(g)psi(gt)p(g)c(se)N(gt)	-6991.0	-	-	-
S(g)psi(g)p(g,se)c(g,se)N(gt)	-	-	-6753.1	-
S(g)psi(g)p(g)c(g,se)N(gt)	-	-9768.7	-	-10145.4
S(g)psi(g)p(g)c(se)N(gt)	-6969.7	-	-	-
S(gt)psi(null)p(g,se)c(g,se)N(gt)	-	-	***-6775.7**	-
S(gt)psi(null)p(g)c(g,se)N(gt)	-	-9768.0	-	***-10268.1**
S(gt)psi(null)p(g)c(se)N(gt)	-6874.1	-	-	-
S(g)psi(null)p(g,se)c(g,se)N(gt)	-	-	-6741.7	-
S(g)psi(null)p(g)c(g,se)N(gt)	-	-9760.0	-	-10147.0
S(g)psi(null)p(g)c(se)N(gt)	-6844.0	-	-	-
Null + p(g,se)c(g,se)N(gt)	-7479.0	-10053.5	**-6716.9**	-10557.6
Null + p(g,se)c(g)N(gt)	-7468.1	-9983.4	-6660.4	-10551.0
Null + p(g,se)c(se)N(gt)	-7483.0	-10049.0	-6707.2	-10527.4
Null + p(se)c(g,se)N(gt)	-6826.6	-9812.2	-6552.3	-10305.9
Null + p(se)c(g)N(gt)	-6813.6	-9742.0	-6495.7	-10299.2
Null + p(se)c(se)N(gt)	-6830.5	-9807.7	-6542.6	-10275.6

Null + p(g)c(g,se)N(gt)	-6816.1	**-9761.7**	-6473.2	**-10125.7**
Null + p(g)c(g)N(gt)	-6803.1	-9691.5	-6416.6	-10119.1
Null + c(g)N(gt)	-6633.7	-9499.7	-6304.2	-10010.5
Null + p(g)c(se)N(gt)	**-6820.1**	-9757.1	-6463.5	-10095.4
Null + p(g)N(gt)	-6798.8	-9689.4	-6412.9	-10085.9
Null + N(gt)	-6630.3	-9497.6	-6300.4	-9977.3
Null + N(g)	-6586.0	-9422.5	-6257.7	-9834.0
Null	-6509.5	-9421.2	-6253.2	-9834.9

Table 2.2. Models for survival, movement and population sizes are compared and results given for the 3 beaver-free springbrooks. Bold text and an asterisk indicate the best model for each spring brook. A model result highlighted in grey indicates that at least some of the parameters could not be estimated so that model was rejected. Bold text indicates the null model with the best p and c parameters that were then used to run different combinations of survival (S) and movement (psi) parameters. Hash marks indicate certain models weren't for some complexes (because they contained the wrong selection of p and c parameters).

	Site 5 (CR)	**Site 6 (CT)**	**Site 7 (NN)**
Model	AICc	AICc	AICc
S(t)psi(t)p(se)c(se)N(t)	**-**	-	***-** **1538.8397**
S(t)psi(t)p(g)c(se)N(t)	***-3156.1**	***-2755.5255**	-
S(t)psi(null)p(se)c(se)N(t)	-	-	-1538.8
S(t)psi(null)p(g)c(se)N(t)	-3134.8	-2755.5	-
S(null)psi(t)p(se)c(se)N(t)	-	-	-1533.3
S(null)psi(t)p(g)c(se)N(t)	-3143.0	-2708.9	-
Null + p(se)c(se)N(t)	-3304.4	-2829.7	**-1533.3**
Null + p(g,se)N(t)	-3292.4	-2753.7	-1529.6
Null + p(se)N(t)	-3135.4	-2753.7	-1529.6
Null + p(g)c(se)N(t)	**-3122.7**	**-2708.9**	-1473.4
Null + p(g)N(t)	-3110.7	-2632.9	-1469.7
Null + N(t)	-3023.1	-2632.9	-1469.7
Null	-3018.4	-2629.2	-1470.3

FIGURES

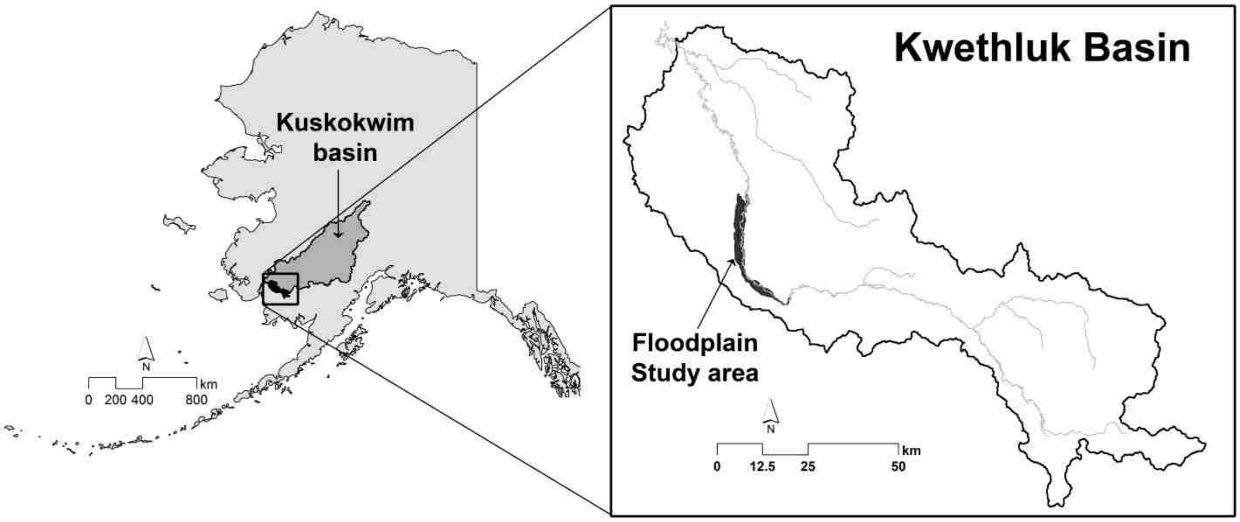

Figure 2.14. The Kwethluk River floodplain study area, a tributary of the Kuskokwim River, located in western Alaska.

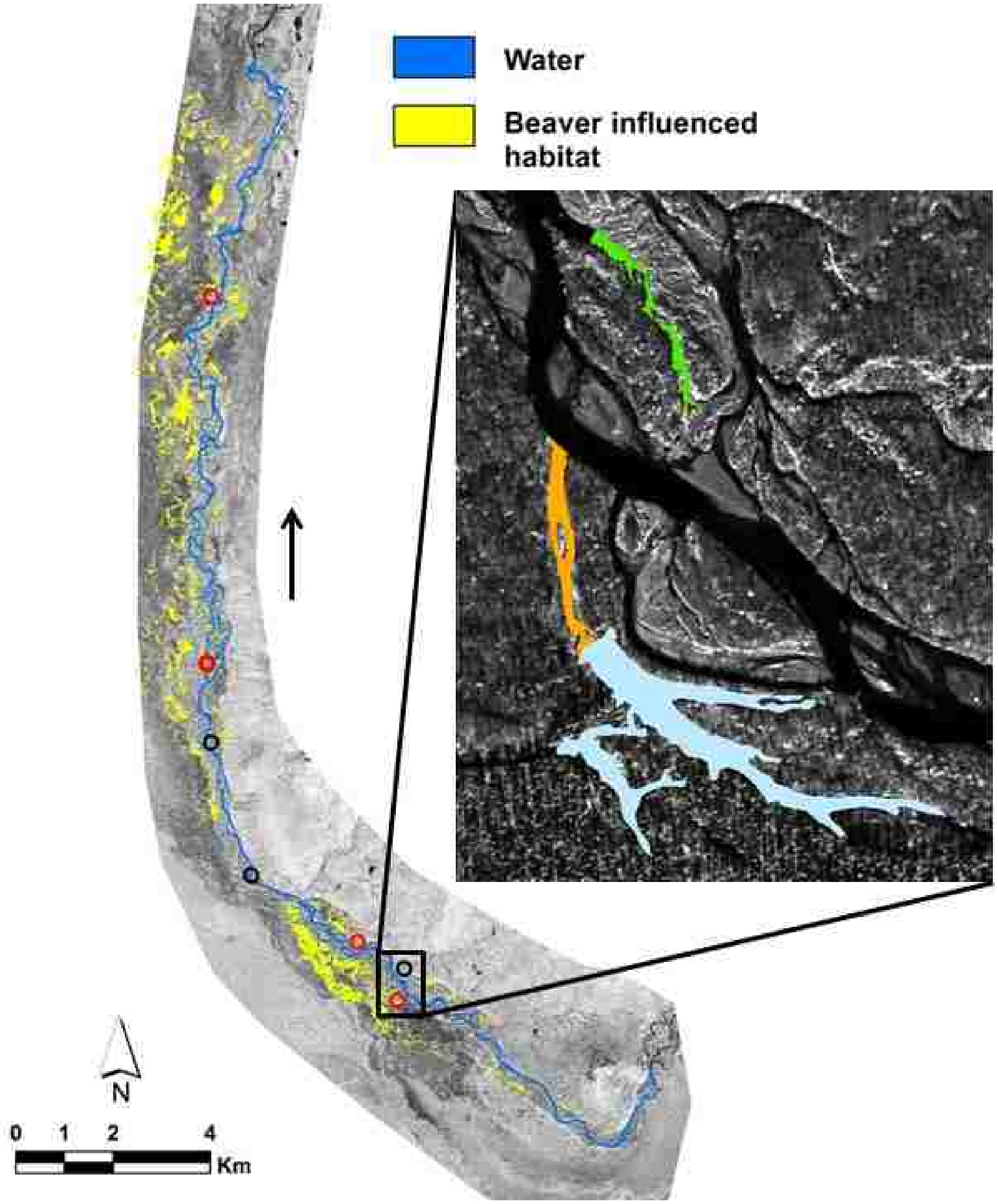

Figure 2.15. The 27-km study reach with water shown in blue and beaver influenced areas shown in yellow. Circles show the locations of mark-recapture study sites (paired beaver ponds and beaver-influenced springbrooks in red and beaver-free springbrooks in black). The inset illustrates an example of one beaver complex (beaver pond in blue and beaver-influenced springbrook in orange) and a beaver-free springbrook (in green). The black arrow indicates direction of flow.

Figure 2.16. Study sites located in parafluvial habitats, including (A) beaver-free spring brooks, (B) beaver-influenced spring brooks, and (C) early-successional beaver ponds (embedded in willow and alder). (D) Dams on early-successional ponds range from 1.1–2m in height.

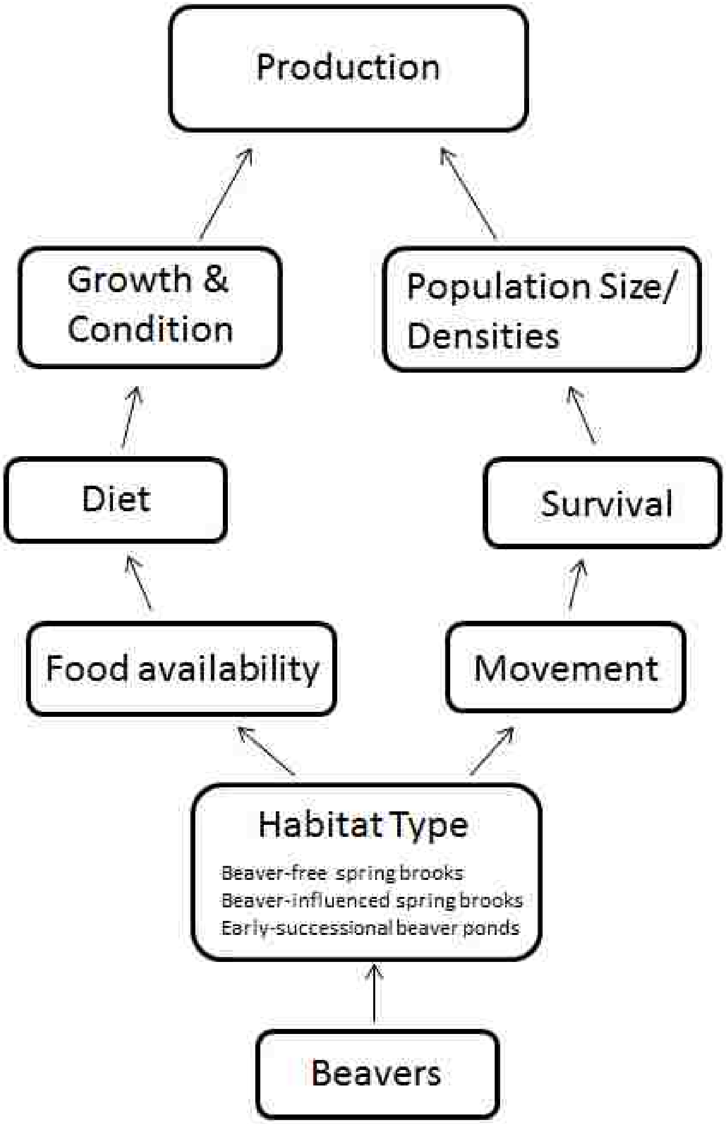

Figure 2.17. Flow diagram of factors and study design used to determine the influence of beavers on production of juvenile coho and Chinook salmon from the parafluvial zone of the Kwethluk River.

Figure 2.18. Photos contrasting conditions at base (A) and flood (B-D) flows. Double pit-tag antennae are visible on a beaver-influenced springbrook at base flow (A), but the antennae are submerged during flood flows (B). During floods, water flows over (C) and around (D) beaver dams during flooding, enhancing possible fish passage between the habitats.

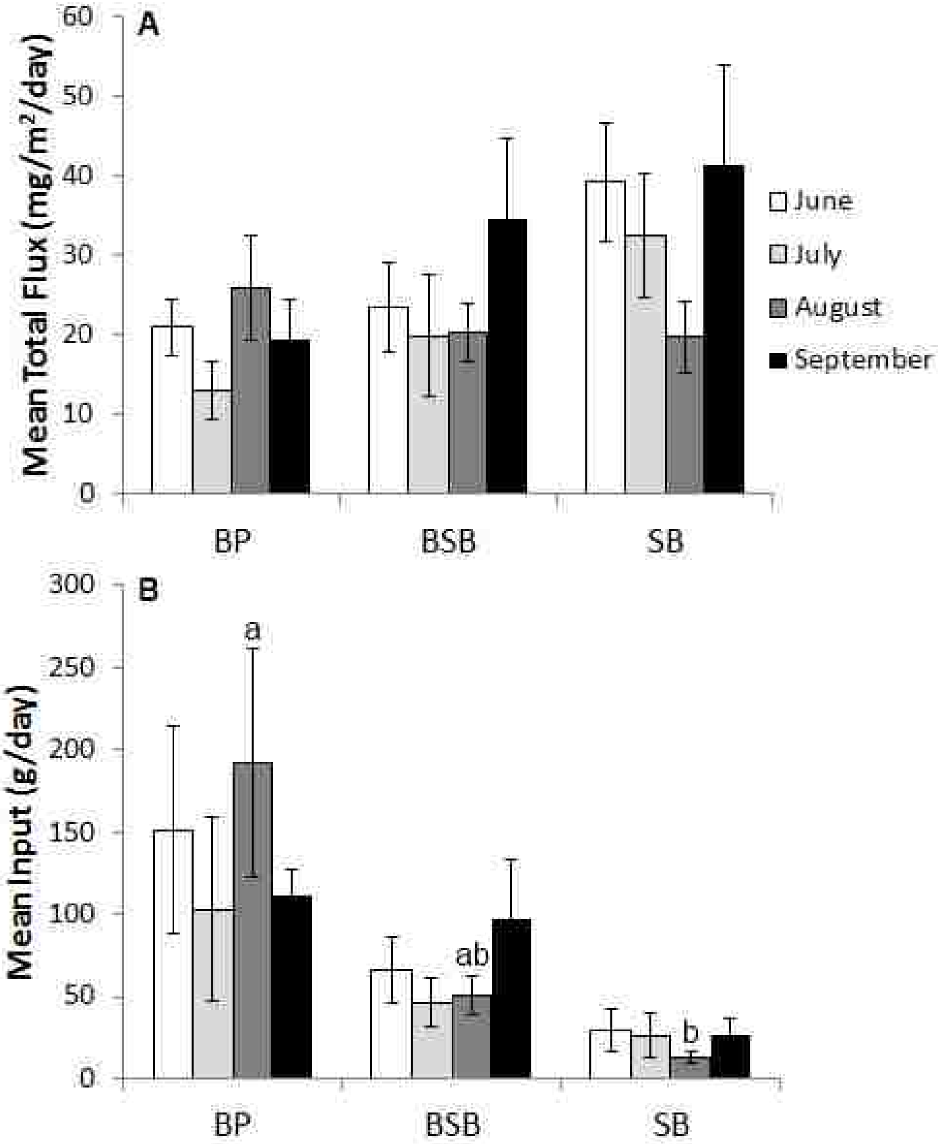

Figure 2.19A&B. Flux and inputs of aerial invertebrate biomass into floodplain habitats. (A) Mean (±1 SE) flux (mg/m^2/day) of invertebrates into pan traps in 4 beaver ponds (BP), 4 beaver-influenced springbrooks (BSB), and 3 beaver-free springbrooks (SB) during four sampling periods (June, July, August, and September). **(**B) The same data given in A) but mean total input is calculated by scaling flux values to the entire area of each site and averaging by habitat type.

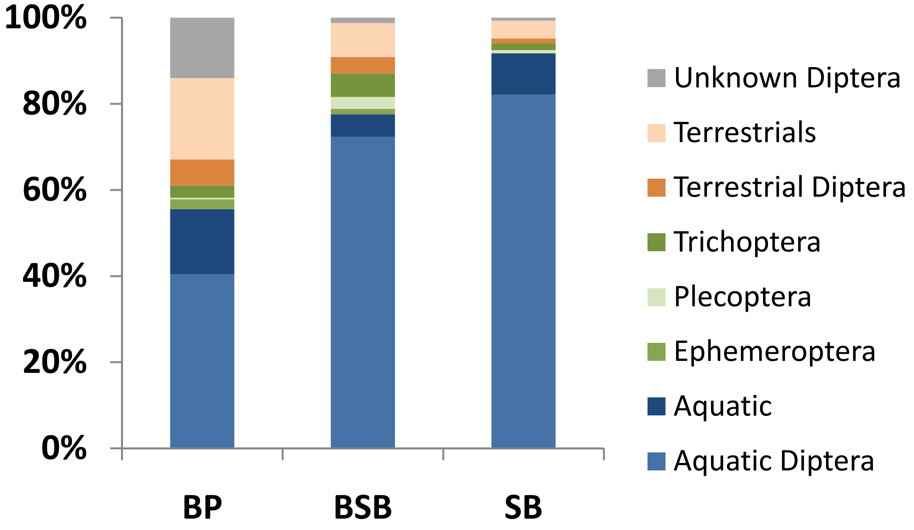

Figure 2.20. Mean composition of juvenile coho and Chinook diets by habitat type (BP = beaver pond, BSB = beaver influenced springbrook, SB = beaver-free springbrook).

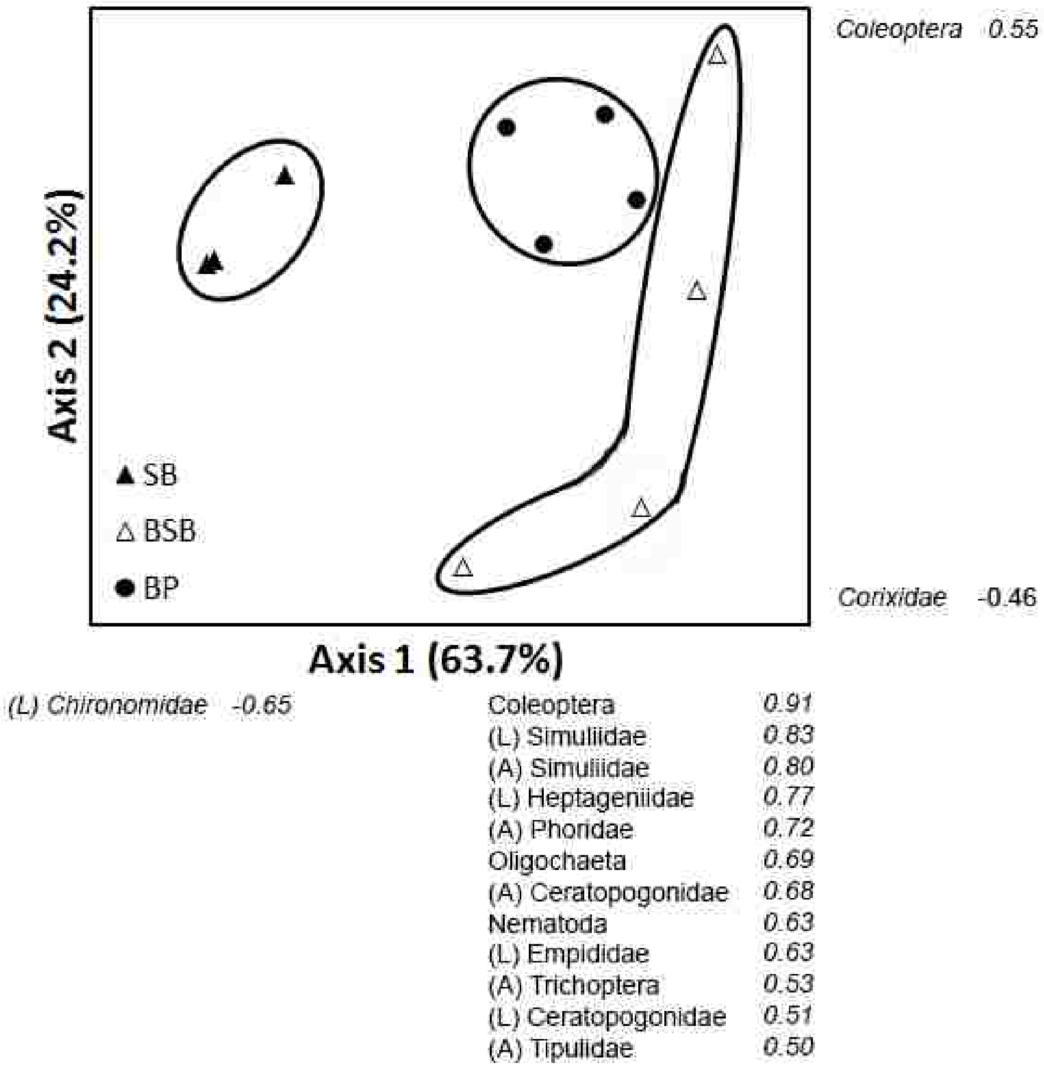

Figure 2.21. Ordination plot obtained by nonmetric multidimensional scaling of the relative abundance of macroinvertebrates in diets of juvenile coho residing in beaver-free springbrooks (SB), beaver-influenced springbrooks (BSB), and beaver ponds (BP). Site position in diet space is shown relative to axes 1 and 2 and diets in the three habitat types were significantly different. Numbers in parentheses next to axis titles represent the % variation explained by each axis. Relative importance of each taxon is indicated by ranking of Pearson correlation coefficients between taxon and each axis as given below the ordination plot. Aerial (A) and Larval (L) forms of macroinvertebrates were present in the diets.

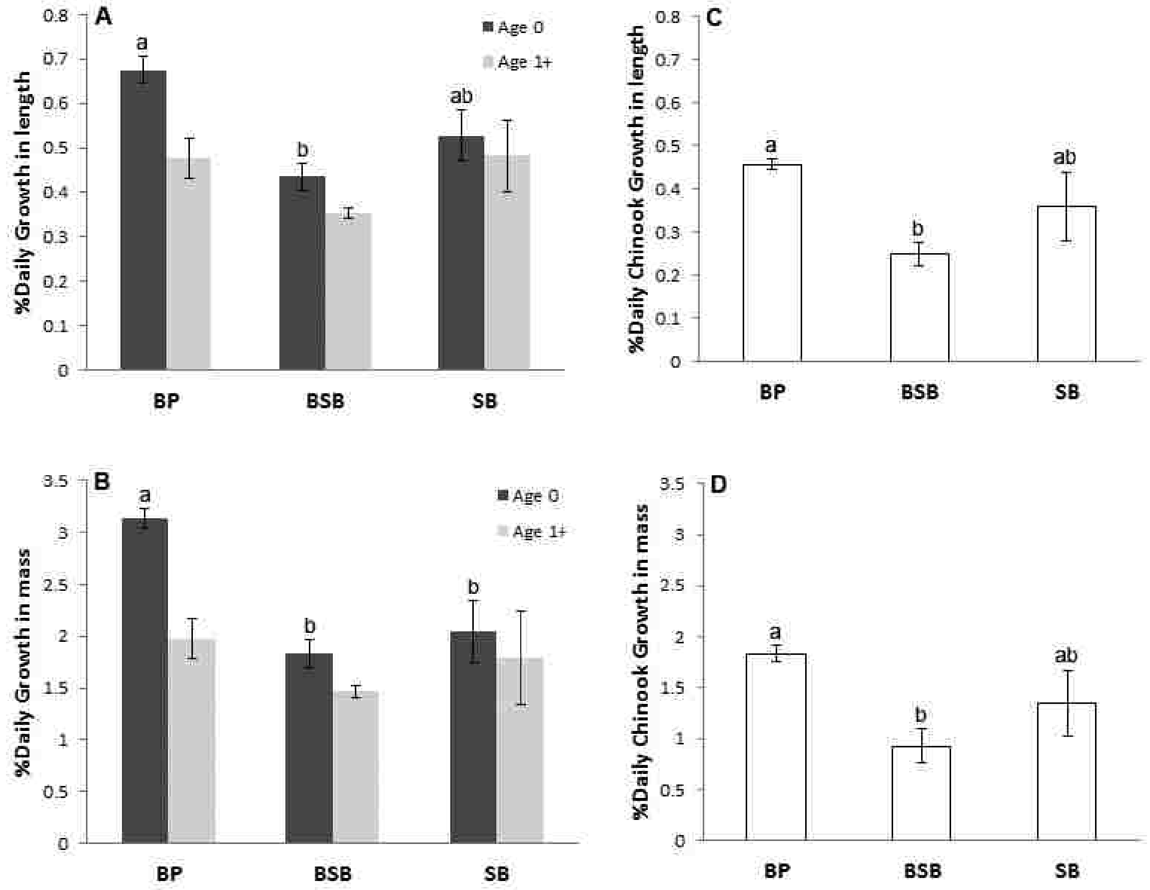

Figure 2.22. Mean (±1 SE) growth for age-0 and age-1+ coho in A) % daily length and B) % daily mass, and for age-0 Chinook in C) % daily length and D) % daily mass, for 4 early-successional beaver ponds (BP), 4 beaver-influenced springbrooks (BSB), and 3 beaver-free springbrooks (SB) based on fish recaptured during June to August.

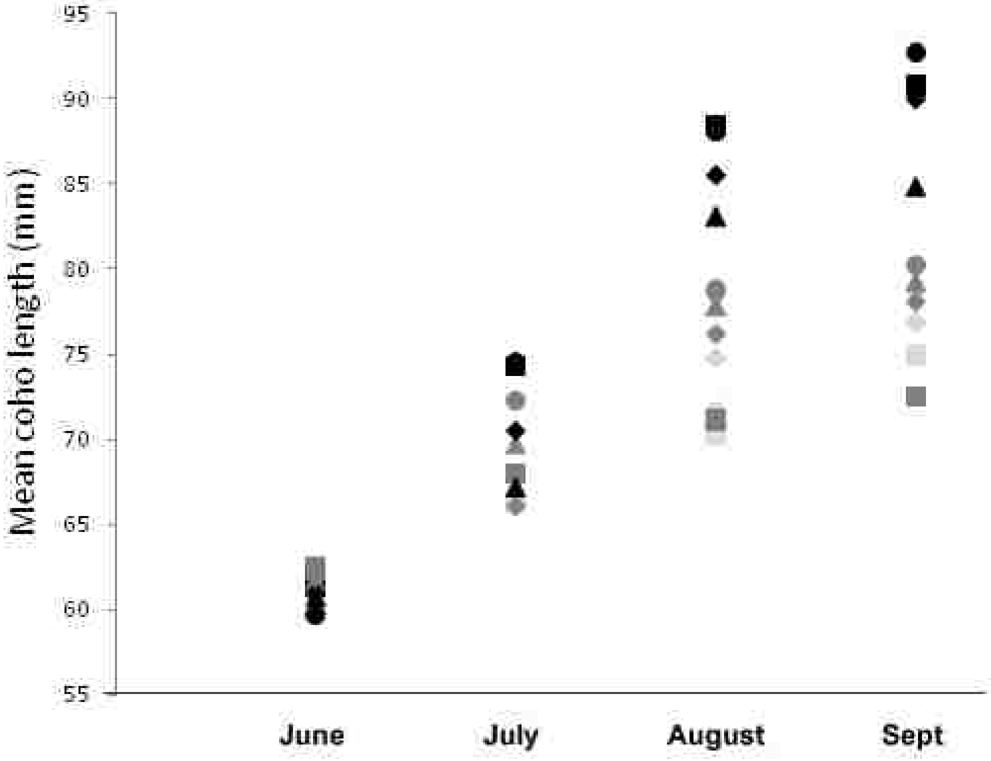

Figure 2.23. Length of age-0 coho by habitat type from June to September (black = beaver ponds, dark grey = beaver influenced springbrooks, light gray = springbrooks). Different symbols within each color group represent individual sites. Young of the year were about the same size in June but grew faster over the summer in beaver ponds than in the springbrooks.

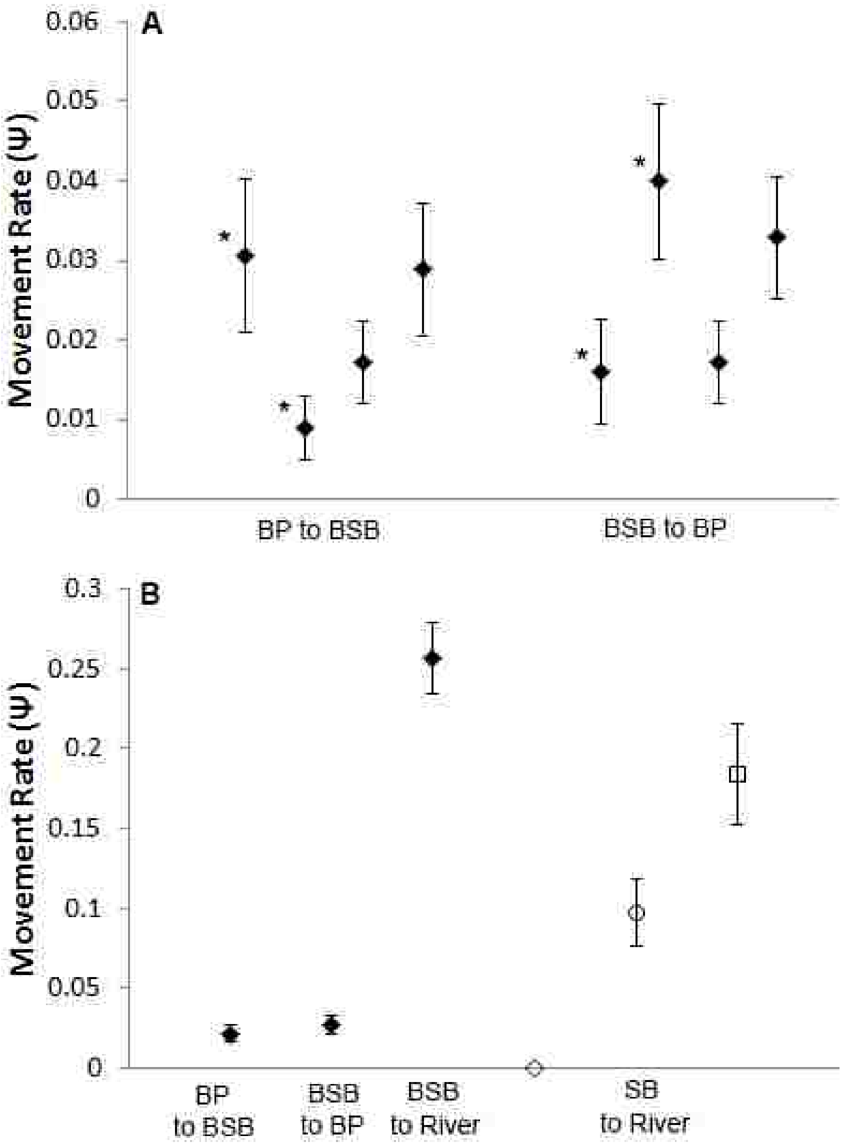

Figure 2.24. Movement rates (% of marked fish that moved) of juvenile salmon (coho and Chinook data pooled) among habitat types based upon mark-recapture data obtained in the four beaver complexes and one of the spring brook sites studied. (A) Mean (±1 SE) movement rates of juvenile coho and Chinook from beaver ponds to beaver-influenced springbrooks (BP to BSB) and from beaver-influenced springbrooks into beaver ponds (BSB to BP). (B) Mean (±1 SE) movement rates with sites pooled by habitat type (closed diamonds: from beaver ponds to beaver-influenced springbrooks (BP to BSB); from beaver-influenced springbrooks to beaver ponds (BSB to BP); from beaver-influenced springbrooks to the river (BSB to river) average over the entire summer period; and open symbols: from beaver-free springbrooks to the river (SB to river) over three time periods (open diamond = June-July (no fish moved), open circle = July-August, open square = August-September). Asterisks indicate sites with PIT-tag antennae; emigration data from these sites were used to parameterize the models in Program Mark.

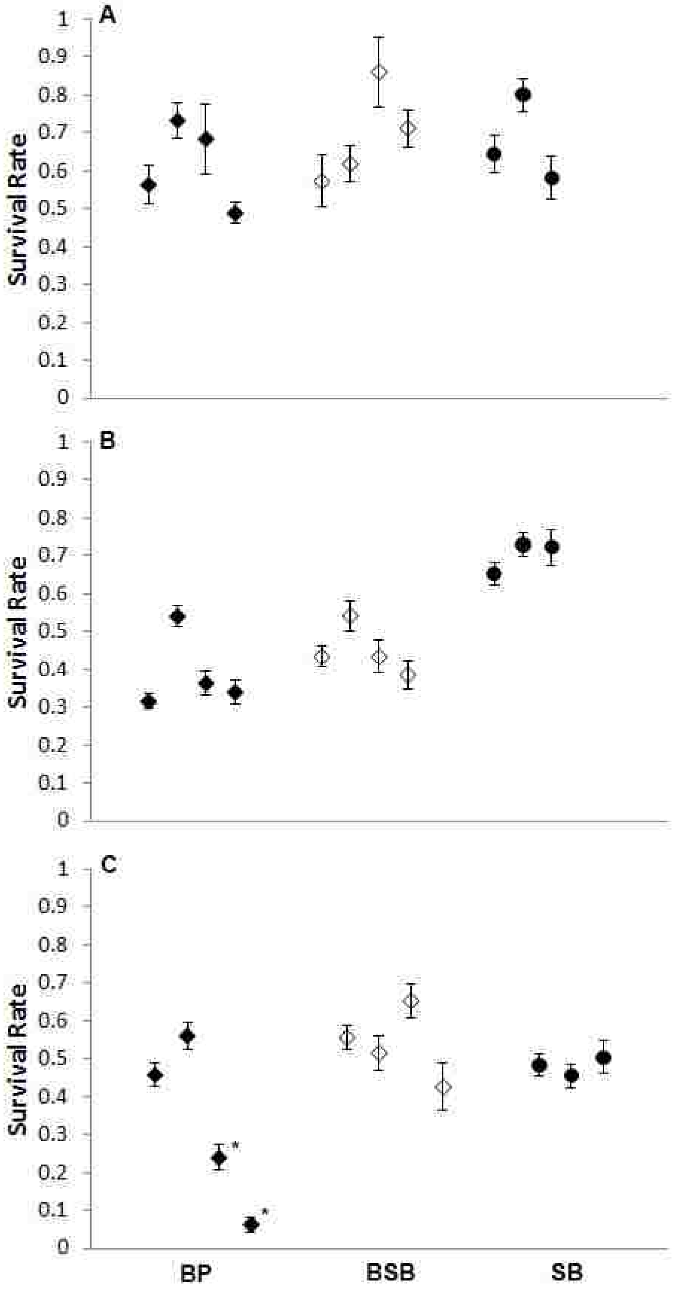

Figure 2.25. Survival rates (±1 SE) of juvenile coho salmon in beaver ponds (BP, closed diamonds), beaver-influenced springbrooks (BSB, open diamonds), and beaver-free springbrooks (SB, closed circles) for three time periods: (A) June-July, (B) July-August, and (C) August-September. * indicate survival rates that may be underestimates due to emigration.

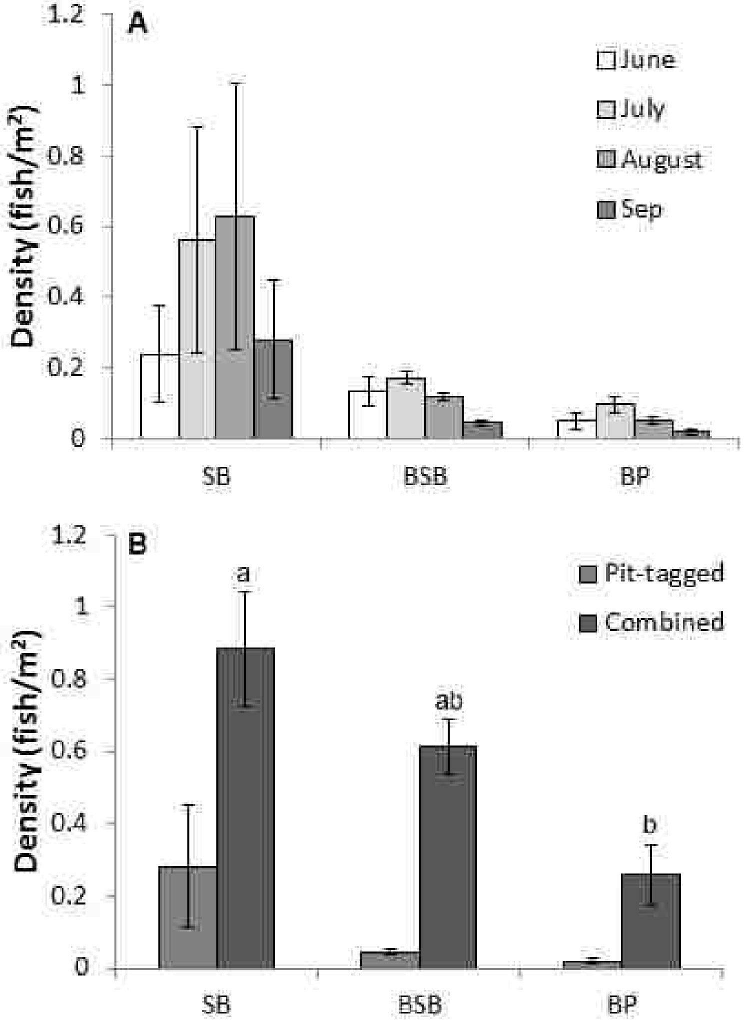

Figure 2.26. (A) Mean (±1 SE) juvenile coho and Chinook density of pit-tagged fish by habitat type for the 4 capture-mark-recapture sites (SB = beaver-free springbrooks, BSB = beaver-influenced springbrooks, and BP = early successional beaver ponds). (B) Mean (±1 SE) juvenile coho and Chinook density in September for pit-tagged fish (light grey) and all juveniles large enough to be tagged (pit-tagged and elastomer tagged, dark grey) for beaver-free springbrooks (SB), beaver-influenced springbrooks (BSB), and early-successional beaver ponds (BP).

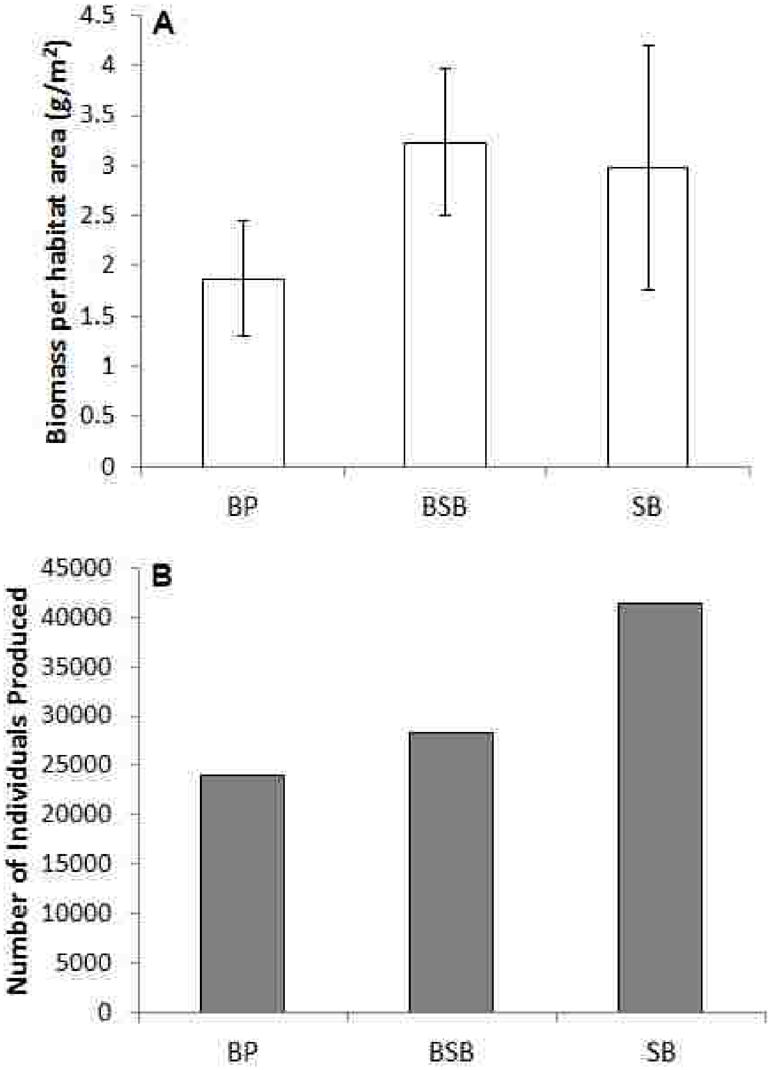

Figure 2.27. (A) Mean Biomass (± 1 SE, g) of juvenile salmon per sq. meter of each habitat type (SB = beaver-free springbrooks, BSB = beaver-influenced springbrooks, and BP = early successional beaver ponds) for the 7 study sites. (B) Number of individuals rearing in each habitat type for the entire floodplain.

CHPATER 3: BEAVERS REDUCE HABITAT CONNECTIVITY AND SALMON PRODUCTIVITY IN EXPANSIVE RIVER FLOODPLAINS

Abstract. We compared two large alluvial rivers known for their production of salmon to determine how beavers might influence juvenile salmon at the floodplain scale. Our goal was to provide perspective on the likely influences of beavers on juvenile salmon habitat use and production by comparing two rivers with similar physical drivers but that differed due to the presence of beavers in one river. We compared species richness, densities, condition and growth of juvenile coho and Chinook salmon between parafluvial and orthofluvial habitats within both rivers, as well as between the rivers. Species richness was similar by habitat type in the Kol (without beavers). In contrast, in the Kwethluk (with beavers) parafluvial habitats had twice as many species as orthofluvial habitats. Salmon density was similar in all habitat types in the Kol, but in the Kwethluk coho densities were 8-12x higher in off-channel spring brooks vs. the main channel and Chinook densities were up to 2x higher in parafluvial spring brooks than other floodplain habitats. In the Kol there was no difference in coho condition by habitat type but Chinook condition was highest in orthofluvial spring brooks. Within the Kwethluk there was no difference in Chinook condition, but the condition of coho was lowest in main channel versus all other habitats (0.89 vs. 0.99 – 1.10). We found that the Kol produces an order of magnitude more salmon biomass and rears 40x the individuals compared to the Kwethluk. We estimated that in the absence of beavers the Kwethluk floodplain could produce 2x the biomass (between June-August, 1174 vs. 667kg) and rear 3x the number of salmon (370,000 vs. 140,000).

Key words: Beaver (*Castor canadensis*), Pacific salmon, ecosystem engineering, salmon ecology, alluvial river floodplains, salmon production

INTRODUCTION

Forty-percent of all wild Pacific salmon are produced in the expansive floodplain rivers of Kamchatka, Russia, with most of the rest coming from the large floodplain river-lake systems of Alaska and British Columbia (Augerot 2005). The expansive floodplains of large rivers provide abundant spawning and rearing habitat for wild salmonids. Dynamic floodplain environments are maintained by processes of cut and fill alluviation, channel avulsion, riparian plant succession, ground- and surface water exchanges and erosion and deposition of live and dead wood that interact to create a complex shifting habitat mosaic (Stanford et al. 2005). Spring brooks in abandoned flood channels often are a dominant habitat type in expansive floodplains (Whited et al., 2013) and are known to be primary rearing areas for all species of Pacific salmon, trout and char (Eberle and Stanford 2010, Armstrong and Schindler 2013). Shallow spring brooks form by water upwelling from the floodplain aquifer, have warm winter and cool summer temperature patterns, and have high ecological connectivity with riparian food webs; therefore enhanced growth and survival of juvenile salmon has been documented in these habitats (Sommer et al. 2001, Jeffres et al. 2008, Bellmore et al. 2013).

Beavers in North American rivers typically dam spring brooks adding extensive pond complexes to the habitat mosaic of the floodplain (Malison et al. In review); whereas, beavers do not exist in the very productive salmon rivers of the Asian Far East, including Kamchatka. So, the interesting conservation question of whether beavers are good for salmon or not, can be approached by contrasting salmon ecology in rivers with and without beavers.

Beavers are well known to exert strong influences on growth and productivity of stream fishes by altering habitat characteristics in low order streams, but ultimate effects are both negative and positive. In low order streams beaver dams may impede or limit fish movement (Schlosser and Kallemeyn 2000, Mitchell and Cunjak 2007), promote siltation of spawning grounds (Taylor et al. 2010) and ponds may be hypoxic owing to microbial decomposition of retained organic matter (Burchsted et al. 2010). On the other hand, positive effects in low order streams include increases in the production of invertebrate food resources (Hanson and Campbell 1963, Keast and Fox 1990), increased density and sizes of fish, including salmon (Gard 1961, Hanson and Campbell 1963, Bryant 1983, Murphy et al. 1989, Leidholt Bruner et al. 1992, Schlosser 1995), higher survival rates (Bustard and Narver 1975, Quinn and Peterson 1996), faster growth rates (Bustard and Narver 1975, Swales and Levings 1989) and increased production (Nickelson et al. 1992, Layman and Smith 2001, Pollock et al. 2004). Less is known regarding the interactions of beavers and salmon in expansive floodplain settings of large rivers even though beavers are ubiquitous in large rivers throughout the range of salmon in North America.

The few studies addressing impacts of beavers on juvenile salmonids in expansive floodplains suggest that the potential for beavers to influence the ecology and production of salmon in rearing habitats is high. For example, in a large Alaskan river floodplain beavers dammed 80% of all spring brook habitats (Malison et al. In review). Parafluvial spring brooks occur close to the active channel network and are scoured annually by floods while orthofluvial spring brooks are located farther from the channel where flooding is infrequent. By building large dam complexes beavers may shrink the usable portion of the floodplain for juvenile salmon. In fact, the conversion of spring brooks to dammed ponds strongly restricted the ability of juvenile salmon to use orthofluvial habitats farther from the channel in an Alaskan river (Malison et al. In review). However, it is difficult to determine how the loss of orthofluvial floodplain habitats may influence salmon production. For example, if beavers were removed from a river, would juvenile salmon use of orthofluvial habitats be similar to their use of parafluvial habitats close to the main channel, or are orthofluvial habitats less important?

If beavers are able to influence juvenile salmon habitat and productivity this could have important implications for salmon conservation. The issue is extremely relevant because beaver populations have expanded in Alaska (with declining demand for pelts) and the re-establishment of beavers in rivers where extirpation occurred decades ago often is considered a management option to enhance salmonid production. However, the massive conversion of floodplain habitat by beavers may actually limit salmon production. Experimental approaches to the question are problematic. Measuring total salmon production in one or more beaver modified rivers prior to and following beaver removal would be ideal; but such an approach is simply not feasible owing to the massive scale (hundreds of km^2) of beaver activity in these floodplain settings (Malison et al. In review). However, lack of beavers in the salmon rivers of the Kamchatka Peninsula (Russian Federation) offers an interesting comparison to shed light on the issue. Thus, our approach was to compare and contrast habitat use and production of juvenile salmon on expansive floodplains of two geomorphically similar salmon rivers, the Kol in Kamchatka, Russia (no beavers) and the Kwethluk River in Alaska (abundant beavers). We focused studies on coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) because they rear in off channel habitats the longest out of the Pacific salmon and may be most strongly influenced by beavers.

Although many other factors, notably harvest, species composition of the ichthyofauna and supporting food webs, and import of marine derived nutrients, certainly also influence salmon productivity in the two rivers, we expected that the potential productivity of coho and Chinook would be much greater in the Kol (without beavers) than in the Kwethluk (with beavers) because spring brooks are more productive habitats than beaver ponds (see chapter 2). Our intent in this paper simply was to contrast the ecology of the two rivers and thereby provide a conservation perspective on the likely influences that beavers have on floodplain rivers. Thus, we measured rearing habitat availability by type (main channel shallow shorelines, tributaries, parafluvial and orthofluvial spring brooks, and early-, mid- and late-successional beaver ponds) in relation to species composition, densities, condition, and growth of juvenile salmon within the parafluvial and orthofluvial zones of the two rivers. Additionally, we conducted an experiment to determine if orthofluvial beaver ponds on the Kwethluk were of sufficient quality that juvenile salmon would rear and grow in them if they could be accessed. Lastly, we determined how beavers influence the production of juvenile salmon at the floodplain scale.

METHODS

Study Areas

The Kol is a 5th order river originating in the Central Mountain Range of the Kamchatka Peninsula, Russia (Figure 3.28). Floodwaters inundate the floodplains to the valley walls frequently, especially in the spring and fall (Eberle and Stanford 2010). The Kol study reach is an expansive anastomosing wandering river that reworks the entire floodplain. Channel avulsions are common, creating a complex network of flood channels that disconnect from the main channel through sediment accretion or levees mediated by wood jams (Figure 3.29). Channel beds that have been scoured low enough to intercept the shallow aquifer result in parafluvial spring brooks that flow along the abandoned flood channels near the river and older orthofluvial spring brooks farther from the river. The Kol is an extremely productive salmon river; with 3-10 million fish returning annually (6 salmon species + anadromous *O. mykiss* and 2 char species). Pink salmon dominate anadromous runs with 5-7 million returning on even years and approximately 500,000 on odd years (Pavlov et al. 2009). This productivity is largely due to a huge marine derived nutrient (MDN) subsidy and extensive networks of spring channels in both the parafluvial and orthofluvial zones which have strong trophic linkages to an expansive and productive floodplain forest (Eberle and Stanford 2010).

The Kwethluk River is a 5th order tributary of the Kuskokwim River on the west coast of Alaska. Similar to the Kol, floodwaters inundate the floodplains in the spring and fall. The study reach is an expansive anastomosing floodplain located between 37 and 64km (from Three-Step to Elbow Mountain) above the confluence of the Kwethluk with the Kuskokwim (Figure 3.28). Similar to the Kol, a complex network of flood channels is present and spring brooks persist at base flow in flood channels where the river has scoured sediments below the water table (Figure 3.29). However, due to abundant beaver habitat modification, combined with riparian plant succession over time, a complex mosaic of early-, mid-, and late-successional beaver ponds are distributed throughout the parafluvial and orthofluvial zones of the river (as described by Mouw et al. 2012) and beavers have reduced the anabranching extent and frequency as compared to the Kol. In fact, 80% of all off-channel habitats are located behind beaver dams (Malison et al. In review). The Kwethluk has far fewer fish return than the Kol but is still an important salmon river in the Kuskokwim basin, AK. Up to ~200,000 fish return annually (all 5 species – *O. mykiss* is resident only - over the past ten years) with coho and chum dominating the runs.

Both rivers have a long legacy of commercial and subsistence salmon harvest, however long-term harvest rates likely are 2-3x higher in the Kwethluk because the Kol is largely uninhabited whereas the Kwethluk Village sits at the base of the Kwethluk and town of Bethel is located downstream (Augerot 2005, Pavlov et al. 2009).

Data Collection

Floodplain Characteristics and Rearing Habitat Availability

To compare floodplain characteristics between the Kol and Kwethluk Rivers we obtained habitat complexity metrics from the Riverscape Analysis Project, which is a publicly available geospatial database of riverine and watershed physical structure of basins around the Pacific Rim (Whited et al. 2012). We quantified spring brooks and beaver ponds in relation to the shallow shorelines of the channel networks at base flow by classifying Quickbird satellite multispectral imagery collected on the Kol in 2004 and the Kwethluk in 2011. Initially, pixels associated with water bodies were classified and delineated using Definiens Developer (version 8.6; Definiens, Westminster, Colorado; www.ecognition.com/) and Erdas Imagine (version 9.3; Intergraph, Norcross, GA; www.geosptail.intergraph.com) software. Following delineation, habitat patches (i.e., ponds, spring brooks, and main channel shallow shorelines) were manually demarcated using heads-up digitizing (manually drawing polygons around features) in Arc/Map (version 10; ESRI, Redlands, California, USA; www.esri.com), following similar methods used by Whited et al. (2013). Image classifications were validated from field observations.

Juvenile Salmon Metrics

In the spring, summer and fall of 2004-2008 we routinely sampled juvenile salmon in representative main channel shallow shoreline, tributary, and parafluvial and orthofluvial spring brook sites on the Kol and Kwethluk River floodplains through the

Salmonid Rivers Observatory Network program (SaRON), a research and conservation cooperative of the Flathead Lake Biological Station, Moscow State University, the Wild Salmon Center (Portland, OR) and the Gordon and Betty Moore Foundation (see http://www2.umt.edu/flbs/Research/SaRON.aspx). Representative sampling sites within in each habitat type were distributed throughout the length of each of the two floodplains. We determined fish density by species in lotic habitats (main channel shallow shoreline, tributary and parafluvial and orthofluvial spring brooks) using 3-pass depletion electrofishing over 50m reaches delimited by block nets. We routinely sampled juvenile salmon in beaver ponds (of all successional stages) in 2006 and 2009-2011 through the SaRON program and as part of complimentary studies (Malison 2013 chapter 2, Malison et al. In review). Ponds were sampled by depletion minnow trapping in 2006 and by using capture-mark-recapture minnow trapping in 2009-2011. In all cases, fish were held in buckets with aerators, anesthetized with clove oil or MS-222, and then identified, measured and weighed. We calculated fish population densities from data collected in both rivers from 2004-2008 using Bayesian inference for depletion estimates (Wyatt 2002). We calculated Fulton's condition factor, K (Ricker 1975), for each fish by dividing mass (g) by length (mm) cubed and multiplying by a scalar of 10^5 to determine if condition varied by habitat type or by river floodplain. We also calculated % daily batch growth rates in mass (m_n) for coho and Chinook in each habitat type in both rivers. Percent daily growth in mass was calculated using the formula: $((m_2-m_1)/(m_1*(t_2-t_1)))*100$. To determine accuracy of batch growth rates we compared batch growth rates to individual growth rates (from PIT-tagged individuals) from habitats sampled on the Kwethluk during 2009-2011.

Enclosure experiment

To determine if use of orthofluvial habitats by juvenile salmonids was restricted because of poor habitat quality we conducted an enclosure experiment in five habitat types including: the main channel, beaver-influenced spring brooks, and early-, mid- and late-successional beaver ponds in the Kwethluk River. Beaver-influenced spring brooks were added as a habitat type in 2009 because they made up a significant portion of the parafluvial habitat used by juvenile salmon. We placed two enclosures (1m x 1m x 2m) in 3 replicates of each habitat type between June 14 and August 22, 2011. We placed eight individually marked coho in each enclosure and measured and weighed each individual every two weeks to calculate growth rates. If individuals died they were replaced with new individuals to keep densities the same in each enclosure. We used growth as a surrogate for habitat quality to determine how late-successional pond habitat in the orthofluvial zone compared to parafluvial habitats.

Floodplain production

We estimated the biomass of individuals produced from off channel habitats in both floodplains by extrapolating biomass/m^2 (calculated from batch growth rates and density estimates) to the total area of each habitat type for each floodplain for the time period between June and August. Because growth data were sparse for Chinook we used coho growth rates for the production estimates. We used the combined density of coho and Chinook in production calculations. We calculated production from off-channel habitats for both rivers (i.e. parafluvial and orthofluvial spring brooks in the Kol and beaver-free spring brooks, beaver-influenced spring brooks, and early-, mid-, and late-successional beaver ponds in the Kwethluk) because the way in which beavers may influence production is by damming off-channel habitats. Malison (2013 chapter 2) calculated total production of juvenile coho and Chinook for the parafluvial zone of the Kwethluk floodplain (including spring brooks, beaver-influenced spring brooks, and early-successional beaver ponds). We calculated total production for mid- and late-successional habitats and combined these data with the estimates from Malison (2013 chapter 2) to determine production from the entire off-channel floodplain study reach. We also estimated the number of individuals that reared in each habitat type because it is possible that patterns in biomass accumulation may be different from the number of individuals produced.

We also estimated what the floodplain scale production of juvenile coho and Chinook would be in the Kwethluk in the absence of beavers by estimating production if all spring brooks were free flowing. To estimate the area that would be covered by free flowing spring brooks instead of ponds we used satellite imagery in ArcMap to delineate known channel courses (i.e. previous spring brook paths) in pond complexes and calculated the percentage of area that would be covered if dams were not present. We estimated that roughly 45% of the area currently covered by beaver ponds in the orthofluvial zone would be covered by orthofluvial spring brooks if dams weren't present. Because juvenile salmon habitat use, condition and growth were similar in the parafluvial and orthofluvial zones of the Kol River (without beavers), we used density and growth estimates from beaver-free parafluvial spring brooks in the Kwethluk to estimate what production might be from beaver-free orthofluvial spring brooks. This gave an estimate of the magnitude of production that could be lost due to beaver habitat modification on the Kwethluk.

Statistical Analyses

We analyzed the effect of habitat type on the number of species, density, condition, batch growth and enclosure growth rates of juvenile coho and Chinook in each river using one-way analysis of variance (ANOVA)(PROC GLM, SAS Institute Inc., Cary, North Carolina). Pairwise comparisons among the least squares means for habitat type were assessed using Tukey's honestly significant difference (HSD). All data sets were tested for normality and, where necessary, log10 transformed in SAS to improve normality and homogeneity of variance prior to statistical analysis. Where the assumption of homogeneity of variance assumption could still not be met Welch's ANOVA was used because the probability of a false positive may be much higher than 5 percent in the one-way ANOVA.

Comparisons of the effect of river type (with or without beavers) were made using t-tests. Because multiple comparisons were done for each variable (for multiple habitat type comparisons) a Bonferroni correction factor (Rice 1989) was used to determine the significance level by dividing 0.05 by the number of tests. All statistical tests were considered significant where $P<0.05$, unless a Bonferroni correction was applied.

RESULTS

Comparative Floodplain Characteristics

The Kwethluk has a larger catchment area and larger total floodplain area than the Kol River, but the mean floodplain elevation, number of floodplains, floodplain to watershed ratio, floodplain sinuosity, and number of nodes is similar for both rivers (Table 3.3). The Kol has over twice as many nodes per length of floodplain as the Kwethluk, showing that the Kol floodplains are more complex. Both rivers are bounded by tundra at the edges of the floodplains and are free from human alteration. The focal study reaches of the two rivers have similar slopes (Kwethluk, 0.0020 and Kol, 0.0022), river width (Kwethluk, 42m and Kol, 50m) and types of sediment supplies (dominated by gravel and cobble) indicating that the primary physical drivers of floodplain complexity are similar. Within the study reaches, the Kol River has almost 1.5x more total aquatic habitat than the Kwethluk but the percentage of off-channel habitat is similar for both rivers (20.5 vs. 22.6 %, Table 3.3). However, over 99% of off-channel aquatic habitats in the Kol are comprised of parafluvial (55%) and orthofluvial (45%) spring brooks (the small remainder being parafluvial ponds) while in the Kwethluk only 17% of the off channel habitat is comprised of spring brooks as a result of beaver interventions. In fact, the majority of off-channel habitat in the Kwethluk is located behind beaver dams (80%) of varying successional stages (described by Mouw et al. 2012).

Species Composition and Fish Densities

Species Composition

Within the Kol River all twelve fish species known to occur in Kamchatka were found in all habitat types (Figure 3.30A). Dolly Varden (*Salvelinus malma*) made up the greatest proportion of fish in main channel habitats and the least in orthofluvial habitats. Coho were most abundant in orthofluvial spring brooks and least abundant in main channel habitats. The total number of fish species and the number of salmon species was similar for all floodplain habitats at the Kol ($F_{[3,22]} = 1.72$, $P = 0.1919$ and $F_{[3,22]} = 1.57$, $P = 0.2251$).

Within the Kwethluk floodplain, sculpin (*Cottus cognatus*) was the most abundant taxon in main channel and tributary habitats, coho and Chinook salmon were co-dominant in backwaters and coho salmon dominated spring brooks and beaver ponds (Figure 3.30B). In contrast to the Kol, the total number of fish species varied significantly with habitat type in the Kwethluk ($F_{[8,53]} = 3.03$, $P = 0.0070$). Significantly more species were present in parafluvial spring brooks and early-successional beaver ponds than in late-successional ponds (Tukey's HSD, $P < 0.0361$), and though not significant, 2x more species were present in tributaries than in late-successional beaver ponds (Tukey's HSD, $P < 0.0791$). The number of salmon species also varied by habitat type ($F_{[8, 15.94]} = 2.50$, P 0.0566), with 1.7-2x more species of salmon present in main channel shallow shorelines, tributaries, spring brooks and early- and mid-successional ponds than in late-successional beaver ponds (Tukey's HSD, $P < 0.0476$).

Though species composition varied by river, coho predominated in off channel habitats in both rivers (44% in the Kol and 46% in the Kwethluk; Figure 3.30A&B). Chinook salmon were less abundant in the Kol vs. the Kwethluk (3 vs. 25%). Coho, sockeye (*Oncorhynchus nerka*), and lamprey (*Lampeta spp.*) made up greater proportions of the fish in orthofluvial vs. parafluvial habitats in the Kol River. This suggests that orthofluvial habitats would be important habitats for coho and sockeye in the Kwethluk if beaver dams weren't present.

Density

In the Kol River total fish, coho, and Chinook densities were similar for all habitat types ($F_{[3,28]} = 2.70$, $P = 0.065$, $F_{[3,7.7543]} = 3.06$, $P = 0.0937$, and $F_{[3,5.6905]} = 3.15$, $P =$ 0.1125; Figure 3.31A).

In contrast, densities of all fish, coho, and Chinook varied by habitat type in the Kwethluk River ($F_{[3,28]} = 12.8$, $P < 0.0001$, $F_{[3,28]} = 6.37$, $P = 0.002$, and $F_{[3,28]} = 2.94$, $P =$

0.0505; Figure 3.31B). Main channel habitats had lower densities compared to off-channel parafluvial and orthofluvial spring brooks (Tukey's HSD, $P < 0.0099$). Tributaries also had lower total densities compared to parafluvial spring brooks (Tukey's HSD, $P = 0.0069$). Coho and Chinook densities were lower in main channel habitats compared to parafluvial spring brooks (Tukey's HSD, $P = 0.0014$ and $P = 0.0462$). Compared to main channel, tributary and spring brooks habitats, densities were 3-12x lower in mid- and late-successional beaver ponds (see Malison et al. In review).

All habitats of the Kol had higher total densities compared to the Kwethluk ($t > 2.18$, $P < 0.0112$), except for parafluvial spring brooks ($t = 2.57$, $P = 0.1108$). Coho densities were higher in main channel habitats in the Kol vs. the Kwethluk ($t = 2.20$, $P = 0.0012$), but similar for other habitats. Chinook densities were higher in Kol main channel habitats than in Kwethluk main channel habitats ($t = 2.16$, $P = 0.0052$).

Fish Condition and Growth

Fish Condition

Juvenile coho in main channel, parafluvial and orthofluvial spring brook habitats all had similar condition factors in the Kol River ($F_{[2,15]} = 0.82$, $P = 0.4582$). However, the condition of Chinook did vary by habitat type ($F_{[2,12]} = 7.49$, $P = 0.0077$), being higher in orthofluvial vs. parafluvial spring brooks (Tukey's HSD, $P = 0.0107$) and higher in main channel habitats vs. parafluvial spring brooks (Tukey's HSD, $P = 0.0317$).

In contrast, the condition of juvenile coho varied significantly by habitat type for the Kwethluk River ($F_{[6,15.4581} = 10.28$, $P = 0.0001$). Main channel coho had lower condition factors than coho in all other habitat types (Tukey's HSD, $P < 0.0015$), except for orthofluvial spring brooks which were similar to the main channel. The condition of juvenile Chinook did not differ by habitat type ($F_{[6,39]} = 1.45$, $P = 0.2204$).

Comparing the two rivers, we found that juvenile coho were in better condition in all habitat types in the Kol River ($t > 2.11$, $P < 0.0043$). Juvenile Chinook were in better condition in main channel and orthofluvial habitats in the Kol vs. the Kwethluk ($t > 2.13$, $P < 0.0042$).

Growth Rates

Within the Kol River mean batch growth rates varied by habitat type for age-0 coho ($F_{[3,4]} = 10.47$, $P = 0.023$; Figure 3.32A), with main channel and orthofluvial spring brook habitats having higher growth rates than parafluvial spring brooks (Tukey's HSD, $P < 0.029$). Growth rates of age 1+ coho did not differ by habitat type ($F_{[3,5]} = 2.28$, $P = 0.197$).

Within the Kwethluk mean batch growth rates were similar among all habitat types for age-0 and age 1+ coho ($F_{[6,18]} = 1.64$, $P = 0.193$ and $F_{[4,14]} = 1.70$, $P = 0.207$; Figure 3.32B). In the one late-successional pond with juvenile salmon (other late-successional sites had no salmon), batch growth rates were 2x lower than in spring brooks and 3-4x lower than in early- and mid-successional ponds.

In comparing the two rivers, age-0 coho grew almost 3x faster in parafluvial spring brooks in the Kwethluk than in the Kol, though the difference was not significant after Bonferroni correction ($t = 2.36$, $P = 0.0166$). Age-0 coho in main channel shallow shorelines, tributaries, and orthofluvial spring brooks grew at similar rates in both rivers ($P > 0.2515$). Age 1+ coho grew at similar rates in parafluvial and orthofluvial spring brooks in both rivers ($P > 0.1375$). Chinook also grew at similar rates in main channel habitats of both rivers (t = 4.30, $P = 0.4684$).

Batch growth rates differed significantly and underestimated growth compared to growth rates from individually tagged coho for age-0 fish ($F_{[4,45]} = 20.64$, $P = <0.0001$). In contrast, growth rates calculated from individuals were similar to batch growth rates for age-1+ coho ($F_{[4,50\,]} = 1.54$, $P = 0.2059$). Using batch growth rates likely underestimates growth, mainly because newly emerged age-0 fish continually enter the sampling pool as they grow large enough to be captured. Though batch rates likely underestimate production estimates we used the same methods in both floodplain reaches, allowing comparisons to be made.

Kwethluk Enclosure Study

Growth rates varied significantly by habitat type in both % daily mass and % daily length ($F_{[4,9]} = 8.13$, $P = 0.0047$ and $F_{[4,9]} = 7.54$, $P = 0.006$, respectively, Figure 3.33) for juvenile coho reared in enclosures. Juvenile coho in main channel enclosures grew significantly faster than coho in beaver-influenced spring brooks and early- and mid-successional beaver ponds based on increases in mass and length (Tukey's HSD, $P < 0.0249$ and $P < 0.0374$, respectively). Coho growth in late-successional enclosures was similar to all other habitat types (Tukey's HSD, $P > 0.1129$). Thus we concluded that the late-successional beaver ponds in the orthofluvial zone would be suitable rearing habitats if they could be accessed.

Floodplain Scale Production – The Kol

Parafluvial and orthofluvial spring brooks produced a similar biomass of juvenile coho and Chinook per square meter (Figure 3.34A). For the entire floodplain, we estimated that parafluvial spring brooks produced 49 kg/day (2692 kg in total) and reared 2,333,549 individuals while orthofluvial spring brooks produced 45 kg/day (2712 kg in total) and reared 2,523,407 individuals for a total of 5404 kg and 4,856,956 individuals (Figure 3.35A).

Floodplain scale production – The Kwethluk with and without beavers

Biomass produced per square meter varied by habitat type on the Kwethluk ($F_{[4,14]} = 4.61$, $P = 0.0139$; Figure 3.7B). Production from the parafluvial zone (including beaver-free and beaver-influenced spring brooks, and early-successional beaver ponds) was estimated to be 7.7 kg/day (464 kg in total) and 93,750 individuals were reared. We estimated that an additional 3.3 kg/day (199 kg in total) was produced from and ~43,400 individuals were reared in mid-successional beaver pond habitats on the Kwethluk (Figure 3.35B). Production from late-successional ponds was extremely low, with almost 50x less salmon being produced than from mid-successional ponds at 0.07 kg/day (4 kg in total) and only 3,100 individuals were reared (Figure 3.35). Combining all parafluvial and orthofluvial off-channel habitats we estimate that 667 kg of biomass was produced and 140,300 juvenile coho were reared in the presence of beavers (Figure 3.35B).

Based on habitat availability in the Kol River we assumed that if beavers were not present on the Kwethluk River, all off-channel habitats would be free-flowing, connected to the main channel, and ideal rearing habitats as they are on the Kol River. In the absence of beavers we estimated that the parafluvial zone would produce 1.5x less biomass but would rear 1.2x the numbers of juvenile coho and Chinook. In the orthofluvial zone, replacing mid-successional ponds with orthofluvial spring brooks would result in 1.5x the biomass (287 kg vs. 199 kg) and a two-fold increase in the number of individuals (~96,300 ind. vs. ~43,400 ind.). Replacing late-successional ponds with orthofluvial spring brooks would result in a fifty-fold increase in production (207 kg vs. 4 kg, and ~154,100 ind. vs. ~3,100 ind.; Figure 3.35). In total for the floodplain we estimated production of biomass would be 2x higher between June-August (1,174 kg vs. 667 kg), and almost 3x the number of individuals would be reared (370,000 vs. 140,000 individuals; Figure 3.35) if beavers were not present. Compared to the Kwethluk, the Kol River produces an order of magnitude greater biomass (in just two months) and rears almost forty times more juveniles per year from off-channel habitats.

DISCUSSION

Beavers reduce the production potential of large alluvial river floodplains by two mechanisms. First and foremost, modification of shallow water habitats essentially shrinks the usable portion of the floodplain by blocking off much of the orthofluvial zone. Very few salmon were present in orthofluvial habitats farther from the main channel in the Kwethluk River, compared to the Kol River where juvenile salmonids of all species were present in all habitats and were very abundant in spring brooks throughout the floodplain. Our enclosure experiment on the Kwethluk showed that growth rates were similar in late-successional pond enclosures compared to all other habitats, suggesting all ponds could support salmon. However, we know nothing about overwinter survival, so the problem could be a combination of access and overwinter survival. In any case, orthofluvial habitats on the Kwethluk are not significantly utilized by any of the salmon species because access is limited. Second, within the parafluvial zone where juvenile salmon predominantly reared, the presence of ponds resulted in fewer individuals being produced per unit area in ponds compared to spring brooks

(Malison 2013 chapter 2). Thus, by reducing connectivity and impounding habitats that are less productive (on a per unit area basis) beavers reduce juvenile salmon production.

The floodplains of both rivers are complex but at the Kol all habitats are completely connected to the main channel. As a result we found that orthofluvial spring brooks were just as important rearing habitats as parafluvial springbrooks and main channel shallow shorelines. In comparison, the Kwethluk floodplain, while equally complex, is largely disconnected due to beaver activity. Because fish condition and densities were similar for the parafluvial and orthofluvial zones of the Kol River, we inferred that juvenile salmon would use parafluvial and orthofluvial spring brooks of the Kwethluk similarly in the absence of beavers. We estimated that over twice the biomass might be produced and that the floodplain could rear three times the number of juvenile salmon if extensive beaver complexes did not shrink the usable floodplain on the Kwethluk River. Thus, we conclude that beaver modification of spring brook habitats reduces production potential of salmon rivers with expansive floodplains.

We estimated that production from the Kol River was an order of magnitude higher in biomass and that 40x more individuals could be reared compared to the Kwethluk. However, factors other than available rearing habitat, such as escapement and basin fertility could strongly influence these estimates. We know that reductions in escapement (i.e. the number of adults returning to spawn) can strongly impact food availability and growth rates of juvenile salmon by influencing riverine fertility (Bilby et al. 1996, Wipfli et al. 2003). The spawning and death of salmon clearly influences the overall productivity of streams (Richey 1975, Wipfli et al. 1998) and this subsidy of marine derived nutrients (MDN) induces positive feedback loops where increases in juvenile salmon production occurs in response to increased MDN in productivity of multiple trophic levels (Wipfli et al. 1998, Schindler et al. 2005). Thus differences in escapement between the Kwethluk and Kol should result in differences in fertility. Indeed, Morris et al. (2013) found that rivers around the Pacific Rim varied with relation to MDN loading from returning salmon, and that the Kwethluk exhibited much lower foliar $\delta^{15}N$ than the Kol. Thus the Kwethluk may have lower production potential because of reduced escapement and fertility owing to harvest management. Nonetheless, it is quite clear that beavers reduce the usable habitat for salmon on the Kwethluk floodplain compared to the Kol.

Regardless of the potential for beavers to influence salmon production, beavers and salmon evolved together in North American rivers and beavers have been part of the North American landscapes since the early Holocene (Robinson et al. 2007). The benefits of beavers for restoration have been recognized (Pollock et al. 2007, Burchsted et al. 2010) and beavers are currently being reintroduced into low order systems in the west as part of restoration efforts. Even if beaver ponds were replaced with spring brooks on the Kwethluk River, it is unclear how the overall production of juvenile salmon on the floodplain would be influenced and the long-term legacy of beaver modification of the floodplain would still be present. If overall salmon production were to increase following dam removal that would suggest that habitat limitation and density dependent effects are currently occurring on the Kwethluk River. However, habitat limitation seems unlikely, even in the presence of beavers, as escapement levels have declined by 12-15x for coho and Chinook in the Kwethluk River over the past 9 years (Miller and Harper 2012). Furthermore, we documented much higher densities of juvenile salmon in the Kol River than the Kwethluk River (up to 14.9 coho/m^2) and these fish also had high condition factors. The Kol floodplain seems to have a much higher capacity to produce salmon smolts than the Kwethluk River. Even if beavers were not present on the Kwethluk our estimates still show that the Kol River could produce 5 times the biomass and 14 times the individuals as the Kwethluk might without beavers, likely due to the 1-2 orders of magnitude higher escapement levels that the Kol receives. Beavers are part of the North American landscape and their modification of off-channel floodplain rearing habitats may result in lower production potentials for North American rivers as compared to far eastern rivers without beavers.

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TABLES

Table 3.3. Watershed and study reach characteristics for the Kwethluk River, AK and the Kol River, Kamchatka Russian Federation. Habitat complexity metrics for comparison of the Kwethluk and Kol Rivers were obtained from the Riverscape Analysis Project, which is a publicly available geospatial database of riverine and watershed physical structure of basins around the Pacific Rim (Whited et al. 2012). Multispectral imagery from the Quickbird satellite for 2004 was quantified for the Kol and imagery from 2011 was quantified for the Kwethluk to determine the types and amounts of aquatic habitats for both study reaches.

	Kwethluk	**Kol**
Watershed area	3846 km2	1502 km2
Total Floodplain area	2.49 x 10^8 m2	1.04 x 10^8 m2
Mean floodplain elevation	212 m	280 m
Floodplains (#)	10	8
Floodplain: Watershed Ratio	0.06	0.07
Floodplain Sinuosity	1.68	1.20
Nodes (#)	224	192
Nodes per length of Floodplain	0.86	1.81
Total aquatic habitat	283 ha	409 ha
Main Channel total area	219 ha	325 ha
Off-channel habitat area	64 ha	84 ha
Spring brook total area	11 ha	83 ha
% off-channel spring brook area	0.17	0.99
Beaver pond area	51 ha	0
% off-channel beaver pond area	0.80	0

FIGURES

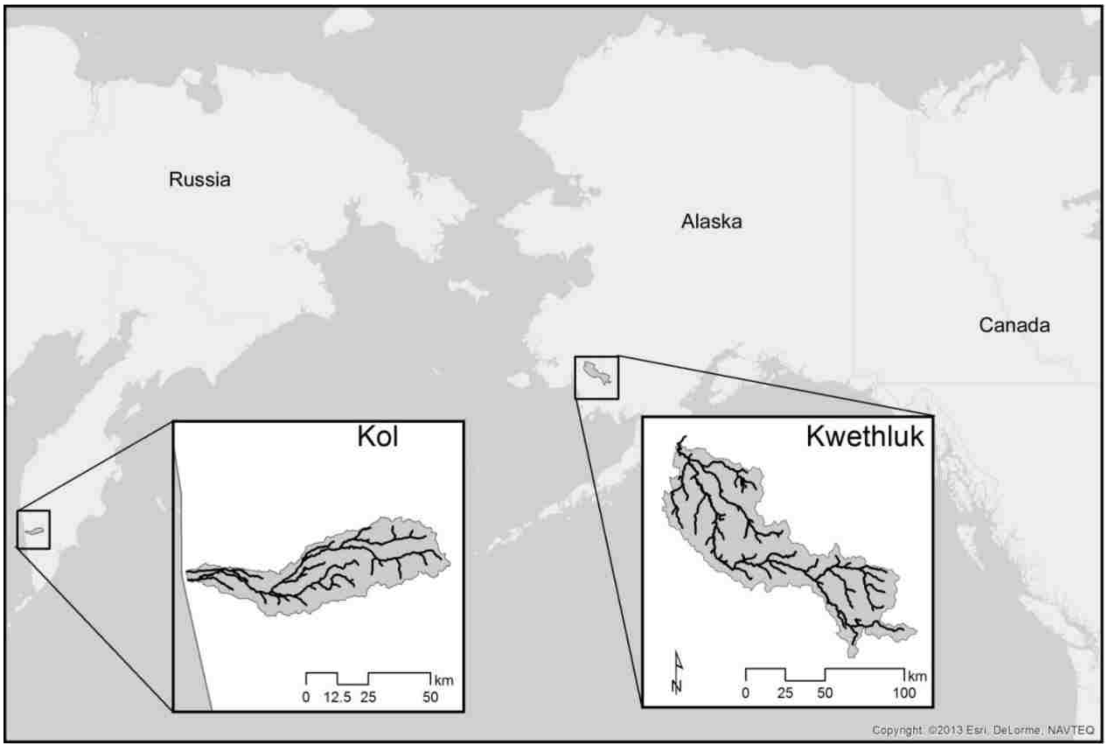

Figure 3.28. Locations of the two study rivers, the Kol River on the Kamchatka peninsula, Russian Federation, and the Kwethluk River, a tributary of the Kuskokwim in western Alaska.

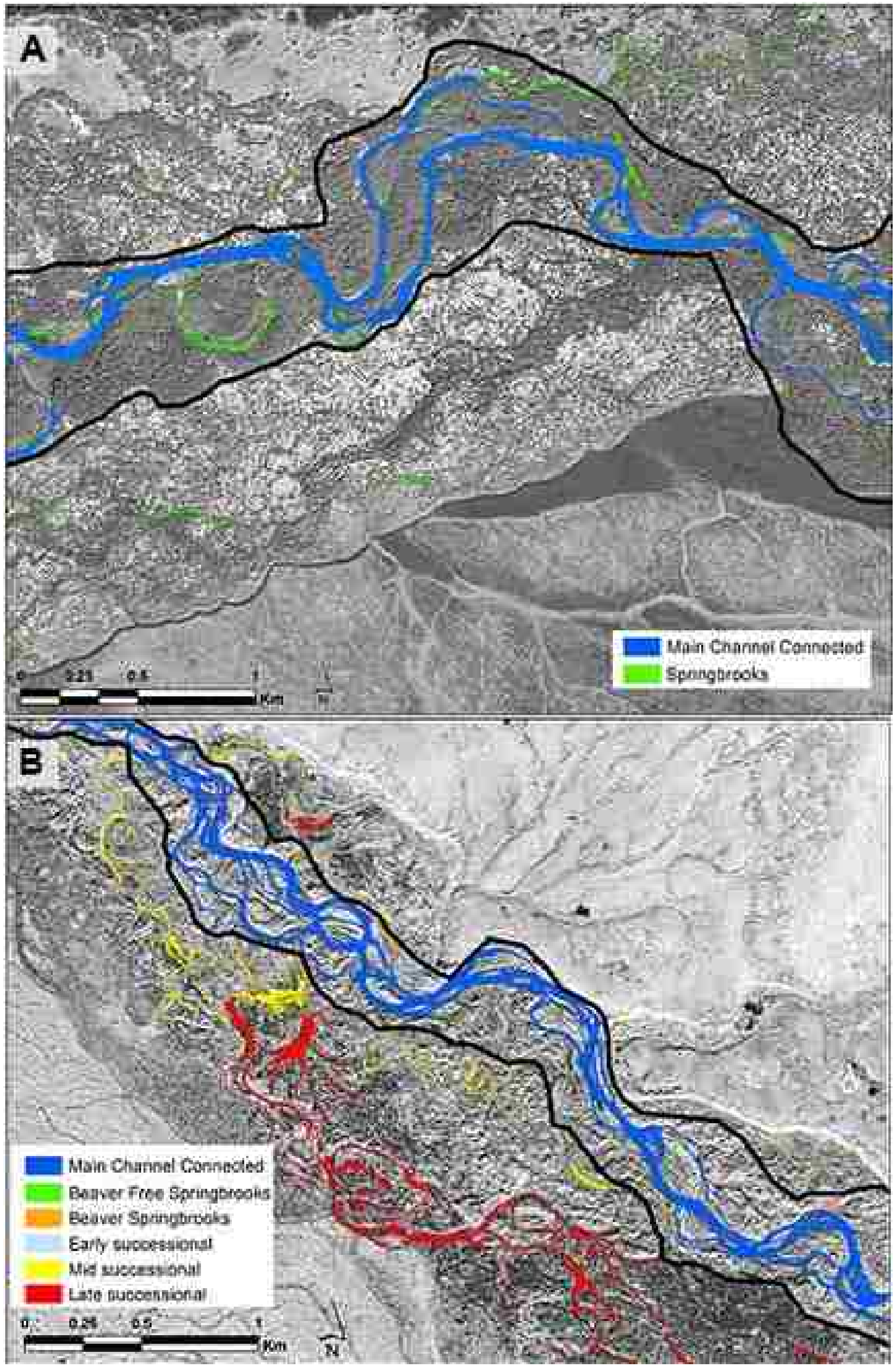

Figure 3.29. Portions of each of the study floodplains contrasting the Kol (A) without beavers and the Kwethluk (B) with 80 percent of the off channel habitats dammed by beavers. Dark blue = main channel, Green = beaver-free spring brooks, Orange = beaver-influenced spring brooks, Light blue = early-successional ponds, Yellow = mid-successional ponds, and Red = Late-successional ponds.

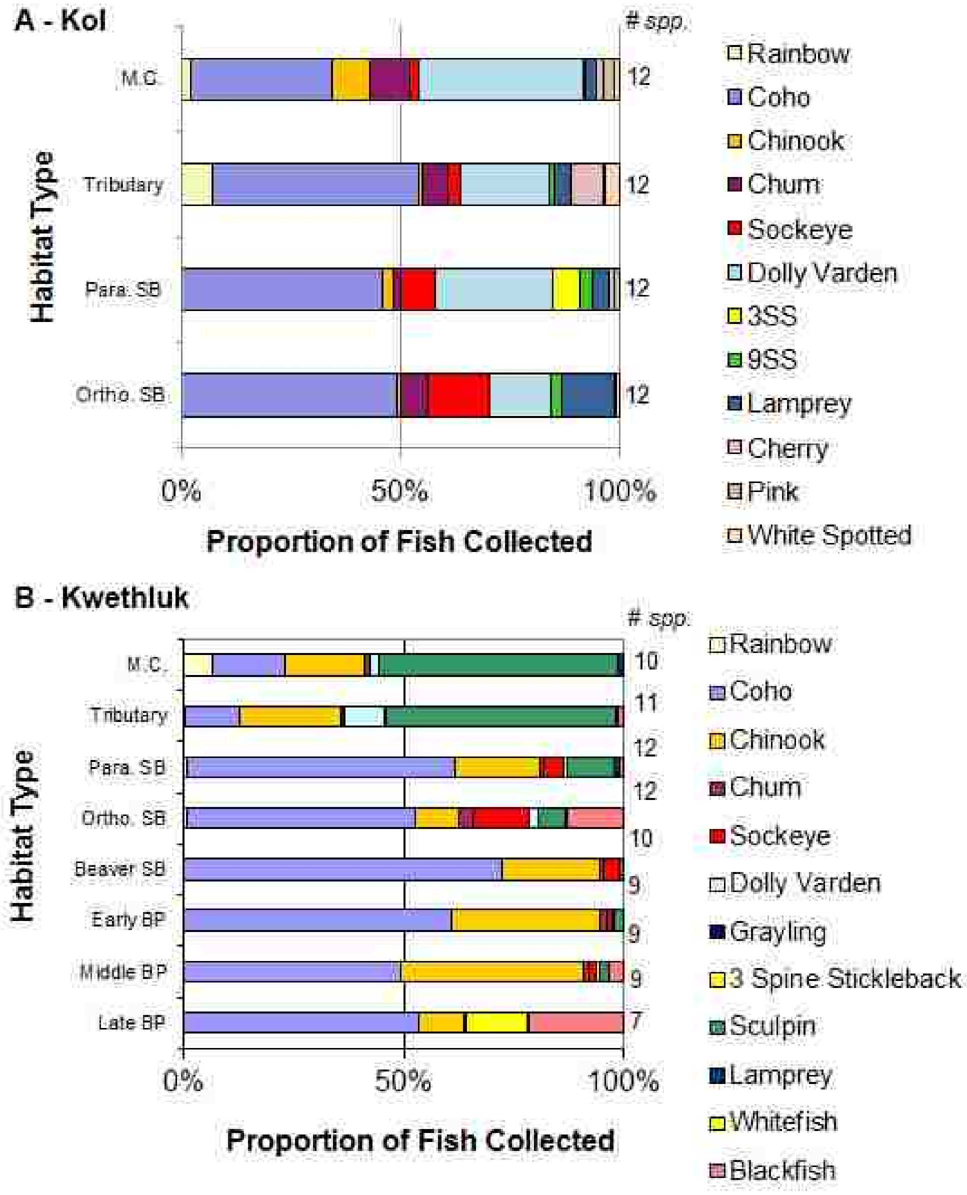

Figure 3.30. Proportion of fish species in the various off-channel habitat types on the Kol (A) and Kwethluk (B) Rivers. Data are means of samples from 2004-2011 (Kol: main channel, n=12; tributaries, n=4; parafluvial spring brooks, n=5; orthofluvial spring brooks, n=5. Kwethluk: main channel, n=11; tributaries, n=3; parafluvial spring brooks, n=11; orthofluvial spring brooks, n=6; beaver-influenced spring brooks, n=6; early-successional ponds, n=9; mid-successional ponds, n=4; and late-successional ponds, n=5. Species included rainbow trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), Chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), Dolly Varden (*Salvelinus malma*), three-spined stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), lamprey (*Lampetra spp.*), cherry salmon (*O. masou*), pink salmon (*O. gorbushcha*), white spotted char (*S. leucomaenis*), arctic grayling (*Thymallus arcticus*), slimy sculpin (*Cottus cognatus*), round whitefish (*Prosopium cylindraceum*), and Alaska blackfish (*Dallia pectoralis*).

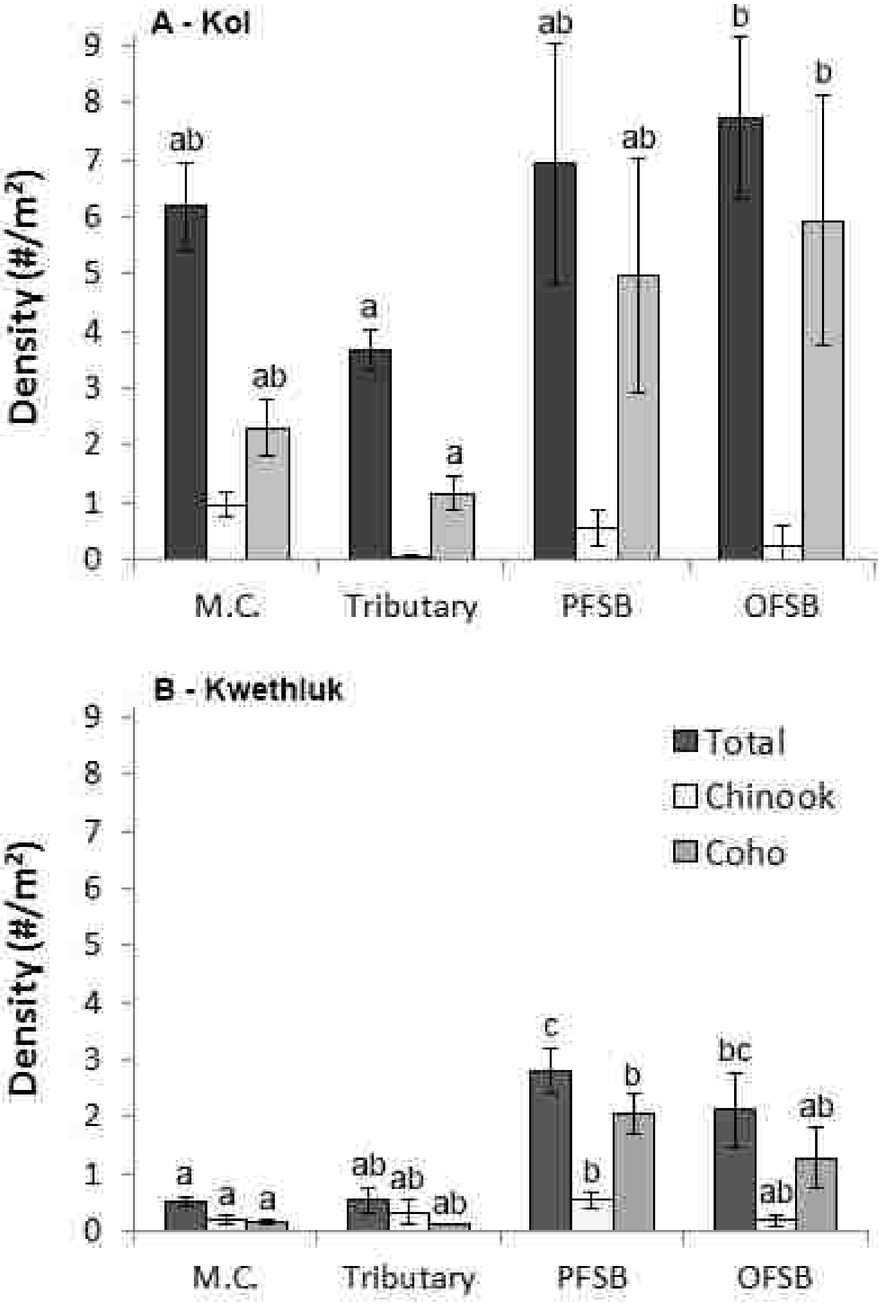

Figure 3.31. Density (± 1 SE) of all salmonids (totals) and Chinook and coho in main channel (M.C.), tributary, parafluvial spring brook (PFSB), and orthofluvial spring brook habitats (OFSB) for the Kol (A) and the Kwethluk (B) Rivers. T-tests contrasting habitat types were significant at $p < 0.05$.

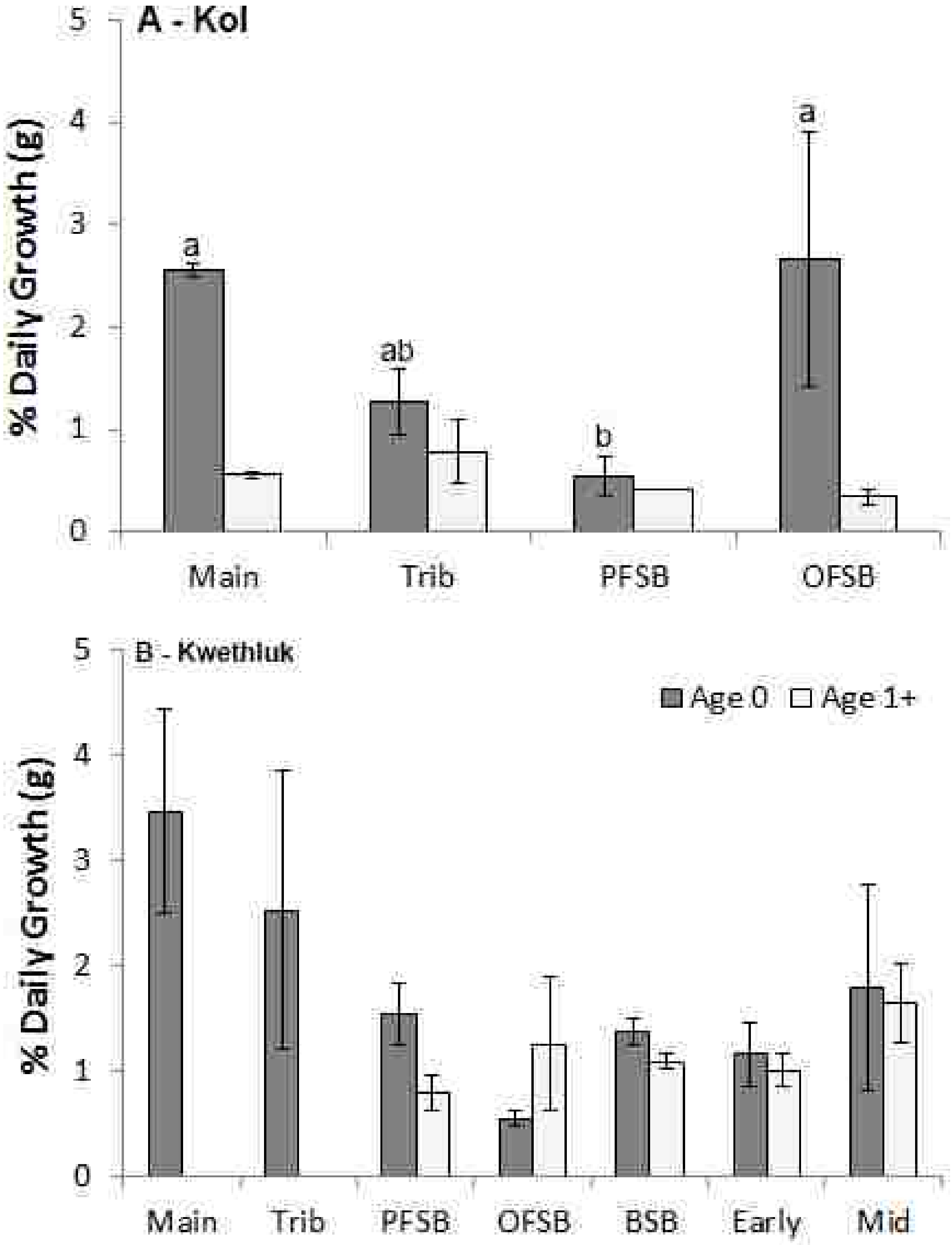

Figure 3.32. Mean (± 1 SE) batch growth rates (mass per day) from June-August of unmarked coho sampled in habitats on (A) the Kol and (B) Kwethluk Rivers (main = main channel shallow shorelines, trib = tributaries, PFSB = parafluvial spring brooks, OFSB = orthofluvial spring brooks, BSB = beaver-influenced spring brooks, Early = Early-successional beaver ponds, and Mid = Mid-successional beaver ponds).

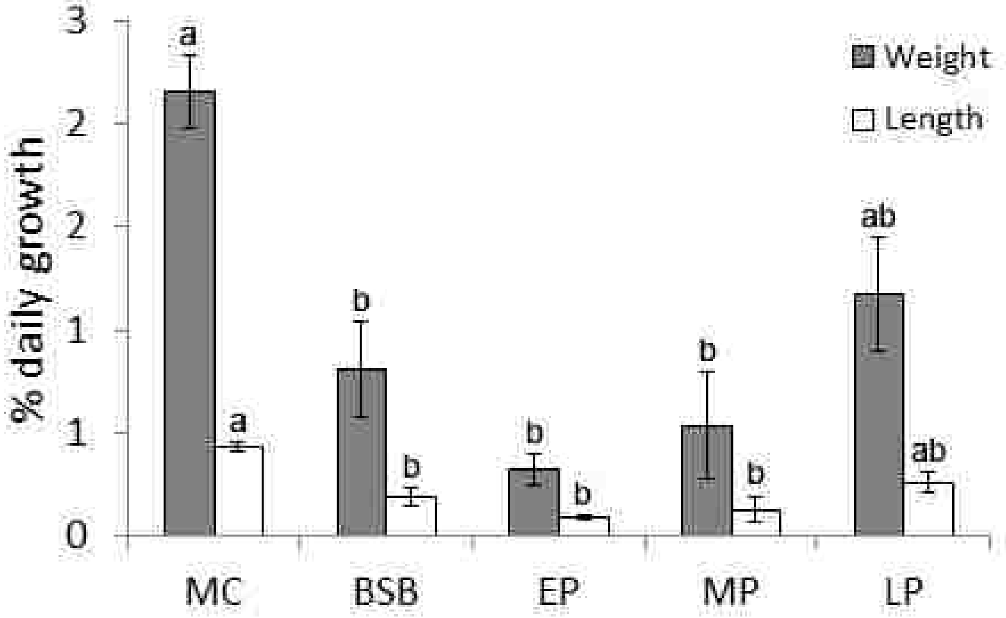

Figure 3.33. Percent daily growth (in mass and length, data are means ±1 SE bars) from June through August of juvenile coho reared within enclosures on the Kwethluk River in five different habitat types: MC = main channel, BSB = Beaver-influenced spring brooks, EP = early-successional beaver ponds, LP = Late successional beaver ponds (n = 3 for each habitat). Tukey HSD tests contrasting habitat types were significant at $p< 0.05$.

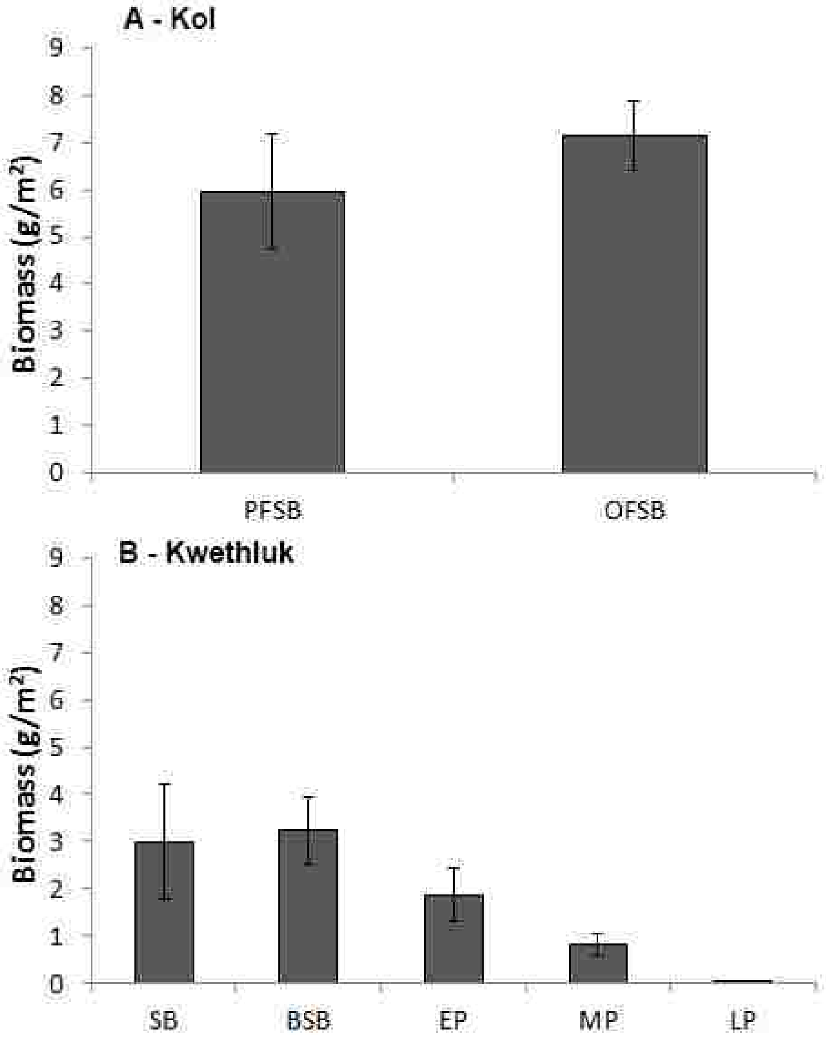

Figure 3.34. Mean (±1SE) juvenile salmon biomass produced per unit area for off channel floodplain habitats in (A) the Kol and (B) the Kwethluk. (PFSB = parafluvial spring brooks, OFSB = orthofluvial spring brooks, SB = beaver-free spring brooks, BSB = beaver-influenced spring brooks, EP = early-successional beaver ponds, MP = mid-successional beaver ponds, and LP = late-successional beaver ponds)

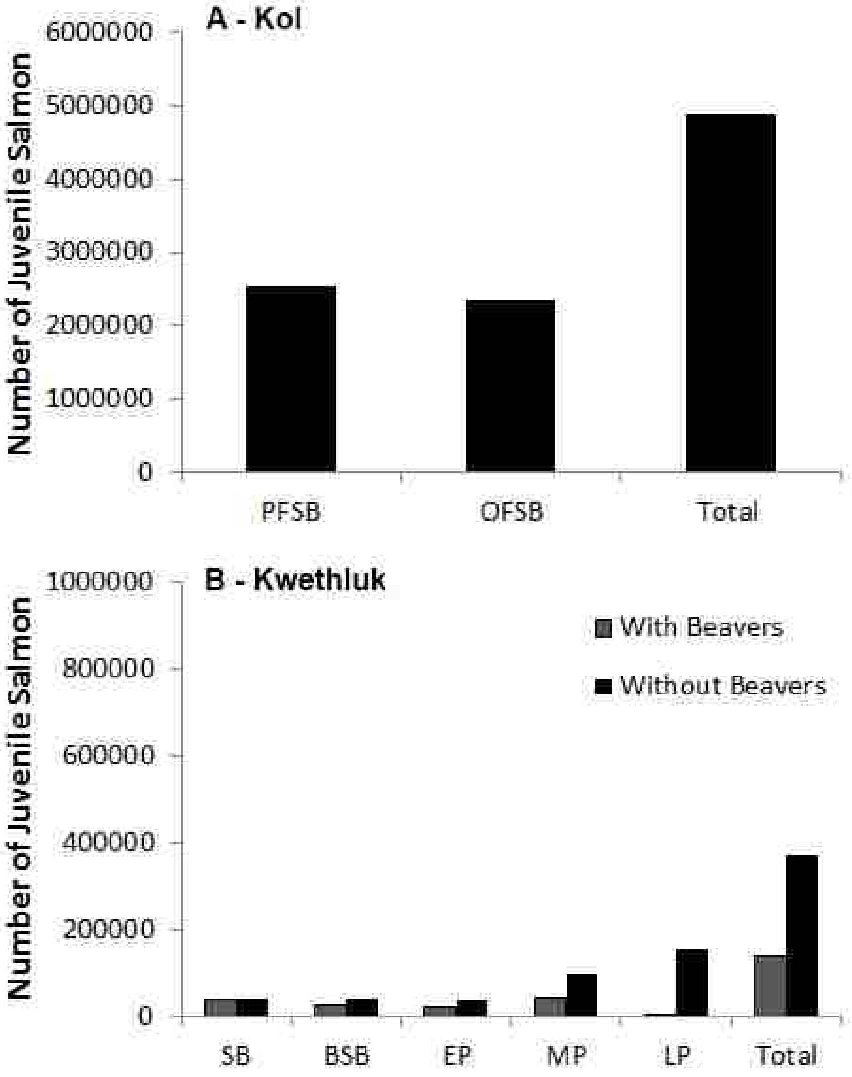

Figure 3.35. The total number of juvenile coho and Chinook reared in floodplain habitats for (A) the Kol River, and (B) for the Kwethluk River with beavers currently, and estimations if beavers were removed. Note the scale of Kol graph is six times larger than that of the Kwethluk.

MAJOR CONCLUSIONS FROM EACH CHAPTER

Chapter 1: Beavers (*Castor canadensis*) influence habitat availability and use by macroinvertebrates and juvenile salmon in a large Alaskan River floodplain

- By damming spring brooks beavers significantly modified a large alluvial floodplain of the Kwethluk River, with 87.5% of the entire off-channel aquatic habitat being composed of beaver ponds and beaver-influenced spring brooks.

- Three successional stages of ponds were present on the floodplain as a result of vegetation succession following initial impoundment of spring brooks. Early-successional ponds were generally closer to the main channel and had high synchrony values (closely tracking water fluctuations in the main channel), while mid- and late-successional ponds were farther from the main channel with more dams blocking aquatic routes and were highly variable in flood response relative to the main channel.

- Physical characteristics were similar among different successional stages of beaver ponds and among different types of spring brooks (by NMDS ordination), indicating that all habitat types were suitable rearing habitats for juvenile salmon.

- Aquatic macroinvertebrate communities differed between beaver ponds and spring brooks with significant differences in species space (by NMDS ordination) driven by the importance of larval mayflies and stoneflies in spring brooks, while cladocerans, snails, copepods, and freshwater clams were dominant in beaver ponds.

- The presence of different types of beaver modified habitats on the floodplain altered the distribution and habitat use of juvenile salmon. Total species and salmon species richness was 2-3x higher, the proportion of fish captured in sites that were young-of-the-year was over 50% compared to <5%, and densities of juvenile salmon were 5-7x higher in spring brooks and early-successional beaver ponds compared to late-successional ponds.

- Beaver ponds had different water level patterns relative to the main channel and spring brooks. Early-successional ponds had high hydrologic synchrony values (closely tracking water fluctuations in the main channel), while mid- and late-successional ponds, being farther from the main channel with more dams blocking flow paths, had lower and highly variable synchrony values.

- Almost no movement of juvenile salmon past dams occurred at base flow. However, summer and fall flooding mediated movement past dams, allowing individuals to “escape” ponds or enter ponds to rear overwinter.

- Beavers reduced habitat connectivity and added variability to macroinvertebrate assemblages within habitats by damming floodplain spring brooks, which are extremely important rearing areas for juvenile salmon in rivers that do not have beavers. Nonetheless, juvenile salmon were able to effectively inhabit and move between early-successional ponds and spring brooks in the Kwethluk, though the presence of beaver dams strongly limited the use of late-successional ponds on the large alluvial river floodplain.

Chapter 2: Juvenile salmonid growth, survival, and production in a large river floodplain modified by beavers (*Castor canadensis*)

- Beavers increased the growth rates of young-of-the-year coho and Chinook in early-successional beaver ponds compared to both beaver-influenced and beaver-free spring brooks (3.1 ± 0.1 vs. 1.83 ± 0.14 and 2.0 ± 0.3 %mass/day for coho and 1.8 ± 0.08 vs. 0.93 ± 0.16 and 1.35 ± 0.32 %mass/day for Chinook)

- Different growth rates resulted in larger coho parr being produced in early-successional beaver ponds by September than both types of spring brooks, even though juvenile coho started out at similar sizes in June.

- Despite higher growth rates and lower densities in ponds, survival rates were consistently highest in beaver-free spring brooks compared to both early-successional ponds and beaver-influenced spring brooks.

- Similar movement rates occurred from spring brooks into beaver ponds and from beaver ponds into spring brooks, both of which were lower than emigration rates out of spring brooks into the main channel complex (1-5% vs. 10-25%).

- Ponds produced a greater biomass of juvenile salmon than either type of spring brook (175 vs. 149 and 140 kg), but reared only about half the individuals that reared in beaver-free spring brooks (24,100 vs. 41,400).

- I found that juvenile salmon were able to survive overwinter in beaver ponds under almost a meter of ice, suggesting that ponds are not “sinks” for juvenile salmon production.

- If beavers were not present and all springbrooks were free flowing, I calculated that slightly less biomass would be produced from the parafluvial zone of the floodplain but 1.5-2x more individuals would be reared, showing that beavers may limit production from the parafluvial zone of the floodplain.

Chapter 3: Beavers reduce habitat connectivity and salmon productivity in expansive river floodplains

- Species richness was similar by habitat type in the Kol River (without beavers). In contrast, species richness of all fish and of salmon differed by habitat type for the Kwethluk River (with beavers), with twice as many total species and salmon species in parafluvial spring brooks and early-successional beaver ponds in the parafluvial zone versus late-successional beaver ponds in the orthofluvial zone (8.5 ± 1.9 and 7.3 ± 1.2 vs. 3.8 ±1.1; 3.7 ± 0.5 and 3.7 ± .4 vs. 1.8 ± 1.3).

- Salmon density was similar by habitat type in the Kol (without beavers). However, in the Kwethluk coho densities were 8-12x higher in off-channel spring brooks than the main channel and Chinook densities were up to 2x higher in parafluvial spring brooks than other habitats.

- Because species richness, densities and growth were similar among habitats in the parafluvial and orthofluvial zones in the Kol River I inferred that if beavers were not present in the Kwethluk River than all floodplain habitats would be free flowing spring brooks that would be utilized by salmon (in both the parafluvial and orthofluvial zone).

- Through an enclosure experiment I found that late-successional ponds in the orthofluvial zone successfully reared juvenile salmon (growth rates were similar to all other habitats), suggesting that underutilization of late-successional ponds may be due to problems of habitat access vs. habitat quality.

- I estimated that if beavers weren't present on the Kwethluk floodplain that there could be twice as much biomass produced between June-August (1174 vs. 667kg) and three times more salmon could be reared on the floodplain (370,000 vs. 140,000).

- Compared to the Kwethluk the Kol can produce an order of magnitude greater biomass (2692 kg in just two months), and rear almost 40x more juvenile salmon from floodplain habitats. Even if beavers were not present on the Kwethluk, the Kol could still produce 5 times the biomass and rear 14x the individuals.

- Therefore, I conclude that presence of beavers may limit the production potential of large alluvial river floodplains, especially at high escapement levels. However, the Kol is still more productive, likely due to the 1-2 orders of magnitude higher escapement levels that the Kol receives.

Synthesis

Beavers modified the majority of the off-channel habitat of a large alluvial river floodplain. This resulted in a mosaic of different successional stages of beaver ponds that were similar in physical characteristics, but strongly differed in physical and hydrological connectivity to the main channel. The presence of beaver modified habitats strongly influenced the distribution and densities of juvenile salmon on the floodplain. By combining the total area of each habitat type with differences in habitat specific growth rates and fish densities I found that the presence of dammed habitats limits the production potential of the floodplain. Primarily this occurred because late-successional ponds in the orthofluvial zone were effectively removed as rearing habitat for juvenile salmon, shrinking the usable portion of the floodplain. Additionally, densities were lower in early-successional beaver ponds, resulting in a lower biomass per unit area being produced in ponds compared to spring brooks in the parafluvial zone. By comparing the ecology of juvenile salmon in parafluvial and orthofluvial habitats of the Kol River, without beavers, I inferred that juvenile salmon would utilize the entire floodplain (i.e. both parafluvial and orthofluvial spring brooks) of the Kwethluk River if beavers were not present. Beavers are part of the North American landscape and their modification of off-channel floodplain rearing habitats may in part result in lower production potentials for North American rivers as compared to far eastern rivers without beavers. However, the large difference in production and the number of juvenile salmon rearing in the Kwethluk vs. the Kol floodplain is likely driven by the large difference in availability of returning adult spawners and associated marine derived nutrient inputs into the basin.