Patterns and Processes of Salmon Colonization

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and have found that it is complete and satisfactory in all respects,
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examining committee have been made.

Chair of the Supervisory Committee:

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Dedication

To my loving family Susan, Samantha, Olivia, and my loving mother Cleopatra.
Thanks for your unconditional love and support

University of Washington

Abstract

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Reproductive migration and homing behavior are characteristic and well-studied traits in salmonid fishes (*Salmo*, *Oncorhynchus*, *Salvelinus* and related genera) and common, if perhaps less precise and less well known, in many other fishes as well. The philopatric nature of salmonids is well documented; however, the converse behavior of straying has allowed salmonid populations to colonize new habitats over their evolutionary history. Salmon can disperse and colonize new habitats, or recolonize formerly disconnected habitats quickly, establishing self-sustaining populations. Natal sites are not static because habitat is a shifting mosaic that changes with large-scale natural and anthropogenic disturbances that force dispersal and colonization of new habitats. Why do salmonids stray and what causes the strays to succeed and become colonists in some cases but not others?

This dissertation investigates how the establishment of self-sustaining salmonid populations in newly opened or reopened habitats is related to the compatibility between specific life history adaptations and geomorphic and ecological conditions that determine stream-habitat characteristics. In this manner, salmon straying can be thought of as active movement to a particular type of place rather than just random dispersal. The hypothesis helps us to focus on four specific factors that can influence successful colonization including: 1) distance from a source population, 2) different habitat preferences among species, 3) local adaptations within species, and 4) competition among and within species.

Chapter 1 examines the current state of knowledge on the patterns and processes of salmonid colonization in the peer-reviewed and non peer-reviewed scientific literature. Chapter 2 investigates the correlation between the occurrence of small salmonid spawning aggregates, habitat characteristics, and competing dominant salmonids at the stream reach and watershed scale in the Wood River system, Alaska. Chapter 3 examines the relative importance of the spatial and temporal relationship between source population distance, stray rates, and habitat characteristics to colonizing pink salmon (*Oncorhynchus gorbuscha*) productivity and abundance in discrete locations within large watershed, the Fraser River, British Columbia. Chapter 4 compares the influences of body size, habitat quality, and competition on the movement and survival of juvenile coho salmon (*Oncorhynchus kisutch*) during the early stages of colonization.

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Homing and straying: the role of colonization in the conservation of salmon and trout

Abstract

The act of homing to natal streams segregates salmon populations and leads to the evolution of population-specific adaptations to local conditions that is the cornerstone of the salmon management and conservation. The links between homing and the benefits of local adaptation also begs the question of why the converse, straying (or dispersal), the reproduction of salmon at a non-natal site, also occurs in all salmonid species. The goal of our paper is to review the scientific literature pertaining to the following questions: 1) Why do salmon stray? 2) How do new populations become established? And 3) how can this information be used for the restoration of salmon populations? The process of imprinting to natal streams has been hypothesized to be sequential and related to a combination of changes in environmental stimuli, developmental and seasonal cues, and an increased tendency to migrate as a fish grows older. There are many sources of mistakes, thus it is not surprising that the homing process is imperfect. Three generalizations have come from the literature. First salmon homing averages 92% (S.D. +/-9.4%), while salmon straying averages 8% (S.D. +/-9.5%). Second the amount of straying is roughly correlated with geographical distance. Lastly straying rates can differ between salmonid species, however such comparisons are difficult to make because data is not necessarily comparable for more than one species from each site, and spatial scale often varies among studies. Straying salmon can establish self-sustaining populations in years to decades and their establishment in newly opened habitats, is the link between compatible life history adaptations and environmental characteristics. The restoration of salmon populations in historically available habitats that have been disconnected and are now reconnected may be as simple as allowing salmon to naturally colonize because of their ability to locally adapt to the right habitat conditions.

Introduction

Homing, defined as the return of mature animals to the general location of their natal site (i.e., where their parents bred), is common and widely distributed among diverse animal taxa (Papi 1992). Spawning site fidelity (or philopatry) occurs in birds (Rhodes et al. 1996), reptiles (Bowen et al. 1994), and fishes in marine (Klimley et al. 1991; Thorrold et al. 2001; Dixson et al. 2008; Rooker et al. 2008), and freshwater environments (Werner and Lannoo 1994; Massicotte et al. 2008). As McCleave (1967) pointed out, this homing to the natal site is a subset of the more general phenomenon of homing, including return to the site of previous reproduction, and homing after natural or experimental displacement. The phenomenon of homing is particularly well studied in anadromous fishes such as salmon and trout (Hasler and Scholz 1983; Quinn 1984; 1993; Dittman and Quinn 1996). Homing segregates populations, leading to the evolution of population-specific adaptations to local conditions that is the cornerstone of the management and conservation of these fishes (Ricker 1972; McDonald 1981; NRC 1996; Garcia de Leaniz et al. 2007).

The links between homing and the benefits of local adaptation that seem to be the hallmark of successful salmon populations beg the question of why the converse, straying (or dispersal), the reproduction of salmon at a non-natal site, also occurs in all salmonid species (Hendry et al., 2004). Straying not only occurs in episodic pulses but also occurs at a relatively low and steady level. Straying is important because it enables salmon to colonize new areas over a relatively short time frame (Hendry et al. 2004; Quinn 2005), and is the behavior that has allowed salmonid populations over the course of thousands of years to colonize their existing habitats (Quinn 1984; Hendry et al., 2004). For example, in streams of southeast Alaska, multiple salmonid populations have established themselves within decades of glacial retreat (Milner and Bailey 1989; Milner and York 2001), allowing us to witness the process that took place countless times throughout the range of salmon in the more distant past. Where fish ladders have been installed or culverts removed, streams have experienced natural colonization of upstream habitats, and self-sustaining populations, within a one to five year period (Bryant et al. 1999; Glen 2002; Pess et al., 2003).

Homing and straying are typically viewed as population-scale phenomena. For example, Sandercock (1991, p. 432) wrote “A return to the parental spawning ground provides a mechanism for enhancing survival by the repeat usage of good sites. Straying can also be a survival mechanism in that it may protect against the loss of an entire stock due to some environmental catastrophe in the home stream (e.g., the volcanic eruption of Mt. St. Helens, Washington)". However, it is important to remember that both phenomena result from the actions of individual fish and must be understood from an individual perspective. It may benefit the population as a whole for some fish to stray but why should any individual fish do so if, on average, it would produce more offspring by spawning at the natal site? In addition, the individual perspective will be different for the parent and the offspring. Any single offspring may maximize its fitness by returning to spawn at the "best" place (that is, statistically most likely to be good for the survival of its offspring), whereas the inclusive fitness of the parents may be maximized if some offspring come back home and others go elsewhere. Even if the "elsewhere" is not quite as good as home, it will spread the risk of no returning offspring for the parent and so be better in the long run for the parent, though perhaps not for all offspring.

The phenomena of homing and straying in salmonids are not only interesting from the standpoint of adaptive significance and sensory mechanisms but they are also central to the conservation and management of salmon. Straying and the establishment of self-sustaining populations is important because many salmon occupy artificially truncated river systems, and some of these populations are listed as either threatened or endangered under the United States Endangered Species Act (ESA) (NRC 1996; Montgomery 2003). Lack of fish passage is a problem throughout North America (e.g., USGAO 2001; Langill and Zomora 2002) and Europe (Yanes et al. 1995; Glen 2002). There are an estimated 1.4 million stream-road crossings in the United States (M. Hudy, USFS, pers. comm., 2 May 2003). In Washington State alone over 7,700 km of historical salmon habitat are inaccessible to migratory fishes because of impassable culverts or road crossings, despite state regulations requiring road crossings to provide fish passage (Roni et al. 2002).

Removal of a blockage, whether it is a small culvert or a series of dams in a large watershed, is considered a key restoration action to aid in the recovery of listed salmon. These actions are currently being implemented throughout watersheds on both coasts of the Atlantic and Pacific oceans and will likely become more prevalent in the next five to ten years, despite their cost (Roni et al. 2002). Although much effort has been made to remove blockages to salmon passage, surprisingly little is known about why salmon colonize new habitats and what occurs after a barrier is removed. Thus the recolonization of habitat from which salmon were extirpated will likely depend on straying, and straying and gene flow are critical to the numerical persistence and genetic diversity of fragmented units within metapopulations (Rieman and Dunham 2001; Schtickzelle and Quinn 2007).

On the other hand, the salmonids are non-native components of the fish fauna throughout much of the world, and their expansion through straying affects their interactions with native fishes. While artificial introductions of anadromous salmonids within their native geographic range have seldom succeeded (Withler 1982), such introductions in places outside their geographic range such the Great Lakes of North America, New Zealand, and South America have been successful within decades (Kwain and Lawrie 1981; Quinn et al. 2001; Ciancio et al. 2005). Non-native salmonids are found in all continents other than Antarctica and in many of the world's major river systems (Crawford and Muir 2008).

Even though we know that salmon can move in and utilize newly opened habitats, the questions of why salmon stray, and how the transition takes place from straying (by individuals) to colonization (successful establishment of a self-sustaining population) remain unanswered. Little research has been done on the relationship between straying and the colonizing of unoccupied areas. There are both physiological and ecological perspectives on straying but we do not really understand the phenomenon itself, or how the actions of individuals give rise to independent, self-sustaining populations.

The goal of our paper is to review the scientific literature pertaining to the following linked questions: 1) Why do salmon stray? 2) How do new populations become established? And 3) how can this information be used for the restoration of salmon populations? The central paradox is that new habitat is only discovered by straying salmon, yet homing by the majority of the fish is the prerequisite for maintenance of a self-sustaining population. We consider two main aspects to the question of straying and the development of self sustaining populations through colonization: proximate causation (physiological and ontogenetic mechanisms) and ultimate causation (adaptive benefits and evolution) (Tinbergen 1963). We attempt to identify the most important factors to consider for salmon recolonization in the context of management actions such as barrier removal, habitat restoration, and natural vs. artificial propagation in newly opened habitats. First, we assess the literature, revealing the shift in focus from understanding the mechanisms of homing by salmon to the consequences of straying for conservation. We discuss physiological mechanisms, ecological, and evolutionary aspects of homing and straying and attempt to identify what is most important with respect to salmon colonization. Second, we identify several generalizations about homing and straying. Third, we give examples from recent studies of how salmon straying in newly created habitats has led to self-sustaining populations. Lastly, we introduce a template that attempts to integrate physiological mechanisms with ecological and evolutionary aspects of straying in relation to population establishment in newly accessible or reconnected habitats. We use the template to then identify the most important parameters in the development and implementation plans for salmon population expansion due to barrier removal.

A historical context to the definition of homing and straying

There is evidence that observers living in Europe centuries ago surmised and even concluded that the Atlantic salmon they observed migrating and spawning in streams had been there before, as juveniles or as spawning adults (Nordeng 1989). Izaak Walton wrote in his classic The Compleat Angler, “Sir Francis Bacon observed, the age of a Salmon exceeds not ten years…Much of this has been observed by tying a Ribband or some known Tape or thred, in the tail of some young Salmons, which have been taken in Weirs as they have swimm’d toward the salt water, and then by taking a part of them again with the known mark at the same place at their return from the Sea …which has inclined many to think, that every Salmon usually returns to the same River to which it was bred, as young Pigeons taken out of the same Dove-cote, have also been observed to do." Bacon lived from 1561 to 1626 so this suggests that at least some people have known or speculated that salmon home for many centuries. The concept of homing was recognized by modern scientists in anadromous fishes during the late 1800's. For example, phenotypic differences in American shad *Alosa sapidissma* from different rivers were noticed "at market" (Milner 1876), and the long-distance and isolated nature of headwater rivers in the Columbia River allowed scientists to "infer that the instinct of location is probably sufficient to attract a colony of [Pacific salmon, *Oncorhynchus* species] as far inland as the headwaters of the longest river, whenever their home has been once established there (United States Commission on Fish and Fisheries 1876)."

By the early-mid 20th century there was abundant evidence that most of the salmon that survived at sea returned to their natal site to spawn (e.g., Foerster 1936). The mechanism by which they accomplished this feat was the subject of various hypotheses (e.g., Powers 1941). Experiments with bluntnose minnows led Hasler and Wisby (1951) to hypothesize that salmon learn or "imprint" the olfactory memory of their natal stream, store this memory during migrations to distant waters, but when mature "remember" and use the odors to relocate the stream for spawning (Hasler and Scholz 1983). This hypothesis was confirmed with subsequent studies in which salmonids were exposed to specific chemicals during the parr-smolt transformation stage, and subsequently ascended otherwise unfamiliar streams scented with those odors 90% of the time (coho salmon, *O. kisutch*: Scholz et al. 1976; brown trout, *Salmo trutta*: Scholz et al. 1978; rainbow trout, *O. mykiss*: Cooper and Scholz 1976). From the standpoint of these experiments, the small percentages of salmon and trout that did not ascend the scented stream predicted were an aberration, and little was written about them. Indeed, the term straying was not even indexed in Hasler and Scholz's review of their large body of work (1983).

The work by Hasler and colleagues was the basis for further investigation into the physiological and ontogenetic mechanisms of imprinting and homing (Dittman and Quinn 1996). Emphasis has been placed on the parr-smolt transformation, a developmental process characterized by physiological and behavioral changes which prepare freshwater residents (parr) for life at sea (Dittman and Quinn 1996). The focus of this work has been on the relationship between the olfactory system, the timing of imprinting, and the changes in plasma levels of the hormone thyroxine and other endocrine events (Dickoff et al. 1978; Hasler and Scholz 1983; Dittman et al. 1996; Morin et al. 1989; 1994; 1997). The process of imprinting has been hypothesized to be sequential and thus related to a combination of changes in environmental stimuli due to changes in habitat, developmental and seasonal cues, and an increased tendency to migrate as a fish grows older (Dittman and Quinn 1996). The odor memories are not only stored in the olfactory lobe of the brain but there is also sensitization of the sensory cells (Nevitt et al. 1994; Dittman et al. 1997). Importantly, with all the complexities of home stream odor detection and learning by juveniles, memory by sub-adult salmon, and responses to those odors by mature adults, there are many sources of mistakes. That is, for entirely mechanistic reasons related to sensory physiology and ontogeny, it is not surprising that the homing process is imperfect.

The ecological and evolutionary benefits of homing have also been discussed extensively (Taylor 1991; Quinn 1993). “Locally adapted” traits specific to the physical and biological characteristics of natal spawning sites typically enhance the survival or reproductive success of individuals in their home environment and select against strays (i.e., fish adapted for some other environment: Ricker 1972; Taylor 1991; Quinn 2005). Examples of local adaptation with respect to salmon homing to their natal river systems include sockeye salmon (Quinn et al. 1995), coho salmon (Taylor and McPhail 1985), and Chinook salmon (Quinn et al. 2000).

Most of the empirical studies on homing have been conducted with hatchery populations because these fish are often marked for fishery management purposes. The question posed by the majority of these studies has been what is the magnitude and pattern of straying in salmon populations (Quinn 1993)? For example, Quinn and Fresh (1984) found that 98.6% of the Chinook salmon released from the Cowlitz River hatchery in the Columbia River system that survived returned to the Cowlitz River. However, the straying rate increased with the age of the returning adult salmon and most strays were within the vicinity, but did not necessarily stray to the nearest river system. Since then there have been a number of other studies using coded wire tagging data to assess the proportion of salmon that stray from hatcheries, the spatial distribution of strays, and the effects of different treatments and practices on straying (Quinn et al. 1991; Unwin and Quinn 1993; Pascual and Quinn 1994; Pascual et al. 1995; Hard and Heard 1999; Candy and Beacham 2000; Thedinga et al. 2000). More recently, radio telemetry has provided rich details on the movements of individual wild and hatchery produced Chinook salmon and steelhead homing and straying in the Columbia River Basin (Keefer et al. 2005a; 2005b; 2008a; 2008b). Much of this work has been motivated, in part, by concerns about straying of hatchery salmon and their potential to interbreed with wild fish. Although this view of straying as a concern has validity in this context, it has distracted attention from the fact that straying is a natural process that cannot and indeed should not be eliminated.

Homing and straying generalizations

One generalization that comes from homing and straying studies over the last 30 years is that regardless of species or origin (wild vs. hatchery), most fish home but some do stray (Hendry et al. 2004; Quinn 2005). Salmon homing averages 92% (S.D. +/-9.4%), while salmon straying averages 8% (S.D. +/-9.5%) (Hendry et al. 2004 Appendix 1 – Straying rates of anadromous salmonids, Keefer et al. 2005b; Keefer et al. 2008c). It has been difficult to determine whether straying differs between hatchery and wild populations because the vast majority of the studies have been conducted on hatchery populations (Quinn 1997). However, in most cases “non-native” populations as well as salmon displaced from their natal rearing sites stray more than native salmon and those reared and released on-site (Quinn 1993, Keefer et al. 2008c).

A second generalization that homing and straying studies have concluded is that the amount of straying from the release site is roughly correlated with geographical distance (Quinn 1997). Quinn and Fresh (1984) and Quinn et al. (1991) found that greater than 95% of all fish that did stray were within 30 km of their home river system or hatchery release site, and other studies also found most straying to nearby sites

(Labelle 1992; Unwin and Quinn 1993; Hard and Heard 1999; Candy and Beacham 2000; Jonsson et al. 2003; Keefer et al. 2008b). Keefer et al. (2008b) found that two types of straying behavior, overshooting a natal stream and the temporary use of another tributary, declined exponentially with increasing distance from the natal tributary. Thus straying is negatively correlated with geographic distance (Hendry et al. 2004). This relationship also has an effect on gene flow which is also negatively correlated with geographic distance, meaning that there is greater genetic differentiation between populations as the distance between populations increase (Hendry et al. 2004). One corollary of this result is that the proportion of salmon straying depends on the spatial scale that is being studied, thus the larger the extent the higher the proportion of salmon that home. Few if any salmon from the Columbia River system fail to return there but as one goes farther up the river into sub-basins, and progressively smaller streams to the spawning grounds one may detect higher rates of straying.

A third generalization that has come from homing and straying studies is that straying rates differ, to some extent, between salmonid species (Quinn 1984; Hendry et al. 2004; Quinn 2005). Hard evidence to support this generalization is scarce because there have not been controlled experiments on all species in the same river, as would be needed to firmly establish differences among species. Nevertheless, sockeye salmon have shown very low straying rates (<0.8%), whereas coho, Chinook, steelhead, and Atlantic salmon have had similar and somewhat higher rates (7.8%, 6.2%, 7.7%, and 7.7%), and straying rates for chum and pink salmon are highest (19.1% and 15.4%)

(Figure 1). It must again be emphasized that such comparisons are difficult to make because rarely are there comparable data for more than one species from each site so the differences between species are confounded by differences among rivers and years. In addition, the spatial scale often varies among studies making them difficult to compare.

Notwithstanding the difficulties in determining empirical rates of straying among species, why might one expect them to vary? Quinn (1984) hypothesized that there is a dynamic equilibrium between homing and straying in all populations, and that three main factors influence the relative frequency of homing and straying among species: 1) variation in the number of recruits per spawner, 2) the extent of specialization for freshwater habitats, 3) variation in age of maturity, and the extent of iteroparity. Thus if a stream is stable in the recruitment of salmon due to attenuated flow conditions during spawning and incubation, such as a river flowing from a lake, then variation in recruitment would be less and consequently homing would be favored over straying. Conversely, in spawning areas prone to dynamic changes that produce great variation in egg-fry survival, (e.g., systems with large variation in flow conditions such as coastal, rain-dominated watersheds), straying might be more prevalent.

An excellent example of dramatic changes in environmental conditions and implications for straying and subsequent homing was the eruption of Mt. St. Helens in Washington on 18 May 1980. When Toutle River origin fish returned (e.g., fall 1980, 1981) they encountered drastically degraded habitat conditions and increased turbidity levels by several orders of magnitude (Leider 1989). Faced with these changes, Toutle

River steelhead straying rates increased from 16% to 45% after the eruption, with most strays moving to watersheds with lower turbidity (Leider 1989). However within four years, or one life cycle of steelhead, straying into nearby rivers decreased to pre-eruption levels and densities of spawning steelhead in two of the major tributaries that returned to pre-eruption streambed elevation had steelhead redd densities that went from 0 redds/km to 5.7 redds/km to 21.5 redds/km within seven years of the eruption (Lucas and Pointer 1987; Leider 1989; Bisson et al. 2006). Did they stray because they could not identify their natal river or because they assessed in some way that it was no longer suitable for reproduction? One cannot answer this question for the wild fish but experiments on Chinook salmon exposed to volcanic ash indicated that the presence of ash did not prevent home-stream recognition but that the fish tended to avoid water laden with the ash (Whitman et al. 1982). Conversely as stream conditions changed and sediment concentrations decreased salmon recognized the change and returned to their natal systems (Bisson et al. 2006).

The second element of Quinn's (1984) hypothesis was that species with less extensive use of freshwater habitats might stray at higher levels than species with extensive specialization for freshwater. For example, the population-level patterns of disease resistance (Buchanan et al. 1983; Bower et al. 1995), migratory orientation (Raleigh 1971; Brannon 1972) and other forms of behavior and morphology (Rosenau and McPhail 1987; Swain and Holtby 1989); that characterize species such as steelhead, Chinook, coho and sockeye salmon presumably derive from the longer period of freshwater residence and greater variation among populations compared to chum and pink salmon (Figure 1). For pink and chum salmon that spawn in the lower portions of coastal streams, conditions are very similar among the streams available to them; straying to a stream other than the natal stream may not have a large effect on fitness (Quinn 2005). Data from the homing and straying studies organized by the amount of time salmon species spend in freshwater indicates at slightly higher stray rate in salmon that spend less time in freshwater (Figure 1).

It was also hypothesized that straying be inversely related to variation in age of maturity because parents whose offspring will all spawn in a single year are more at risk of having no grandchildren (owing to some future one-time disaster) than those with offspring spawn in different calendar years Quinn (1984; Figure 1). At one end of the spectrum are pink salmon with a fixed 2-yr cycle. As Bakshtansky (1980) pointed out, an event occurring in a stream can extirpate an entire year class. It may thus optimize the parents' fitness to have some offspring home and have others stray, to reduce the probability that the entire line will be lost. Chinook salmon are at the upper end of the spectrum; they may spend up to 5 yrs at sea, and can return at 2-5 yrs of age. Thus, even with the complete loss of one or more year classes, the parents might still have some surviving grandchildren even if all of their children spawned in the natal streams. Variation in age at maturity is thus a form of straying in time to balance the straying in space. It is important to note that the preceding hypotheses are not mutually exclusive and that the information gathered since they were put forth in 1984 seems to support them, to a greater or lesser extent. Data on wild salmon populations remains very limited, particularly at consistent extents and for multiple species.

Salmon straying and colonization of newly opened habitats

In addition to the studies specifically focused on homing and straying, there have been studies based on the result or potential results of straying to newly, naturally created salmon habitats (Leider 1989; Milner and Bailey 1989; Milner and York 2001; Milner et al. 2007; Milner et al. 2008) or recently opened/re-opened salmon habitats (Bryant 1999; Young 1999; Burger et al. 2000; Quinn et al. 2001; Glen 2002; Pess et al., 2003; Anderson et al. 2008; Pess et al. 2008; Kiffney et al. in press). The time period for colonization and establishment of self-sustaining populations, regardless of whether the new habitats are newly opened or re-opened, for many of the preceding studies occurred within five to thirty years, and most falling between one to two decades (Withler 1982; Bryant 1999; Burger et al 2000; Glen 2002; Pess et al. 2003; Milner et al. 2007; Kiffney et al. 2009).

Pink salmon, coho salmon, sockeye salmon, and Dolly Varden (*Salvelinus confluentus*) that strayed from nearby streams colonized newly created streams that had recently been developed due to deglaciation in Glacier Bay and established self-sustaining populations within 20 years (Milner et al. 2007). Where fish ladders have been installed or culverts removed, natural colonization has led to self-sustaining populations within 1 to 5 years (Bryant et al. 1999, Glen 2002, Pess et al. 2003). Recolonization and establishment of pink salmon in the Fraser River above Hell’s Gate landslide required approximately 20 years to establish large spawning populations (Pess et al. 2007). Expansion of habitat area can thus allow salmonids to utilize a greater diversity of habitat types and conditions.

These results emphasize that one of the most important attributes associated with successful salmon colonization, and the establishment of persistent, self-sustaining populations in newly opened habitats, is the link between compatible life history adaptations and geographic, hydrologic, and ecological characteristics (Quinn 1984; Allendorf and Waples 1996; Burger et al. 2000). For example, as the Glacier Bay landscape evolved over time certain habitat features such as lakes became separated from the stream network resulting in a loss of sockeye populations (Milner et al. 2007). Burger et al. (2000) also found that life history adaptation needed to be compatible with local habitat conditions in order for sockeye salmon donor populations to successfully colonize a lake system in Alaska after passage facilities allowed them to circumvent a waterfall, thus underscoring the need to consider life history traits in other introduction and recovery programs.

Further evidence for the link between life history adaptation and environmental and ecological condition again comes from Milner's work in Alaska (1989; 2008). Milner and Bailey (1989) compared the salmonid spawning density in two recently deglaciated, geomorphically similar, and adjacent streams in southeast Alaska. They found that low turbidity was a dominant factor associated with higher spawning density. Streams with lower turbidity levels also had higher proportion of preferred spawning temperature range (12 to 15° C), a more attenuated hydrology, and more extensive riparian vegetation structure. In each case, colonization and re-colonization occurred and the abundance of spawning populations varied as a function of different habitat preferences among species, local adaptations, habitat type (e.g., channel slope, sediment character), and habitat quality (turbidity levels, temperature, cover). Colonization of these streams over time varied for each species and resulted in more coldwater oriented species utilizing streams first (i.e., Dolly Varden), while other salmonid species (i.e. pink, coho, and chum salmon) appeared 2 to 10 years later as maximum stream temperatures warmed from 7.1° C to 16.6° C (Milner et al. 2008).

Thus habitat conditions must be favorable, and allow for increasing growth and survival at key life stages, which can then result in higher population growth rates that lead to self-sustaining populations (Withler 1982). It is important to note that the success of colonization is never certain and newly accessible areas vary in suitability; Withler (1982) found only a very small number of successful colonization efforts, both natural and artificial, among hundreds of attempts within the range of Pacific salmon. Even though we know that salmon locate and utilize newly opened habitats, establish self-sustaining populations, and develop diverging life history traits in newly opened habitats, the questions of why salmon stray and what causes successful colonizing remain unanswered.

Homing and straying and its application to salmon recolonization

Despite low but persistent levels of ongoing straying, not all salmon species are present in all streams within their ranges, and the ranges do not entirely coincide. If we combine this with the fact that so many transplants within the range of salmon species failed, we can only conclude that salmon occupy the majority of accessible river that is currently suitable for them. Changes in distribution may result from changes in the suitability of rivers for one species or another, or from increased access. Today much of the research focus is the recolonization of formerly disconnected habitats (Anderson et al. 2008; Pess et al. 2008; Kiffney et al. 2009), thus the questions we posed in the introduction are directly relevant. What are the key factors that determine salmon colonization and population persistence after blockages are removed? How do different fish management strategies, habitat conditions, and population dynamics affect salmon recolonization? How does salmon recolonization affect other ecosystem attributes?

The establishment of self-sustaining populations in newly opened habitat may be related to the compatibility between specific life history adaptations and the physical and ecological characteristics of the new habitats (Quinn 1984; Allendorf and Waples 1996; Burger et al. 2000). The concept that self-sustaining populations can be established, or population size increased, when a sufficient number of colonists have life history traits or adaptations compatible with available habitats is important because it focuses on specific factors that can influence successful recolonization (Table 1) (Pess et al. 2008). The potential effect each of these variables has on dispersal and recolonization will vary according to species, local adaptations within species (e.g. extent of freshwater use), and unique habitat characteristics that are compatible with both (Quinn 1984).

Barriers are a key factor in determining the ability of salmonids to recolonize. Numerous large barriers isolate salmonids in space and over time, whereas few, small barriers that are not always effective at stopping salmon from moving will allow for the exchange of individuals within and between potentially separate populations. The ability to maneuver past natural barriers varies considerably with species and migration timing. For example, steelhead, coho, and Chinook salmon have superior jumping ability compared to pink and chum salmon (Reiser et al. 2006), but water depth and other physical features also determine how high salmon can jump, and whether waterfalls or cascades constitute barrier to migration or not. Some of these features are fixed whereas others vary seasonally.

The theory of island biogeography (MacArthur and Wilson 1963) proposes that the distance from source population and size of newly opened habitat area are two important factors that can determine the likelihood of dispersal and colonization of new habitats. Habitats closer to a source population are more likely to receive immigrants than those which are a greater distance. In addition, larger areas of habitat increase the likelihood of colonization.

Population size and straying rate are another set of factors that will influence the dispersal and ability of salmonids to recolonize. Large population size can result in a relatively larger number of strays even though the stray rate is low. This is why a relatively low stray rate from a large hatchery can pose potential issues for nearby small, wild salmon populations. A large increase in an already large Fraser River pink salmon population (e.g., ~ millions), combined with other factors allowed for habitat recolonization and the establishment of self-sustaining pink salmon populations in the Fraser River above Hell's Gate (Pess et al. 2007). An increase in the stray rate of a source population can also allow for colonization opportunities. Significantly higher stray rates, such as what occurred after Mt. St Helens resulted in more steelhead in the nearest rivers for a period of three to four years (Lieder 1989). Conversely, low population size or low straying rates result in fewer individuals seeking non-natal habitats and reduces the probability of dispersal and recolonization.

As we have already discussed, salmonid colonization and recolonization can in part be explained in terms of life-history characteristics such as local adaptations to habitats and adjustments to changing environmental conditions (Quinn 1984; Leider 1989; Burger et al. 2000; Keefer et al. 2005b; Milner et al. 2007). Straying rate can vary by species, as noted above (Figure 1) (Hendry et al. 2004; Keefer et al. 2005b). Potential differences by species can be due to differences in life history needs. For example Chinook salmon are likely candidates to colonize large river systems with estuaries due to their relatively larger size, the need to spawn during natural low flow periods such as the summer and fall months, and their extended use in estuaries as outmigrating smolts. Sockeye salmon typically require lake environments for rearing and may increase and decrease in population size as a function of lake area and connectivity (Milner et al. 2007). Both coho salmon and steelhead are more freshwater-dependent than other salmonid species, and less estuarine dependent thus their ability to utilize the newly opened mainstem, floodplain, and tributary habitat is typically quite strong. Both species also utilize mainstem margins, floodplain channels, and typically maximize their extent in tributaries in a watershed. Within a given species, run-timing and different life history strategies may also result in different stray rates. For example Keefer et al. (2005b) found that early steelhead in the Columbia River system are more likely to stray into tributaries because they are typically exposed to high mainstem river temperatures (e.g. > 20º C) for longer time periods than late migrants, increasing the likelihood to stray into cooler lower Columbia River tributaries.

In addition, interactions with existing fish populations will also affect salmonid colonization potential. Interactions between existing resident and newly arrived anadromous salmonids could have a positive or negative effect on the extent and rate of anadromous salmonid colonization. Interspecific competition between different salmonid species is affected by fish density and local habitat features (Harvey and Nakamoto 1996; Volpe et al. 2001; McMillan et al. 2006). Low levels of habitat diversity and complexity can lead to greater competition and result in growth and survival levels being significantly less for one species relative to the other (Harvey and Nakamoto 1996). Such competition can typically result in “residents” having a competitive advantage relative to “challengers” (Volpe et al. 2001; Glova and Field-Dodgson 1995). Interactions between resident and anadromous salmonids can also be positive. Downstream migrating residents may accelerate colonization extent and rates due to positive spawning interaction with upstream moving anadromous populations (McMillan et al. 2007). The downstream movement of upstream resident populations can also lead to the establishment of self-sustaining spawning populations (Roghair and Dolloff 2005), that result in outmigrating smolts (Ruzycki et al. 2003).

Most of the salmon competition literature has considered competition for food and space by juvenile and the competition by adults for breeding space have gotten less attention and can play a role in salmon colonization. One example is habitat segregation between spawning sockeye salmon and non-dominant pink salmon.

Observations in southeast Alaska showed pink salmon concentrated in the lower portions of a river system and sockeye salmon predominately upstream (Fukushima and Smoker 1998). Differences in flow depth, velocity, and stream channel gradient were also observed in the nest sites used by these species (Fukushima and Smoker 1998). Sympatric salmonid populations typically exhibit some sort of spawning habitat segregation which would allow the establishment of populations, given that there was separation in space or time (Witzel et al. 1983; Bagliniere et al. 1994; Fukushima and Smoker 1998).

Identifying and understanding how each of these variables affects species-specific salmonid recolonization provides a template for salmonid response in any watershed. For example, pink salmon which typically have larger but highly variable population sizes, higher straying rates, minimal variation in life history characteristics, and a short freshwater residence are prime candidates for the colonization of newly opened habitats (Quinn 2005). Other species such as steelhead have lower population sizes, lower straying rates, greater variation in their life history, and greater freshwater residence time are thus less likely to establish spawning populations first (Quinn 2005). Conversely, pink salmon may be limited in their spatial extent to colonize due to their relative limited ability to swim over natural barriers, whereas steelhead may have the greatest spatial extent because of their ability to maneuver past barriers.

Summary

It is unknown as to why salmon ultimately stray from their natal streams, however straying is a natural process that occurs at the individual level, whether it is the result of mechanistic or sensory physiology and ontogeny reasons. Straying has population-scale implications that allow for the establishment of self-sustaining populations. Populations can become established in years to decades and vary based on initial source population size, distance to a source population, habitat area, stray rate, their ability to adapt to local habitat characteristics once in the new habitats, and their interaction with existing fish populations. The restoration of salmon populations in historically available habitats that have been disconnected and are now reconnected may be as simple as allowing salmon to naturally colonize because of their ability to locally adapt to the right habitat conditions, especially if there is minimal competition.

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Tables

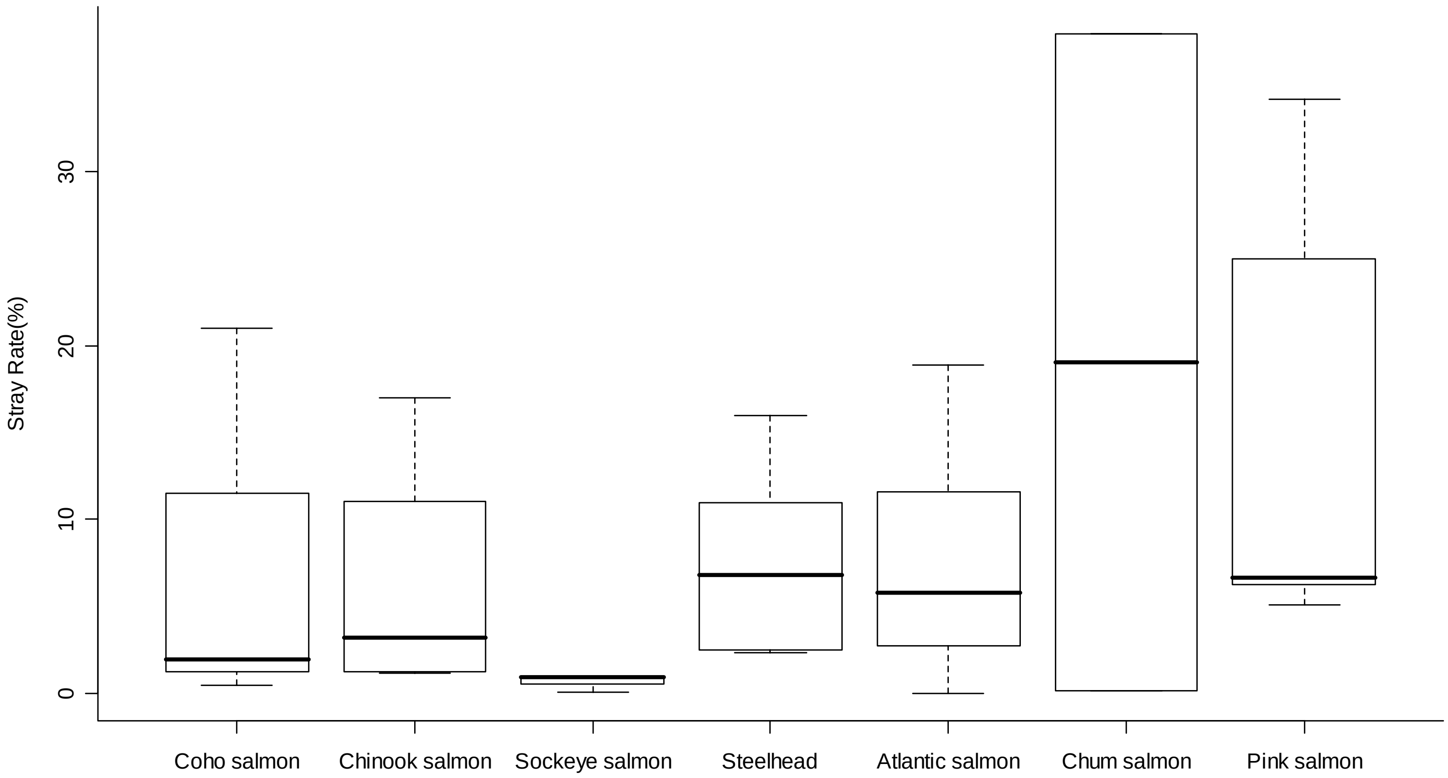
Table 1. Variables that affect salmonid colonization

Variables which affect salmonid recolonization	Likely to disperse & colonize	Not likely to disperse & colonize
Barriers to movement	Few, small	Many, large
Distance from source population	Near	Far
Habitat area	Large	Small
Population size	Large	Small
Population stray rate	High	Low
Life history adaptation to local habitat characteristics	High	Low
Habitat type and condition	Similar habitat types to source population, Good condition	Different habitat types to source population, Poor condition
Interaction with existing fish population	Positive	Negative

Figure Captions

Figure 1. Stray rates as a function of salmonid species. Stray rate data comes from numerous sources that were synthesized in Hendry et al. 2004 – Appendix 1 – Straying rates of anadromous salmonids and recent work by Keefer et al. 2005. The number of studies for each species is Coho salmon n = 2, Chinook salmon n = n = 8, Chum salmon n = 2, Pink salmon n = 3, Sockeye salmon n = 4, Steelhead n = 4, and Atlantic salmon n = 8.

Figure 1.


Stray Rate(%)
0
10
20
30
Coho salmon
Chinook salmon
Sockeye salmon
Steelhead
Atlantic salmon
Chum salmon
Pink salmon

Spatial distribution and dynamics of pink salmon, chum salmon, and Chinook salmon in a watershed dominated by sockeye salmon: insights into the processes of straying and colonization

Abstract

We explored the habitat associations of three species of Pacific salmon, pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and Chinook salmon (*O. tshawytscha*) in the Wood River system of Bristol Bay, Alaska in streams where sockeye salmon (*O. nerka*) are numerically dominant. We developed multivariate models to investigate the relationships among the occurrence of non-dominant salmon, habitat characteristics, and competition with locally dominant sockeye salmon, using four decades of data on salmon presence and abundance, and habitat survey data. In streams meeting the fundamental requirements for salmon reproduction, as evidenced by the presence of sockeye salmon, we found a range of occurrence of the other species, from non-existent to episodic to nearly perennial. The frequency of occurrence and abundance of non-dominant species increased with watershed drainage area and stream depth and, to a lesser extent, decreased with sockeye salmon density. Conversely, sockeye salmon densities decreased with watershed drainage area and stream depth. In addition, habitat partitioning between spawning sockeye and pink salmon was evident at the reach scale within one stream in which they were both found. Pink salmon tended to occupy habitats lower in the drainage network than sockeye salmon even though the species spawned simultaneously. We conclude that increasing watershed area results in larger stream habitat area and a

greater number of deeper and wider habitat types, thus allowing for the sympatric occurrence and persistence of other salmon species with sockeye.

Introduction

Salmonid fishes present excellent opportunities to study the characteristics of populations that are small, ephemeral, or transitioning in abundance in the presence of numerically dominant species. Salmonids share many fundamental habitat requirements, especially with respect to the reproduction. There is broad overlap in the thermal requirements and the stream gravel substrate in which almost all species breed (Kondolf and Wolman 1993; Quinn 2005, and references therein). The occurrence of sub-dominant species however can vary both spatially and temporally within and across watersheds (Labbe and Fausch 2000, Scarnecchia and Roper 2000, Esin and Leman 2008). What controls the occurrence of non-dominant salmonids? How does this vary among and within streams? The occurrence, establishment, and persistence of small, self-sustaining non-dominant populations is typically related to the compatibility between specific life history adaptations and the physical, ecological, and biological characteristics of the new habitats (Quinn 1984, Allendorf and Waples 1996, Burger et al. 2000). The study of small, self-sustaining populations is important because it focuses on specific factors that can influence the successful occurrence of non-dominant species as well as the factors preventing them from becoming more numerous, in the face of competition with other species. On the other hand, the observation of a given species does not necessarily constitute documentation of a self-sustaining population because low levels of dispersal from large source populations may create the appearance of a population where in fact there is only a sink (Cooper and Mangel 1999). Thus, the factors associated with such episodic occurrences are also important for understanding both the species in question and the broader subject of population sources and sinks.

Spawning site characteristics vary among species, and reflect variation in body size; larger fish tend to spawn in deeper and faster water, and in streambed areas with larger substrate size (Crisp and Carling 1989, Groot and Margolis 1991, Kondolf and Wolman 1993, Quinn 2005, Beechie et al. 2008). For example, Chinook salmon have the largest average body size of the Pacific salmon species and spawn in the largest substrate size (Groot and Margolis 1991; Quinn 2005). Chum salmon are considerably larger than sockeye salmon, and pink salmon are typically the smallest, and spawn in areas with the smallest streambed particle size (Groot and Margolis 1991; Quinn 2005). Salmonids select water depths and velocities that are suited to their ability to hold a position in the stream and to dig redds (Beechie et al. 2008). Typically the water must be deep enough for the fish to spawn in, usually deeper than the female's body depth (Crisp and Carling 1989). Velocities must be low enough that both males and females can hold position in the water, but fast enough to transport material dislodged from the stream bed during redd excavation downstream (Beechie et al. 2008). Body size of spawning salmonids is also related to streambed gravel size, thus larger species of salmon tend to use larger sized material for redd sites (Kondolf and Wolman 1993, Crisp 2000, Quinn 2005, Beechie et al. 2008), and egg burial depth also increases with increasing body size of females (Devries 1999, Quinn 2005). However, gravel size, water depth, and water velocity are related, making it difficult to determine the key attribute for spawning site selection (Quinn 2005).

While spawning habitat preferences result in different preferred spawning locations among salmon species, there is also considerable overlap in habitat use, and some level of inter-specific overlap and competition is common (Fukushima and Smoker 1998; Quinn 1999). Inter-specific competition varies with sex, species, and density, and results in differences in spawning habitat use (Fukushima and Smoker 1998, Quinn 1999). For example, Quinn (1999) found that inter-specific competition among sockeye, chum, and pink salmon was greatest among females for redd sites, and certain species such as pink salmon had a greater propensity towards inter- rather than intra-specific competition.

In many regions one cannot explore the correlations between habitat, local adaptations, and the occurrence of non-dominant salmon because the populations have declined so much as a result of fishing, degradation and loss of habitat, hatcheries, climate change, and the introduction of non-native species (NRC 1996, Montgomery 2003). However, in Bristol Bay region of southwest Alaska, where the dominant species in the vast majority of watersheds is sockeye salmon (*Oncorhynchus nerka*), several other salmonid species occur throughout the region including pink (*O. gorbuscha*), chum (*O. keta*), Chinook (*O. tshawytscha*), and coho salmon (*O. kisutch*), rainbow trout (*O. mykiss*), Arctic char (*Salvelinus alpinus*) and Dolly Varden (*S. malma*) (Oswood et al. 2000, Quinn 2005). This is an excellent area to investigate the correlation between these relationships because the habitat condition and salmonid populations have not been altered by anthropogenic influences such as land development, hatchery production, and invasive species, and the fisheries have been managed in a careful and sustainable manner (Hilborn et al. 2003). The numerically dominant sockeye salmon have especially broad overlap in habitat use patterns with pink and chum salmon because in all three species the juveniles usually leave the stream in which they were spawned to migrate to sea (pink and chum salmon) or to a nursery lake (sockeye). The presence of large lakes is important to the life history of the sockeye salmon but it is not clear why the other species should not also be abundant in the otherwise suitable habitat. The region also has a diversity of stream characteristics (e.g., width, depth, gravel size, etc.) that facilitates comparisons of adult salmon occurrence and abundance because the selection of spawning sites by salmon is based on such factors as water depth, velocity, gravel size, and temperature (Groot and Margolis 1991, Quinn 2005, Beechie et al. 2008).

The objective of this study was to examine the correlations between the occurrence of three different salmon species with the habitat characteristics and density of competing, numerically dominant sockeye salmon at the watershed and reach scale in streams of the Wood River system, Alaska. We hypothesized that the frequency of occurrence and abundance of non-dominant adult salmon would increase with habitat area due to increased quantity and diversity of suitable holding and spawning habitat, and greater scope for habitat segregation among species. We also hypothesized that the occurrence and abundance of non-dominant salmon would vary as a function of salmon species and their relative size. Thus Chinook and chum salmon, being the largest bodied, were predicted to occur in larger stream systems, whereas the smaller pink salmon were predicted to have a broader range of suitable habitat, including large rivers to the smallest streams.

Materials and Methods

Study area

The Wood River system has a drainage area of 3,590 km^2 and is a series of four large lakes (lake size from 90 to ~210km^2) interconnected by rivers that are relatively wide (> 60m), deep (up to 4.5 m), short (3 to 6 km), and low-gradient (< 0.50%) that become the Wood River and drain into the Nushagak River and Bristol Bay, Alaska (Figure 1). There are over 50 watersheds that make up the Wood River system, ranging in drainage area from 2.5 km^2 to 172.2 km^2 (average = 31.3 km^2) and in elevation from 15 to 1,531 m (average = 210 m). The hydrology of the streams in these watersheds is a mix of snowmelt (chiefly April through June) and spring-fed, and some have small lakes, spring-fed ponds or beaver ponds.

Approach

We approached the subject of relative abundance of salmon species at two spatial scales - stream and reach, and two forms of data - fish occurrence and abundance. The stream scale (e.g., several km) scale approach used long-term (40 yr) presence/absence data for pink, chum, and Chinook salmon. We used non-dominant salmon occurrence and abundance as an indicator of either potentially small, persistent populations or colonists because their populations are relatively low in many of the smaller streams throughout the Wood River system, yet they have been documented in 28 streams for over 35 years by the University of Washington's Fisheries Research Institute (FRI) program during annual surveys for spawning sockeye salmon. The finer, reach scale (e.g., 100s of m) approach used spatially explicit pink salmon abundance data collected in 2005 and 2006. Data on both scales were used to test hypotheses pertaining to the occurrence and abundance of small salmon spawning aggregates. Each scale used either descriptive or statistical techniques to determine the correlations between fish occurrence/abundance and physical habitat characteristics and adult sockeye densities.

Data

Fish occurrence data used in our analysis were based on annual surveys of spawning sockeye salmon collected by the University of Washington Fisheries Research Institute (FRI) from 1968 to 2007. In addition to counts of live and dead sockeye salmon, the presence or absence of pink, chum, and Chinook salmon was recorded. In some cases there were counts but in others only the presence was noted so only occurrence data were examined. It is important to note that all 28 streams where pink, chum, and Chinook salmon have been documented could not be used for our analysis because of inconsistent annual data collection. Fifteen of the 28 streams were used that had consistent data collection which occurred between 1968 and 2007. The entire reach of stream used by sockeye salmon or, for larger streams, an index reach, was surveyed by two or more observers on foot between 1 and 4 times from the beginning of July through the beginning of September over the entire period of record. The streams or index reaches averaged 2.6 km long (range: 0.35 - 7.6 km).

We collected stream habitat data from all 28 streams in the Wood River system with long-term data on abundance and occurrence of salmon. Stream measurements included bankfull and wetted width, bankfull and wetted depth, stream channel gradient, and stream bed particle size using Wolman pebble counts (Wolman 1954). We also collected information on habitat type, wood loading, in-channel cover type (e.g., cut-banks, wood, boulder clusters), riparian vegetation type, and the amount of in-channel cover relative to wetted width. We sampled the upper, middle, and lower segment of each spawner survey index reach at 10 to 20 channel widths per segment, which is approximately 20 to 30% of the total index reach length. For stream segments within the index reach that we did not sample we classified according to stream channel type using the Montgomery and Buffington (1997) system.

Analysis

We used several steps to correlate adult pink, chum and Chinook salmon occurrence and abundance with physical habitat characteristics and with sockeye salmon abundance in the Wood River system. First, we identified similarities and differences in pink, chum, and Chinook salmon frequency of occurrence among streams using simple summary plots of data from 1968 to 2007. We also plotted abundance for these species from 2004 to 2007 because focused counts for the non-dominant species were obtained in these later years.

Next, we explored stream habitat associations using correlations and principal components analysis (PCA) on variables that were continuous, non-ratio, and not normalized to identify which stream habitat characteristics explained the greatest amount of habitat variation among streams in the Wood River system. The correlation and PCA reduced the number of stream habitat variables from 32 to a smaller set of “less correlated” stream habitat variables for explaining relationships among streams and salmon occurrence and abundance. We then examined ecological resemblance among streams using the Gower’s similarity coefficient (Gower 1971), which averages multiple descriptors to gauge the extent of similarity. Binary, descriptive and quantitative variables were used to calculate a normalized distance to identify the relative similarity among streams. The correlation and PCA, in combination with Gower's coefficient, allowed us to group streams according to a distilled set of habitat variables.

We then used the reduced set of informative, "less correlated" stream habitat variables to examine the correlations among pink, chum, and Chinook salmon occurrence and abundance and stream habitat characteristics using a linear model selection approach. We used species frequency of occurrence (i.e., proportion of years in which the species was observed), or abundance as the response variable; stream habitat characteristics and sockeye salmon density as measure of competition were the independent variables. We implemented a linear modeling approach using Akaike's Information Criterion, adjusted for small sample sizes (AIC*c*), to determine which model best fit the data (Burnham and Anderson 2002). The difference between the AIC*c* of a candidate model and the one with the lowest AICc provided the ranking metric (ΔAIC*c*). Generally speaking, ΔAIC*c* between 0 and 3 indicates substantial support for a model being as good as the best approximating model, ΔAIC*c* between 4 and 7 represents less support, and ΔAIC*c* of greater than 7 indicates very little support for a candidate model relative to the best model (Burnham and Anderson 2002). Akaike weights (w_I) were calculated, representing the strength of evidence in favor of model i being the best model. The ratio of Akaike weights (w_I / w_j) indicates the plausibility of the best-fitting model compared to other models (Burnham and Anderson 2002). Models with an evidence ratio of 10 or less were considered plausible (Burnham and Anderson 2002). If models were not clearly the "best" model based on the preceding critiera, then models within three AIC*c* were considered competing models and results were averaged to determine the maximum likelihood estimate for the intercept and each of the independent variables that are part of the models (Burnham and Anderson 2002, Haring and Fausch, 2002).

Results

Stream-scale salmon occurrence patterns

All three species of non-dominant salmon (pink, Chinook, and chum) were seen in at least one year in 5 of the 15 streams consistently surveyed from 1968 to 2007 (Figures 2a and 2b). The number of streams with all three non-dominant salmonids was considerably greater in Lake Nerka (4 out of 7) than in Lake Aleknagik streams (1 out of 8). The number of streams with two non-dominant salmonids (chum and pink salmon) was the same as all three species (5 out of 15). Only two of the 15 streams had only pink salmon and both were in the Lake Aleknagik system (Figure 2a). Hansen did not have an observed occurrence of pink, Chinook, and chum salmon from 1968 to 2007.

Pink salmon were seen at least once in the majority of streams in lakes Aleknagik and Nerka (11 out of 15). Pink salmon occurrence was greater in Lake Nerka (7 out of 7) than Lake Aleknagik streams (5 out of 8). The proportion of years present by stream for pink salmon ranged between 0 and 65% and averaged 20% for all streams (Figures 2a and 2b). Ice and Hidden Lake creeks had pink salmon occurrence levels at or greater than 50% from 1968 to 2007. Pink salmon occurrence in all streams varied according to year (Table 1). Even-year pink salmon occurred in 5 of the 8 Lake Aleknagik streams for even years, and 4 out of the 8 streams in odd-years. Pink salmon occurred in more Lake Nerka streams during even-years than in odd-years (Table 1). Even-year pink salmon occurrence levels were greater than odd-year pink salmon occurrence levels for all streams with the exception of Happy and Fenno creeks (Table 1).

Chum salmon were seen at least once in all but one stream (14 out of 15), respectively for lakes Aleknagik and Nerka. The proportion of years present by stream for chum salmon ranged between 0 and 67% and averaged 22% for all streams consistently surveyed (Figures 2a and 2b). Ice, Pick, and Fenno creeks had chum salmon occurrence levels greater than 50% from 1968 to 2007. Chinook salmon were seen in 5 out of 15 streams, and 4 of the 5 streams where Chinook had occurred drain into Lake Nerka (Figures 2a and 2b). However, the proportion of years present was considerably higher (39% v. 0 to 11%) in Ice Creek, a tributary to Lake Aleknagik (Figure 2a), than the Lake Nerka streams. In no stream were Chinook salmon reported in > 50% of the years from 1968 to 2007.

One of the strongest patterns in the occurrence of pink and chum salmon was temporal (Figure 3). The occurrence of pink, Chinook, and chum salmon in Aleknagik and Nerka streams increased from less than 10% of all streams surveyed in the1970s to over 25% in the years 2000 through 2007. Pink salmon occurrence by decade increased from 3% of all streams surveyed in the 1970s to 24% in the 21st century (Figure 3). Chum salmon followed a similar trend, increasing from 8% of all streams surveyed in the 1970s to 44% by the 21st century. Chinook salmon occurrence by decade did not show the increasing trend seen for pink and chum salmon and averaged 3 to 4% for each decade (Figure 3).

Stream-scale salmon abundance

Relative abundance patterns from 2004 to 2007 were similar for Lake Aleknagik streams occurrence patterns; Ice Creek had the largest number of salmon other than sockeye (Figure 4a). Pink salmon abundance in Lake Aleknagik streams was greatest in

Ice Creek, averaging in the 100s from 2004 to 2007. All of the other streams in Lake Aleknagik were well below Ice Creek in terms of pink salmon abundance. Chum salmon averaged in the 10s in Ice Creek, and fewer than 10 in the other streams surveyed in the Lake Aleknagik system. Chinook salmon only occurred in Ice Creek among the Lake Aleknagik streams (Figure 4a). Lake Nerka streams had, on average, more pink salmon streams (Figure 4b). Elva and Lynx creeks both had 100s of pink salmon from 2004 to 2007, while Fenno, Hidden Lake, and Kema had 10s of pink salmon. Chum salmon averaged in the 10s in Fenno and Pick creeks but all other Lake Nerka streams had fewer (Figure 4b). Chinook salmon were scarce in all the Lake Nerka streams.

Habitat characteristics

A wide range of stream habitat characteristics were found in the Wood River system (Tables 2a and 2b). Lake Aleknagik streams had slightly larger drainage areas, however the streams in Lake Nerka generally were steeper, wider, deeper, and had larger average stream particle size (D50) (Table 3). Many of the habitat variables were correlated to each other because; 1) they are derived from one of the other variables (e.g., width to depth ratios), 2) a percent of a total estimate (e.g., % habitat depth), or 3) are an indicator of the overall drainage area in a watershed (e.g., width, depth, stream channel gradient, and stream particle size) (Table 4). For example several key variables were highly correlated (e.g., > 0.50) with drainage area, including bankfull width, bankfull depth, wetted width, wetted depth, average depth by habitat type, and the number of key pieces of wood or logjams in a watershed (Table 4).

A PCA on the habitat variables revealed that several stream habitat categories were important in differentiating streams in Lake Aleknagik and Lake Nerka (Figure 5,

Table 5). Only the first two axes of the ordinations of sample sites were interpreted because they explained the greatest amount of the variability in the data. The first axis described an increasing gradient between streams with small drainage areas (and, consequently, shallow, narrow, and steeper channels) to streams with larger drainage areas (i.e., deeper, wider, and lower slope (Figure 5). The second axis described a gradient between sites with small streambed particles, a larger proportion of the area in pools, and more in-stream channel cover to streams with larger streambed particles, less pool area and less stream cover. These two axes explained 61% of the variance, suggesting strong linear relationships among the habitat variables. Several general categories of habitat variables were identified with the correlation and PCA analysis including stream habitat area and associated stream widths and depths (drainage area, bankfull depth, bankfull width, riffle depth, and residual pool depth), in stream cover (average bank cover width, pool area, and logs per channel width), stream channel gradient, and streambed particle size (D15, D50, and D84).

Gower's similarity index (Figure 6) revealed several groupings among the streams of the Wood River system. Streams with smaller drainage areas had lower gradients, were shallower, narrower, and had less wood structure (Eagle, Mission, Hansen, Big Whitefish, Yako, Bear, A, and C creeks). These streams were typically near 5 m bankfull width and had little water flow during the summer habitat surveys (average width of 2.6 ±0.36 m, average depth of 0.2 ±0.04 m). The second grouping (Fenno, Hidden Lake, Kema, Lynx, Pick Stovall, Silver Salmon, and Youth) had similar stream channel slopes as the first group, but had three times the average bankfull (12.9 ±02.43m) and wetted width (6.5 ±0.94m), and twice the bankfull (0.9 ±0.13 m) and wetted depth (0.4 ±0.04 m) relative to the first group. Wood loadings were also slightly higher than the first group. The third group of streams (Cottonwood, Happy, Berm, Joe, and Sam) are between the first and second grouping in terms of drainage area, widths, and depths, but have stream channel gradients that are two times greater (1.2 ±0.12%) than the first two groups. The fourth group (Little Togiak Creek, Sunshine, Rainbow, and Ice Creeks) are the largest low gradient streams and drainage areas that are 5 to 16 times the size of the other groupings (133 ±17 km^2). This increase in drainage area was mainly responsible for the greater widths and depths. The fifth group of streams (Elva Creek and the Little Togiak River) differentiated themselves from the other groups average stream bed particle size (D50) that was two to four times larger than the other groups (78 ± 23 mm). N-4 did not group with any of the other streams due to the combination of a relatively high stream gradient (2.5%) and being relative small in channel width (6.0 m bankfull width).

Correlating salmon occurrence and abundance with habitat characteristics

Correlating pink, chum, and Chinook salmon occurrence with habitat attributes from the different streams in the Wood River system revealed that drainage area (km^2) was an important, positively correlated factor in the development of suitable habitat for species besides sockeye salmon (Table 6a, Appendix). Drainage area was in all of the candidate models for pink and Chinook salmon occurrence and 40% of the candidate models for chum salmon occurrence (Table 6a, Appendix). Glide depth was positively correlated parameter in each of the chum and Chinook salmon occurrence models that had the best AIC*c* scores (Table 6a, Appendix).

Another set of candidate models was developed without drainage area because many of the habitat attributes, particularly width and depth, were correlated with drainage area (Table 4). After eliminating drainage area, pink salmon occurrence was best explained by models having wetted width, a variable highly and positively correlated to drainage area (Table 6b, Appendix). Glide-depth associated models were the best for chum salmon, and Chinook salmon occurrence had at least one depth or width variable associated with each candidate model (Table 6b, Appendix).

Candidate models correlating pink, chum, and Chinook salmon abundance in the recent years to habitat attributes were similar to occurrence models using the longer time series of data (Table 6c, Appendix). Pink salmon abundance was correlated to drainage area and streambed particle size (D50), which were part of each of the best models (Table 6c, Appendix). Chum salmon abundance included drainage area in all the candidate models (Table 6c, Appendix). Chinook salmon abundance models had considerably lower correlation coefficients (0.18 to 0.48), and the lack of difference in the evidence ratios (w_I / w_i) between the candidate models and the null model suggests that none of the models explained Chinook salmon abundance adequately (Appendix). The two best models, based on the ΔAIC*c*, to explain sockeye salmon density only had depth variables (Table 7), especially bankfull depth and glide depth. In both cases density was negatively correlated with depth (Figure 7), in contrast to the positive relationships with depth found for pink and chum salmon occurrence and abundance (Figure 8).

The relationship between dominant sockeye salmon and non-dominant salmon

Sockeye salmon density was a significant variable in only one of the best pink occurrence models and two of the best Chinook salmon occurrence candidate models (Table 6a and 6c). Sockeye salmon density was negatively correlated with pink salmon occurrence (Table 6a), while it was positively correlated with Chinook salmon occurrence and abundance (Tables 6a and 6c). Stream specific average pink and chum salmon occurrence typically decreased in Wood River streams as stream specific average sockeye density increased (Figure 9). Occurrence levels were less than 25% where average sockeye densities were > 0.40/m^2, and went to 0 where densities were > 0.60/ m^2. Sockeye salmon density did not strongly affect occurrence and abundance of pink, chum, and Chinook salmon because the effects of other variables, notably drainage area, were so prominent (Figure 10). For example pink, chum, or Chinook salmon did not occur in two watersheds in the Wood River system with drainage areas < 8 km^2, and occurrence ranged from 10% to 51% for watersheds with drainage areas between 8 and 50 km^2. Occurrence exceeded 50% in the two watersheds > 50 km^2.

Habitat area and segregation between sockeye and pink salmon

Drainage area is a surrogate for many of the physical habitat attributes including overall habitat area surveyed (Figure 11). We examined the distribution and abundance of pink and sockeye salmon in Ice Creek, one of the larger watersheds in the Wood River system, to see if habitat segregation occurred during spawning between sockeye and pink salmon. Reach-scale abundance data revealed differences in peak location of spawning for sockeye and pink salmon (Figure 12). Sockeye salmon abundance was higher in the upper portion of the 5 km index reach, above river kilometer 3.9, while pink salmon abundance was greatest in the lower 2 km of Ice Creek. Overlap between the two species did occur throughout the 5 km index reach.

It is important to note that there is direct overlap between the observed timing of sockeye and pink salmon in Ice Creek, where peak spawning for sockeye occurs during the first two weeks in August (Groot and Margolis 1991) and 100% of all pink salmon that have been seen in Ice Creek, and all other systems throughout Lake Aleknagik and Nerka, also occurred in August (Figure 13). In general observed spawn timing for sockeye, pink, chum, and Chinook salmon in independent streams draining into Lakes Aleknagik and Nerka occurs between the end of July and the end of August (Figure 13) (Groot and Margolis 1991, Hodgson and Quinn 2002, Hilborn et al. 2003). This does not include the large connecting rivers between lakes (“trunk rivers”), the Wood River proper, and the beach areas (Groot and Margolis 1991).

Predicting pink, chum, and Chinook salmon occurrence and abundance

Maximum likelihood estimates for intercept and slope parameters for each of the “best” pink, chum, and Chinook salmon occurrence and abundance models revealed differences in the estimated probability of occurrence and population estimates (Tables 6 a, b, and c and Figures 15, 16, and 17). The best models for occurrence, including drainage area, estimated that the probability of occurrence for pink salmon is 2 to 5 times greater than for both chum and Chinook salmon for a given watershed area (Figure 14). All three probabilities decrease dramatically when drainage area is taken out of the best models (Figure 15). Pink salmon were estimated to still occur at a higher proportion than chum and Chinook with an increase in stream channel width and depth, but overall occurrence estimates are not as large as with drainage area. Lastly, abundance estimates suggested that pink salmon can number in the 100s in larger drainage areas with relatively large substrate (Figure 16). However, over 75% of the watersheds in the Wood River system are less than 50 km2 and have a D50 of 35 mm or less, and these features result in an estimates of 100 or fewer fish (Figure 16). Both Chum and Chinook salmon abundance estimates are considerably lower than pink salmon abundance estimates, ranging in the 10s even in the largest watersheds with the largest stream channel widths and depths.

Discussion

Correlating salmon occurrence and abundance with habitat characteristics

Drainage area, stream depth, width, the amount of in-channel cover, and streambed particle size were important descriptive variables related to the distribution of pink, chum, and Chinook salmon. Occurrence and abundance of all three species increased with an increasing drainage area. Numerous aquatic and terrestrial studies (Thomas et al. 1992, Rieman and McIntyre 1995, Magnuson et al. 1998, Dunham and Rieman 2000, Harig and Fausch 2002) have supported the species-area relationship which states that the probability of a species being present in a habitat increases with increasing area (MacArthur and Wilson 1963).

The species area relationship begs the question of what is the significance of habitat area. The positive relationship between species richness and area has been hypothesized and, in part shown, to be an "epiphenomenon associated with sampling effort," meaning larger areas contain more individuals, and thus sample the species pool more effectively (Connor and McCoy 1979, Angermeir and Schlosser 1989). However, fish-habitat associations that include drainage area and other factors such as stream depth, width, and habitat complexity are well documented, and patterns of species abundance and distribution result from a combination of metapopulation dynamics, habitat diversity, and passive sampling (Rieman and Dunham 2000, Haring and Fausch 2002, Pess et al. 2002, Connor and McCoy 1979). Nonetheless, mechanistic interpretations from species area relationships are typically not possible because it is difficult to interpret what the slope of the species area regression means with respect physical conditions and biological processes that are associated with occurrence and abundance such as habitat availability, habitat selection, immigration, and extinction (Magnusson et al. 1998).

Several features correlated with and determined by drainage area were important for understanding the physical habitat conditions that allow for non-dominant salmon occurrence and abundance in the Wood River system. Larger watersheds provided a greater amount of habitat area (Figure 11) which could be used by pink, chum, and Chinook salmon, and watershed area can be a useful predictor of salmonid occurrence and abundance (Haring and Fausch 2002). The increase in area has been hypothesized to result in a greater diversity of habitat types that may be needed to promote the survival at each life stage of enough individuals to sustain populations (Haring and Fausch 2002). Area has also been hypothesized to allow existing populations to be less vulnerable to natural and anthropogenic disturbance and reduce the potential for extinction (Lande 1993). An increase in habitat area alone, without changes to habitat types or increased resilience to disturbance, can also result in an increase in the occurrence and abundance of animals (Steffan-Dewenter 2003). This was the case in the Wood River system for pink, chum, and Chinook salmon, but not the case for sockeye salmon.

Streams with large drainage areas tended to be wider and deeper than streams in smaller basins (Table 3). These attributes, in turn, were associated with higher levels of occurrence and abundance of pink, chum, and Chinook salmon. Similar positive relationships between presence and abundance and stream width and depth have been found in previous studies (Angermeier and Schlosser 1989, Nelson et al. 1992, Dunham and Rieman 1999. Haring and Fausch 2002). Bull trout occurrence within occupied patches has been found to be positively correlated to stream width (Dunham and Rieman 1999, Ripley et al. 2005). Angermeier and Schlosser (1989) found that habitat volume predicted species richness more precisely than habitat area, thereby suggesting that the area and depth of streams influence the distribution of fishes. However, stream width and depth were not always positively correlated to all salmon that occurred within the Wood River system (Tables 6a, b, and c, Figure 7). Stream depth variables such as bankfull depth were negatively correlated to sockeye density. This has also been found for other species such as coastal cutthroat trout, where there was a decrease in cutthroat trout presence with increasing channel width (Rosenfeld et. al. 2000).

More mechanistically-oriented studies have also identified the importance of stream depth to adult pink, chum, and Chinook salmon. Migratory behavior of both pink and chum salmon was monitored in the Shibetsu River, Japan, where they found that preferred swimming depth for chum salmon was between 0.2 and 0.4m, and 0.6 and 0.8m for pink salmon (Akita et al. 2007). Both species migrated at these depths along defined riverbanks and near the bottom of the streambed (Akita et al. 2007). Minimal flow depth to spawn for pink salmon is typically considered to be 0.15m to 0.2m (Raleigh 1985, Bjornn and Reiser 1991). Chum salmon have also been shown to avoid the “very shallow” and “deep” sites when excavating redds (Quinn 2005). Chinook salmon, the largest bodied of all salmon, also typically favor relatively deeper (>0.3m) locations during spawning (Healey 1991).

All the streams in the Wood River system where pink, chum, and Chinook salmon were not observed between 1968 and 2007 had an average wetted depth less than the 0.15m which was identified as a minimal spawning depth for pink salmon reported in the literature (Bjornn and Reiser 1991). In addition many of the same streams do not have well defined, deep riverbanks at the mouth of the streams where they drain into Lakes Aleknagik or Nerka (George Pess, personal observation, 2004 and 2005). The combination of flows less than 0.15m deep and an ill-defined stream channel mouth could inhibit pink salmon from entering these smaller stream systems in the Wood River system. This is in sharp contrast to sockeye salmon, which do enter these systems in large numbers (Hilborn et al. 2003).

Average cover width (m), which in the case of the Wood River watersheds is predominantly undercut banks, was negatively correlated with pink salmon occurrence and abundance but positively correlated with Chinook salmon occurrence and abundance. It is not clear why there was a negative effect of cover on pink salmon but the positive effect on Chinook salmon abundance is consistent with published reports on other salmon species. The distribution of over-summering steelhead in the New River, northwestern California, was more strongly controlled by physical characteristics of pools, including cover, than by the availability of thermal refuges (Nakamoto 1994). Pool spacing, a larger-scale form of holding water and cover, was a dominant correlate of adult Chinook and coho salmon in the Puget Sound region of Washington State (Montgomery et al. 1999). Similarly, the amount of cover in a given holding location was an important component of preferred holding habitat for adult masu salmon in the Masuhoro River, Japan (Edo and Suzuki 2003). An increase in channel cover, whether it be in the form of undercut banks, depth, or structure such as wood provides visual isolation that can minimize interactions from well-documented terrestrial predators such as bears in the Wood River system (Quinn and Buck 2001, Quinn et al. 2001).

Streambed particle size (D50) was also an important component of several of the best candidate models for pink and chum salmon occurrence and abundance. However, the correlation varied positively and negatively by species and metric (occurrence or abundance), making it difficult to interpret (Tables 6a, b, and c). Median particle size at the redd site has been positively correlated to the average length of female salmonids (Kondolf and Wolman 1993). Larger females thus can typically spawn in larger substrates (Quinn 2005). Pink salmon, typically being smaller salmon (Quinn 2005), would thus have a negative relationship with an increase streambed particle size. However this is only the case of occurrence and not abundance. Conversely chum salmon can be larger bodied salmon (Quinn 2005) that would be positively correlated with an increase in streambed particle size however they are negatively correlated in both occurrence and abundance

Habitat area and segregation between sockeye and pink salmon

The occurrence of pink salmon was positively related to watershed drainage area and stream size but negatively related to sockeye salmon density. Conversely, sockeye salmon densities decreased with watershed area and stream depth. Does this inverse relationship reflect actual competition or habitat segregation, allowing multiple species to co-exist at the reach scale in larger watersheds?

Habitat segregation between spawning sockeye salmon and non-dominant pink salmon was evident at the reach scale in Ice Creek (Figure 12). Pink salmon tended to occupy habitats lower within the drainage network than sockeye salmon, even though there spawn timing was similar (Figure 13) (Groot and Margolis 1991, Hodgson and Quinn 2002). Observations in southeast Alaska also showed pink salmon concentrated in the lower portions of a river system and sockeye salmon predominately upstream (Fukushima and Smoker 1998). Differences in flow depth, velocity, and stream channel gradient were also observed in the nest sites used by these species (Fukushima and Smoker 1998). Sympatric salmonid populations typically exhibit spawning habitat segregation similar to what was observed in Ice Creek (Witzel et al. 1983, Bagliniere et al. 1994, Fukushima and Smoker 1998).

Does pink, chum, and Chinook occurrence allow for the development of self-sustaining populations in the Wood River system?

The lack of consistent pink, chum, and Chinook occurrence and low abundance levels suggest that the majority of streams draining into Lakes Aleknagik and Nerka are likely not small, persistent populations but rather the salmon are strays from larger "source" populations elsewhere. However, two streams had pink salmon occurrence and abundance levels that might indicate small, self-sustaining populations – Ice and Lynx creeks. Both streams had occurrence levels near or greater than 0.50 and abundance levels at or greater than 100 individuals, and the habitat necessary for segregation from sockeye salmon. It is important to note that we cannot answer the question based on existing data. More intensive enumeration surveys, coupled with genetics work on fish within these systems as well as those in nearby watersheds (e.g., Nushagak River) might determine if these fish are self-sustaining or strays from other populations. However, the existing data can give us valuable insight into hypothesizing which streams can potentially be self-sustaining, albeit small populations.

There are two main potential sources of pink, chum, and Chinook salmon strays into Lake Aleknagik and Nerka streams – the "trunk " rivers connecting each of the four lakes in the Wood River system, and the nearby Nushagak River. Pink salmon strays are likely to come from the Agulukpak River, a trunk river that connects Lake Beverly with Lake Nerka, the Agulowak River, a trunk river that connects Lake Nerka to Lake Aleknagik, or the Nushagak River, which is a larger tributary to Bristol Bay (Rogers and Burgner 1967, Baker et al. 2006). The Nushagak had an average estimated pink salmon escapement between the years of 1968 and 2007 of 1.3 million pink salmon (Baker et al. 2006). Chum and Chinook salmon are more likely to come from the Nushagak alone with an average annual escapement of 256,000 and an average annual return of 173,000 respectively. Other potential sources for Chinook salmon in the Wood River include the Togiak, Naknek, Alagnak, and Egegik (Baker et al. 2006)

Limitation of the study

There are two main limitations to this study. The first limitation is related to the occurrence and abundance data. Visual surveys on foot have many potential limitations and biases in the form of observation and process error (Korman and Higgins 1997, Jones et al. 1998). Some of the factors influencing observer efficiency include, but are not limited to, observer experience, weather conditions, fish behavior, survey method, and physical stream characteristics such as turbidity, water level, and habitat type (Korman and Higgins 1997, Jones et al. 1998, Korman et al. 2002). Accuracy of counts may decrease with an increase in fish density and can lead to a high between-observer variation (Jones et al. 1998). Additionally, spawner surveys in the Wood River system have been focused on sockeye salmon thus the data collected for pink, chum, and Chinook salmon were not always given equal priority. Despite these limitations, patterns and trends emerged over space and time suggesting that salmon other than sockeye were more common in larger systems than smaller systems. Non-sockeye salmon are typically more easily noticed in small, shallows streams, thus the lack of occurrence in such habitats is particularly striking.

Summary

This study demonstrates the utility of evaluating the role of habitat conditions on salmon occurrence and abundance. Presence/absence, abundance, and descriptive models at a hierarchy of scales provide hypotheses for more causative relationships between habitat variables and fish presence or abundance. While the relationships developed from our study cannot give definitive insight into the absolute habitat requirements needed for non-dominant salmonids to persist and sustain in the Wood River system, it does provide consistency between the correlative results and our mechanistic understanding of the relationship between salmonids and their habitats.

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Tables

Table 1. Even and odd year occurrence (%) of pink salmon in the Wood river system – 1968 through 2007.

Stream	Even-year	Odd-year
Lake Aleknagik		
Bear Creek	0.17	0.05
Eagle Creek	0.00	0.00
Hansen Creek	0.00	0.00
Happy Creek	0.00	0.05
Ice Creek	0.65	0.48
Mission Creek	0.05	0.00
Yako Creek	0.20	0.05
Whitefish Creek	0.15	0.00
Lake Nerka		
Elva Creek	0.25	0.10
Fenno Creek	0.15	0.19
Hidden Lake Creek	0.50	0.14
Kema Creek	0.20	0.00
Lynx Creek	0.45	0.00
Pick Creek	0.20	0.00
Stovall Creek	0.10	0.05

Table 2. Habitat characteristic data for 28 streams in the Wood River system. a. Lake Aleknagik streams. b. Lake Nerka streams

a.

	Bear Creek	Big Whitefish Creek	Eagle Creek	Hansen Creek	Happy Creek	Ice Creek	Mission Creek	Silver Salmon Creek	Sunshine Creek	Yako Creek	Youth Creek
Drainage area (km2)	14.0	11.7	4.0	3.0	18.0	93.0	4.0	32.0	172.0	13.0	79.0
Bankfull width (m)	6.3	5.2	3.0	5.9	10.1	22.3	3.0	7.4	26.3	6.5	27.5
Bankfull depth (m)	0.5	0.5	0.5	0.5	0.5	0.8	0.4	0.7	1.3	0.7	1.7
Bankfull width to depth ratio (m/m)	12.7	10.4	6.0	11.9	19.2	27.2	8.3	10.0	19.2	9.8	16.0
Gradient (%)	0.50	1.00	1.50	0.50	1.50	0.52	0.37	0.67	0.22	0.56	0.64
Wetted width (m)	3.35	3.47	1.75	3.03	4.14	8.66	1.70	5.23	10.13	3.52	12.71
Wetted depth (m)	0.30	0.27	0.36	0.08	0.32	0.63	0.14	0.43	0.92	0.29	0.52
Wetted width to depth ratio (m/m)	10.81	15.27	5.39	35.67	13.10	14.17	11.84	13.30	11.27	12.64	27.31
% pool	43	35	75	24	36	38	54	34	49	29	29
% riffle	36	15	11	67	58	34	23	11	26	51	41
% rapid	0	33	2	0	0	0	0	0	0	7	0
% glide	21	16	12	9	6	28	22	56	26	13	30
Channel widths (cw)/pool	4.2	4.0	1.7	8.7	2.1	4.3	4.3	10.1	2.7	7.0	3.7
Ave residual pool depth (m)	0.29	0.31	0.17	0.15	0.30	0.82	0.14	0.52	1.00	0.25	0.48
Ave riffle depth (m)	0.18	0.27	0.10	0.05	0.26	0.48	0.09	0.18	0.48	0.21	0.31
Ave glide depth (m)	0.37	0.35	0.10	0.10	0.38	0.48	0.11	0.33	0.74	0.37	0.50
Dominant cover type	1	1	1	1	1	2	1	6	3	3	2
Subdominant cover	3	2	7	7	8	1	7	3	2	2	3
Average cover width (m)	0.39	0.65	0.39	0.53	0.64	0.55	0.15	0.29	0.30	0.40	0.36
% width covered by bank	0.14	0.18	0.33	0.17	0.15	0.06	0.09	0.06	0.03	0.13	0.03
# key logs or logjams	1.0	0.7	1.2	0.3	6.7	7.1	0.5	0.0	7.7	0.5	1.2
# key logs or logjams/cw	0.2	0.1	0.4	0.1	0.7	0.3	0.1	0.0	0.4	0.1	0.0
D15	9	7	6	9	13	11	10	8	11	15	13
D50	16	19	11	14	25	19	21	17	20	27	27
D84	30	32	20	22	45	27	42	31	35	46	53
Channel type	1	1	1	1	2	1	1	1	1	1	1

b.

	A Creek	Berm Creek	C Creek	Cottonwood	Elva Creek	Fenno Creek	Hidden Lake Creek	Joe Creek	Kema Creek	Little Togiak Creek	Little Togiak River	Lynx Creek	N-4	Pick Creek	Rainbow Creek	Sam Creek	Stovall Creek
Drainage area (km2)	3.0	3.0	3.0	10.0	31.0	38.0	8.0	10.8	20.0	117.0	86.2	26.2	3.0	20.0	150.0	10.0	31.0
Bankfull width (m)	2.5	4.9	5.0	10.0	13.6	9.5	6.4	6.7	16.4	20.0	35.9	15.1	6.0	11.7	43.2	9.8	9.0
Bankfull depth (m)	0.5	0.6	0.7	1.1	1.0	0.8	0.7	0.7	0.6	1.3	1.5	0.9	0.4	0.7	1.3	0.7	0.9
Bankfull width to depth ratio (m/m)	5.0	8.1	7.1	9.0	13.6	12.0	9.9	10.3	26.1	15.4	23.9	17.0	15.0	16.7	34.2	16.5	10.3
Gradient (%)	0.3	0.9	0.5	1.1	1.8	0.5	0.6	1.4	0.6	0.3	0.1	0.7	2.5	0.7	0.3	1.0	0.3
Wetted width (m)	1.30	1.88	1.60	4.88	6.72	6.31	4.21	3.58	5.01	8.20	17.92	6.90	4.10	6.45	11.91	3.61	4.90
Wetted depth (m)	0.10	0.16	0.14	0.30	0.40	0.51	0.22	0.39	0.37	0.67	0.32	0.34	0.11	0.51	0.72	0.35	0.41
Wetted width to depth ratio (m/m)	13.00	12.24	11.43	16.92	16.94	14.28	19.77	9.05	13.49	13.14	56.00	27.33	38.99	12.77	16.55	10.24	12.16
% pool	15	2	26	5	12	47	43	24	53	50	30	21	49	36	31	28	40
% riffle	85	23	61	30	47	18	16	9	21	30	18	45	45	17	40	32	11
% rapid	0	32	0	17	24	0	0	36	0	0	0	5	0	0	0	8	0
% glide	0	43	13	48	17	35	41	31	26	19	52	30	6	46	28	32	49
Channel widths (cw)/pool	13.8	15.0	4.1	13.3	9.6	6.2	5.3	5.7	1.6	6.9	3.9	6.7	13.4	7.2	2.1	5.4	5.2
Ave residual pool depth (m)	0.16	0.00	0.16	0.19	0.43	0.62	0.25	0.47	0.53	0.55	0.19	0.37	0.16	0.62	0.97	0.46	0.45
Ave riffle depth (m)	0.07	0.08	0.10	0.23	0.27	0.20	0.18	0.16	0.18	0.46	0.35	0.23	0.08	0.45	0.31	0.17	0.17
Ave glide depth (m)	0.02	0.17	0.14	0.29	0.35	0.32	0.23	0.37	0.18	0.79	0.46	0.35	0.09	0.44	0.65	0.31	0.33
Dominant cover type	2	2	1	3	4	2	1	3	1	3	5	2	2	1	3	3	1
Subdominant cover	2	3	3	6	3	3	2	2	3	6	3	4	1	3	8	6	3
Average cover width (m)	0.21	0.26	0.39	0.29	0.24	0.35	0.32	0.21	0.35	0.10	0.00	0.21	0.10	0.34	0.27	0.26	0.32
% width covered by bank	0.16	0.14	0.24	0.07	0.04	0.05	0.08	0.07	0.07	0.02	0.00	0.04	0.03	0.05	0.03	0.08	0.07
# key logs or logjams	1.0	0.5	4.0	0.0	1.6	3.8	0.0	4.0	1.6	3.8	0.0	2.1	0.0	0.0	4.8	6.1	0.0
# key logs or logjams/cw	0.4	0.1	0.8	0.0	0.1	0.3	0.0	0.5	0.1	0.2	0.0	0.1	0.0	0.0	0.1	0.7	0.0
D15	8	16	7	17	69	15	6	10	5	17	30	12	13	6	18	21	12
D50	20	28	13	52	102	30	12	31	11	28	55	23	31	13	46	48	25
D84	36	52	20	128	184	53	23	57	19	48	112	50	57	20	76	90	46
Channel type	2	2	1	2	1	1	1	2	1	1	1	1	4	1	1	2	1

Table 3. Habitat characteristics (Average ±SE) for streams in Lakes Aleknagik and Nerka.

	Aleknagik	Nerka	Combined
Drainage area (km2)	40.3 (±16.1)	33.5 (±10.5)	36.2 (±8.8)
Bankfull width (m)	11.2 (±2.8)	16.4 (±2.7)	12.5 (±1.9)
Bankfull depth (m)	0.8 (±0.1)	0.9 (±0.1)	0.8 (±0.1)
Bankfull width to depth ratio (m/m)	13.7 (±1.9)	17.8 (±1.8)	14.3 (±1.3)
Gradient (%)	0.7 (±0.1)	0.8 (±0.2)	0.8 (±0.1)
Wetted width (m)	5.2 (±1.1)	7.0 (±1.0)	5.6 (±0.7)
Wetted depth (m)	0.4 (±0.1)	0.4 (±16.1)	0.4 (±16.1)
Wetted width to depth ratio (m/m)	15.5 (±2.6)	20.9 (±2.9)	17.3 (±2.0)
% pool	40.5 (±4.3)	36.7 (±3.8)	34.2 (±3.0)
% riffle	33.7 (±5.7)	25.9 (±4.8)	32.9 (±3.6)
% rapid	3.9 (±3.0)	4.5 (±3.0)	5.9 (±2.2)
% glide	21.7 (±4.1)	32.9 (±3.7)	27.0 (±2.9)
Channel widths (cw)/pool	4.8 (±0.8)	5.8 (±1.0)	6.4 (±0.6)
Ave residual pool depth (m)	0.4 (±0.1)	0.5 (±0.1)	0.4 (±0.05)
Ave riffle depth (m)	0.2 (±0.04)	0.2 (±0.03)	0.2 (±0.02)
Ave glide depth (m)	0.3 (±0.06)	0.4 (±0.05)	0.3 (±0.04)
Average cover width (m)	0.4 (±0.05)	0.2 (±0.03)	0.3 (±0.03)
% width covered by bank	0.1 (±0.03)	0.05 (±0.01)	0.1 (±0.01)
# key logs or logjams	2.4 (±0.9)	2.0 (±0.5)	2.1 (±0.5)
# key logs or logjams/cw	0.2 (±0.1)	0.2 (±0.1)	0.2 (±0.1)
D15	10.2 (±0.8)	13.7 (±3.6)	14.1 (±2.3)
D50	19.7 (±1.6)	29.4 (±5.5)	28.0 (±3.6)
D84	34.8 (±3.2)	54.4 (±10.7)	52.0 (±7.0)

Table 4. Correlation coefficient among habitat variables in the Wood River system, Alaska.. Bold numbers are correlations of greater than 0.50.

	DA	BW	BD	BWDR	G	WW	WD	WWWR	%P	%RI	%RA	%G	CWP	ARPD	ARD	AGD	DCT	SCT	ACW	%WCB	#KP	#KP/CW	D15	D50	D84	CT
Drainage area (km2)	1.00																									
Bankfull width (m)	0.87	1.00																								
Bankfull depth (m)	0.77	0.83	1.00																							
Bankfull width to depth ratio	0.67	0.84	0.45	1.00																						
Gradient (%)	-0.43	-0.36	-0.35	-0.18	1.00																					
Wetted width (m)	0.78	0.92	0.87	0.70	-0.31	1.00																				
Wetted depth (m)	0.86	0.68	0.65	0.58	-0.30	0.61	1.00																			
wetted width to depth ratio	0.11	0.38	0.32	0.28	0.04	0.56	-0.23	1.00																		
% pool	0.17	0.00	-0.15	0.12	-0.02	0.00	0.26	-0.15	1.00																	
% riffle	-0.10	-0.06	-0.11	-0.03	0.01	-0.17	-0.33	0.16	-0.39	1.00																
% rapid	-0.27	-0.25	-0.12	-0.28	0.40	-0.24	-0.16	-0.19	-0.51	-0.23	1.00															
% glide	0.16	0.26	0.39	0.13	-0.29	0.39	0.27	0.10	-0.17	-0.69	0.07	1.00														
channel widths/pool	-0.36	-0.39	-0.20	-0.45	0.29	-0.31	-0.43	0.14	-0.60	0.27	0.31	0.06	1.00													
Ave residual pool depth (m)	0.78	0.64	0.48	0.67	-0.30	0.52	0.92	-0.23	0.23	-0.23	-0.21	0.22	-0.43	1.00												
Ave riffle depth (m)	0.76	0.67	0.64	0.59	-0.28	0.70	0.82	0.03	0.11	-0.21	-0.13	0.26	-0.34	0.72	1.00											
Ave glide depth (m)	0.85	0.73	0.74	0.57	-0.33	0.70	0.88	-0.03	0.08	-0.23	-0.07	0.26	-0.37	0.75	0.88	1.00										
Dominant cover type	0.37	0.40	0.49	0.18	-0.02	0.49	0.31	0.25	-0.30	-0.14	0.13	0.40	0.25	0.23	0.26	0.38	1.00									
Subdominant cover type	0.04	0.11	0.02	0.12	-0.04	-0.05	0.01	-0.10	0.11	0.12	-0.18	-0.13	-0.23	-0.06	-0.11	0.03	-0.11	1.00								
Ave cover width (m)	-0.17	-0.23	-0.32	-0.01	0.04	-0.30	-0.01	-0.34	0.06	0.14	0.06	-0.29	-0.32	0.07	0.03	-0.07	-0.49	0.07	1.00							
% width covered by bank	-0.52	-0.59	-0.58	-0.53	0.13	-0.66	-0.46	-0.38	0.14	0.21	0.08	-0.48	-0.10	-0.51	-0.51	-0.56	-0.50	0.21	0.52	1.00						
# key logs or logjams	0.53	0.36	0.20	0.47	-0.07	0.18	0.58	-0.33	0.12	0.13	-0.09	-0.22	-0.44	0.62	0.44	0.49	0.04	0.16	0.23	-0.08	1.00					
# key logs or logjams/cw	-0.05	-0.17	-0.20	-0.08	0.10	-0.29	0.04	-0.44	0.06	0.27	0.04	-0.42	-0.30	0.06	-0.08	-0.04	-0.15	0.18	0.24	0.44	0.73	1.00				
D15	0.15	0.26	0.34	0.14	0.28	0.32	0.10	0.21	-0.37	0.12	0.29	0.02	0.19	0.04	0.18	0.19	0.49	0.02	-0.30	-0.35	0.02	-0.11	1.00			
D50	0.16	0.32	0.40	0.18	0.31	0.35	0.11	0.23	-0.45	0.08	0.36	0.11	0.23	0.06	0.15	0.21	0.55	0.10	-0.36	-0.42	0.04	-0.10	0.94	1.00		
D84	0.10	0.29	0.41	0.13	0.31	0.34	0.05	0.27	-0.49	0.05	0.37	0.18	0.28	-0.02	0.12	0.16	0.55	0.12	-0.40	-0.42	-0.03	-0.14	0.89	0.98	1.00	
Channel type	-0.31	-0.27	-0.31	-0.13	0.68	-0.27	-0.38	0.18	-0.18	0.22	0.20	-0.24	0.55	-0.32	-0.35	-0.35	0.02	-0.11	-0.25	-0.07	-0.02	0.12	-0.02	0.13	0.17	1.00

Table 5. PCA results including eigenvectors for habitat variables in the Wood River system, Alaska

PCA element	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
Eigenvalue	4.67	3.84	1.41	1.14	0.91	0.79	0.41	0.29
Cumulative % variance	0.33	0.61	0.70	0.79	0.86	0.91	0.96	0.97
Eigenvectors								
Drainage area (km2)	0.41	-0.09	0.02	0.21	-0.09	0.08	-0.01	0.17
Bankfull width (m)	0.42	-0.05	0.00	0.13	-0.09	-0.02	0.45	0.19
Bankfull depth (m)	0.41	0.04	-0.15	0.03	-0.09	0.08	0.37	-0.35
Gradient (%)	-0.18	0.27	0.46	0.27	0.12	-0.38	0.13	-0.11
% pool area	-0.01	-0.31	0.22	0.39	0.60	0.02	-0.11	-0.06
channel widths per pool	-0.16	0.34	-0.35	0.16	-0.35	-0.13	-0.37	0.00
ave residual pool depth (m)	0.32	-0.18	0.23	0.18	-0.25	-0.16	-0.40	0.53
riffle depth (m)	0.36	-0.12	0.09	0.06	-0.16	-0.34	-0.36	-0.67
ave cover width (m)	-0.12	-0.26	0.28	-0.47	-0.22	-0.56	0.24	0.09
# key logs or logjams per channel width	-0.09	-0.09	0.58	-0.16	-0.36	0.62	-0.10	-0.19
D15	0.21	0.38	0.18	-0.24	0.26	-0.01	-0.22	0.03
D50	0.22	0.42	0.18	-0.15	0.13	0.01	-0.03	0.13
D84	0.20	0.43	0.12	-0.13	0.12	0.02	0.06	0.01
channel type	-0.20	0.26	0.19	0.56	-0.33	-0.03	0.27	-0.01

Table 6. Maximum-likelihood estimates of intercept and slope parameters for the “best approximating” models predicting pink, chum, and Chinook salmon occurrence or abundance. a. Pink, chum, and Chinook salmon occurrence with drainage area. b. Pink, chum, and Chinook salmon occurrence without drainage area. c. Pink, chum, and Chinook salmon abundance. Only models with greater than 1/10 of that for the highest ranking model are presented. Standard errors are in parentheses

Table 6.

a.

Species	Model	Intercept	Drainage area	Glide depth	Wetted depth	Cover width	D50	Sockeye density
Pink	Drainage area	0.059 (0.041)	0.006 (0.001)	--	--	--	--	--
	Drainage area, cover width	0.142 (0.102)	0.006 (0.001)	--	--	-0.240 (0.269)	--	--
	Drainage area, sockeye density	0.101 (0.068)	0.005 (0.001)	--	--	--	--	-0.101 (0.131)
	Drainage area, glide depth	0.013 (0.077)	0.005 (0.001)	0.238 (0.338)	--	--	--	--
Chum	Drainage area, glide depth	0.093 (0.066)	0.003 (0.001)	0.908 (0.289)	--	--	--	--
	Wetted depth, glide depth	0.190 (0.061)	--	0.939 (0.323)	0.480 (0.275)	--	--	--
	Drainage area, glide depth, D50	0.065 (0.068)	0.002 (0.001)	0.980 (0.287)	--	--	-0.002 (0.001)	--
	Glide depth	0.164 (0.063)	--	1.415 (0.185)	--	--	--	--
Chinook	Drainage area, glide depth	-0.026 (0.03)	0.007 (0.001)	-0.27 (0.13)	--	--	--	--
	Drainage are, glide depth, sockeye density	-0.055 (0.033)	0.007 (0.001)	-0.283 (0.123)	--	--	--	0.077 (0.048)
	Drainage area	-0.078 (0.018)	0.006 (0.001)	--	--	--	--	--
	Drainage area, sockeye density	-0.107 (0.028)	0.006 (0.001)	--	--	--	--	0.070 (0.058)

Table 6.

b.

Species	Model	Intercept	Wetted width	Glide depth	Wetted depth	Cover width	D50
Pink	Wetted width	-0.186 (0.083)	0.089 (0.016)	--	--	--	--
	Wetted width, D50	-0.15 (0.084)	0.095 (0.016)	--	--	--	-0.003 (0.002)
	Wetted width, glide depth	-0.191 (0.084)	0.095 (0.016)	0.334 (0.448)	--	--	--
	Wetted width, cover width	-0.135 (0.140)	0.089 (0.016)	--	--	-0.147 (0.320)	--
Chum	Wetted depth, glide depth	-0.19 (0.061)	--	0.939 (0.323)	0.48 (0.275)	--	--
	Glide depth	-0.164 (0.063)	--	1.415 (0.185)	--	--	--
	Glide depth, D50	-0.125 (0.182)	--	1.458 (0.182)	--	--	-0.002 (0.002)
Chinook	Wetted depth	-0.229 (0.078)	--	--	0.937 (0.194)	--	--
	Wetted depth, glide depth	-0.246 (0.081)	--	0.369 (0.429)	0.673 (0.364)	--	--

Table 6

c.

Species	Model	Intercept	Drainage area	Glide depth	Cover width	D50	Wetted width	Bankfull width
Pink	Drainage area, D50	-43.524 (10.016)	1.77 (0.146)	--	--	1.707 (0.296)	--	--
	Drainage area, cover width, D50	-15.122 (27.715)	1.789 (0.142)	--	-72.318 (49.532)	1.561 (0.301)	--	--
	Drainage area, glide depth, D50	-31.217 (14.315)	2.015 (0.252)	-72.233 (60.836)	--	1.775 (0.297)	--	--
Chum	Drainage area	-1.273 (1.071)	0.197 (0.021)	--	--	--	--	--
	Drainage area, D50	-0.131 (1.418)	0.199 (0.021)	--	--	-0.05 (0.042)	--	--
	Drainage area, cover width	0.181 (2.709)	0.198 (0.022)	--	-4.190 (7.138)	--	--	--
	Drainage area, glide depth	-2.13 (2.034)	0.182 (0.037)	4.471 (8.931)	--	--	--	--
Chinook	Wetted width, cover width	-8.468 (3.416)	--	--	16.584 (7.801)	--	0.861 (0.39)	--
	Bankfull width, cover width	-6.934 (3.239)	--	--	15.138 (8.071)	--	--	0.282 (0.144)

Table 7. Model selection results for factors that sockeye salmon density in the Wood River system 1968 to 2007. Models are ranked from most plausible (ΔAIC*c*=0) to least plausible; p is the number of parameters. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i).

Model	Log likelihood	p	ΔAIC*c*	Akaike weight (w_i)	R^2	w_I / w_i
Bankfull depth, Glide depth	4.805	3	0.000	0.395	0.579	1.000
Bankfull depth	3.015	2	0.404	0.323	0.480	1.224
Bankfull depth, Glide depth, Cover width	5.067	4	3.181	0.081	0.591	4.905
Bankfull depth, Cover width	3.077	3	3.457	0.070	0.484	5.631
Bankfull depth, D50	3.018	3	3.573	0.066	0.480	5.970
Bankfull depth, Glide depth, D50	4.857	4	3.601	0.065	0.581	6.052
Null	-2.541	1	8.764	0.004	0.000	79.997

Figure Captions

Figure 1. Map of Wood River lakes, Southwest Alaska

Figure 2. Pink, chum, and Chinook occurrence by stream. a. Streams draining into Lake Aleknagik. b. Streams draining into Lake Nerka. Clear bars indicate pink salmon, black bars indicate chum salmon, and grey bars indicate Chinook salmon occurrence. Straight lines with hash marks at top are standard error bars.

Figure 3. Occurrence of pink, chum, and Chinook salmon in all streams surveyed in the Wood River system - 1968 through 2007. Clear bars indicate pink salmon, black bars indicate chum salmon, and grey bars indicate Chinook salmon occurrence. Straight lines with hash marks at top are standard error bars.

Figure 4. a. Pink, chum, and Chinook abundance by stream. a. Streams draining into Lake Aleknagik. b. Streams draining into Lake Nerka. Clear bars indicate pink salmon, black bars indicate chum salmon, and grey bars indicate Chinook salmon abundance. Straight lines with hash marks at top are standard error bars.

Figure 5. Principal components analysis (PCA) of stream habitat variables in the Wood River system, Alaska. The first axis described an increasing gradient between streams with small drainage areas (and, consequently, shallow, narrow, and steeper channels) to streams with larger drainage areas (i.e., deeper, wider, and lower slope). The second axis described a gradient between sites with small streambed particles, a larger proportion of

the area in pools, and more in-stream channel cover to streams with larger streambed particles, less pool area and less stream cover. These two axes explained 61% of the variance.

Figure 6. Gower's Similarity index for Lake Aleknagik and Nerka streams

Figure 7. Average sockeye density from 1968 to 2007 vs. stream bankfull depth in the Wood River system. Average sockeye density = 0.10*(bankfull depth)$^{-2.35}$. $R^2 = 0.53$. p = 0.006. Each point denotes a stream in the Wood River system.

Figure 8. Pink and chum salmon occurrence from 1968 to 2007 vs. glide depth in the Wood River system. Solid black rectangles indicate chum salmon occurrence, while clear diamonds indicate pink salmon occurrence.

Figure 9. Stream specific average pink and chum salmon occurrence vs. stream specific average spawning sockeye density (adult sockeye per meter2) between 1968 and 2007. Clear diamonds indicate average pink salmon occurrence while black, solid rectangles indicate average chum salmon occurrence.

Figure 10. Pink, chum, or Chinook salmon occurrence between 1968 and 2007 vs. average spawning sockeye density (fish per meter^2) between 1968 and 2007. Solid, black diamonds indicate average pink salmon occurrence for drainage areas less than 8km^2, while clear rectangles indicate average pink salmon occurrence for drainage areas greater

than 8km^2 and less than 50km^2. Grayed triangles denote drainage areas greater than 50km^2.

Figure 11. Drainage area (km^2) vs. habitat area surveyed (m^2) in spawner survey index reaches of the Wood river system. Habitat area = 828.38(drainage area) – 1269. $R^2 = 0.83$. $p < 0.0001$.

Figure 12. Distribution of adult sockeye and pink salmon in Ice Creek, Wood river system 2005.

Figure 13. Percent of stream surveys and pink, chum, and Chinook salmon observed in Lake Aleknagik and Nerka streams by month. Striped bars indicate stream surveys, clear bars indicate pink salmon, black bars indicate chum salmon, and grey bars indicate Chinook salmon.

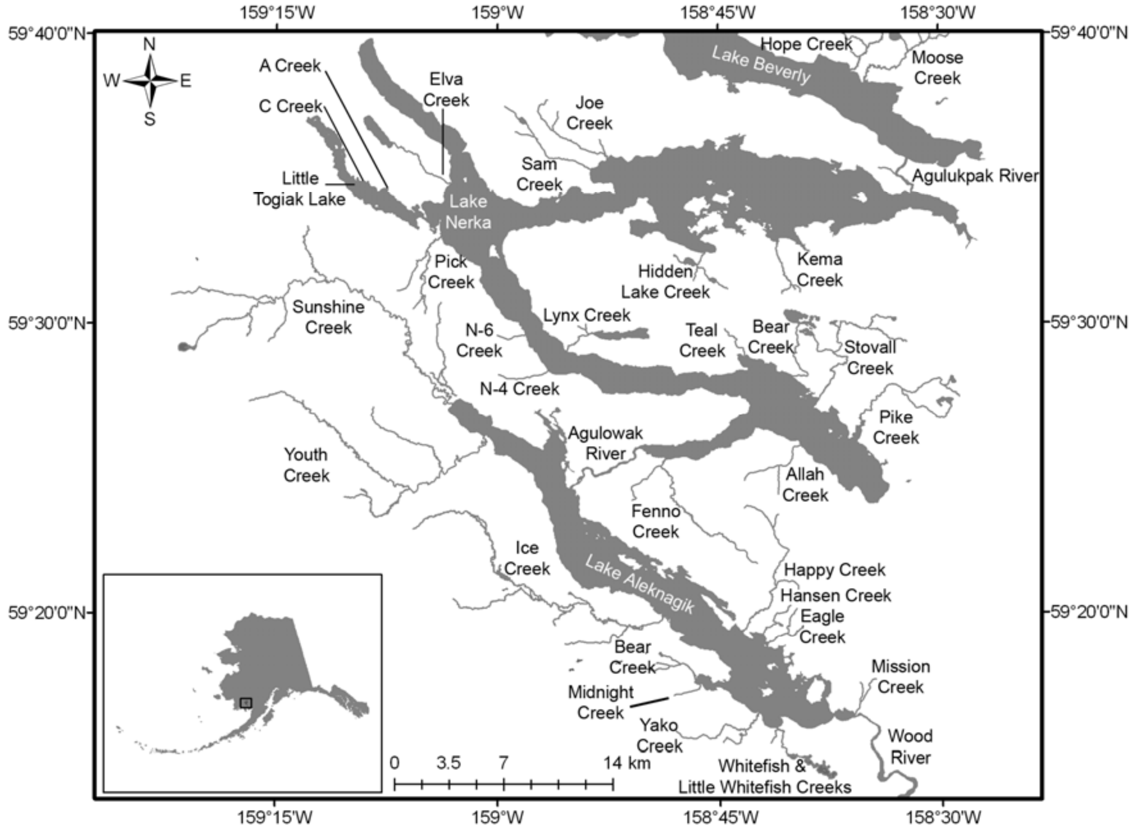
Figure 14. The most plausible candidate models (Table 6a) for predicting the occurrence of pink, chum, and Chinook salmon from stream habitat attributes, including drainage area. The solid black line denotes estimated pink salmon occurrence. The large dark hashed line denotes estimated chum salmon occurrence, and the small hashed line denotes estimated Chinook salmon occurrence.

Figure 15. The most plausible candidate models (Table 6b) for predicting the occurrence of pink, chum, and Chinook salmon from stream habitat attributes, excluding drainage

area. The solid black line denotes estimated pink salmon occurrence. The large dark hashed line denotes estimated chum salmon occurrence, and the small hashed line denotes estimated Chinook salmon occurrence.

Figure 16. The most plausible candidate model for predicting the abundance of pink salmon from stream habitat attributes. The solid white area denotes estimated pink salmon abundance between 0 and 100 individuals. The solid black area denotes estimated pink salmon abundance between 100 and 200 individuals. The solid grey area denotes estimated pink salmon abundance between 200 and 300 individuals. The clear, speckled area denotes estimated pink salmon abundance between 300 and 400 individuals, and the clear vertically hashed area denotes estimated pink salmon abundance between 400 and 500 individuals.

Figure 1.


159°15'W
159°W
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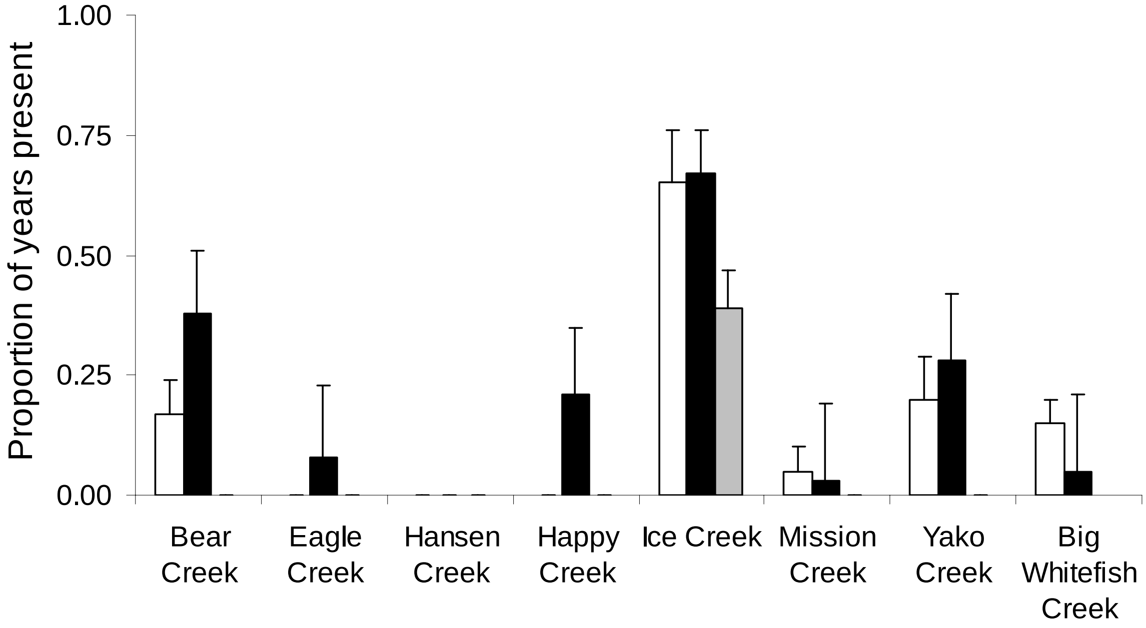
N
W
E
S
A Creek
C Creek
Little Togiak Lake
Elva Creek
Joe Creek
Sam Creek
Lake Nerka
Hope Creek
Lake Beverly
Moose Creek
Agulukpak River
Pick Creek
Hidden Lake Creek
Kema Creek
Sunshine Creek
Lynx Creek
N-6 Creek
Teal Creek
Bear Creek
Stovall Creek
N-4 Creek
Pike Creek
Agulowak River
Youth Creek
Allah Creek
Fenno Creek
Ice Creek
Lake Aleknagik
Happy Creek
Hansen Creek
Eagle Creek
Bear Creek
Mission Creek
Midnight Creek
Yako Creek
Wood River
Whitefish & Little Whitefish Creeks
0
3.5
7
14 km

Figure 2.

a.



Proportion of years present
1.00
0.75
0.50
0.25
0.00
Bear Creek
Eagle Creek
Hansen Creek
Happy Creek
Ice Creek
Mission Creek
Yako Creek
Big Whitefish Creek

Figure 2.

b.

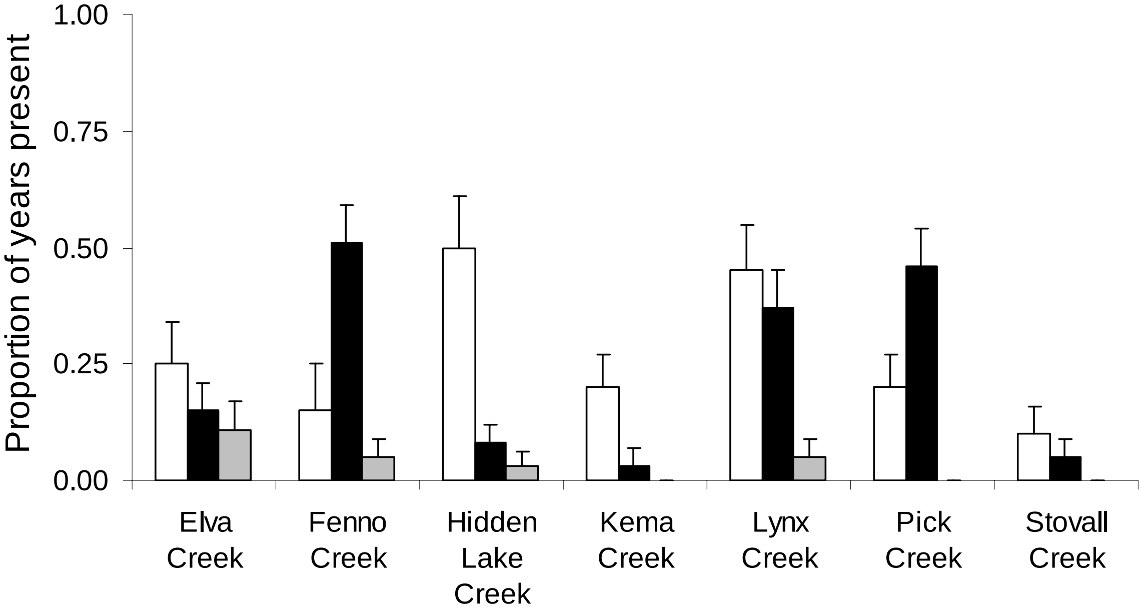

Proportion of years present
1.00
0.75
0.50
0.25
0.00
Elva Creek
Fenno Creek
Hidden Lake Creek
Kema Creek
Lynx Creek
Pick Creek
Stovall Creek

Figure 3.

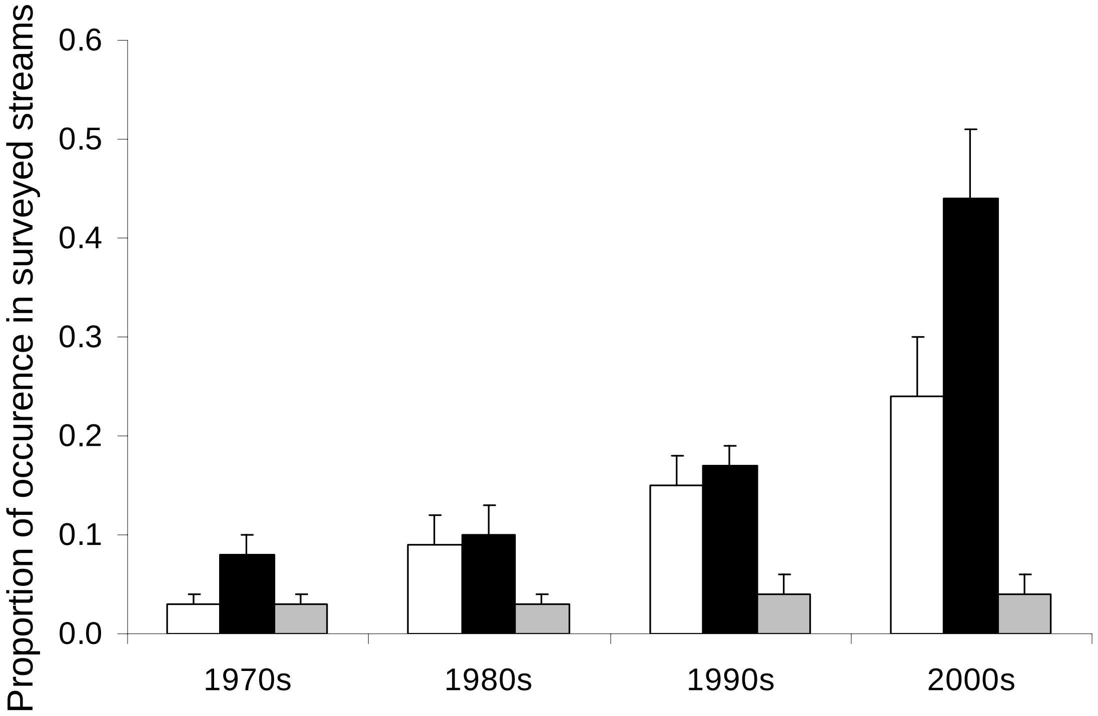

Proportion of occurence in surveyed streams
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1970s
1980s
1990s
2000s

Figure 4.

a.

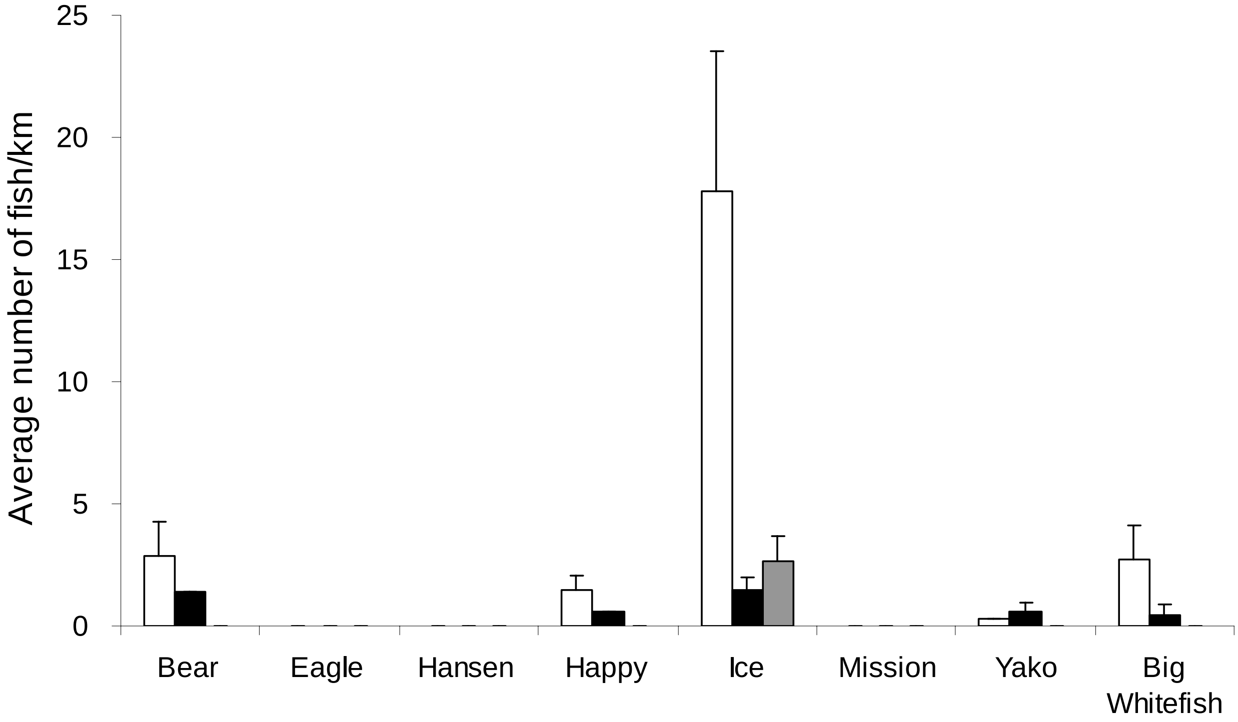

25
20
15
10
5
0
Average number of fish/km
Bear
Eagle
Hansen
Happy
Ice
Mission
Yako
Big Whitefish

Figure 4.

b.

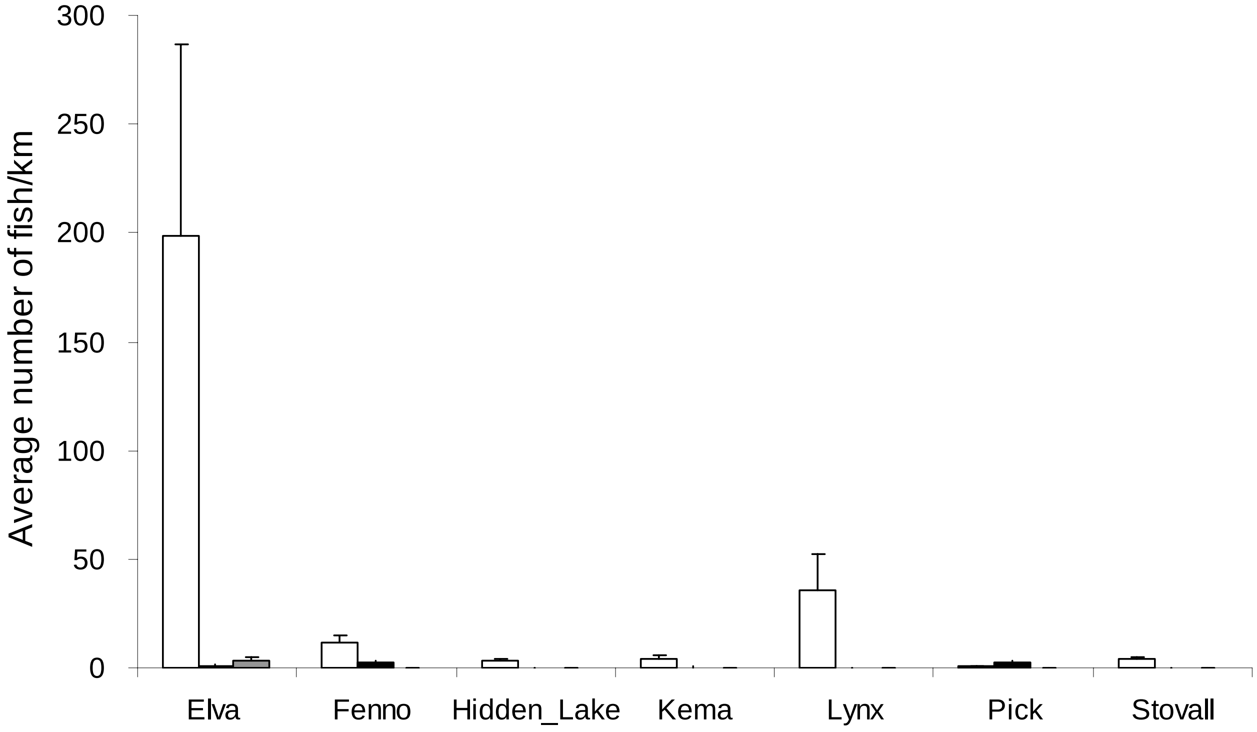

300
250
200
150
100
50
0
Average number of fish/km
Elva
Fenno
Hidden_Lake
Kema
Lynx
Pick
Stovall

Figure 5.

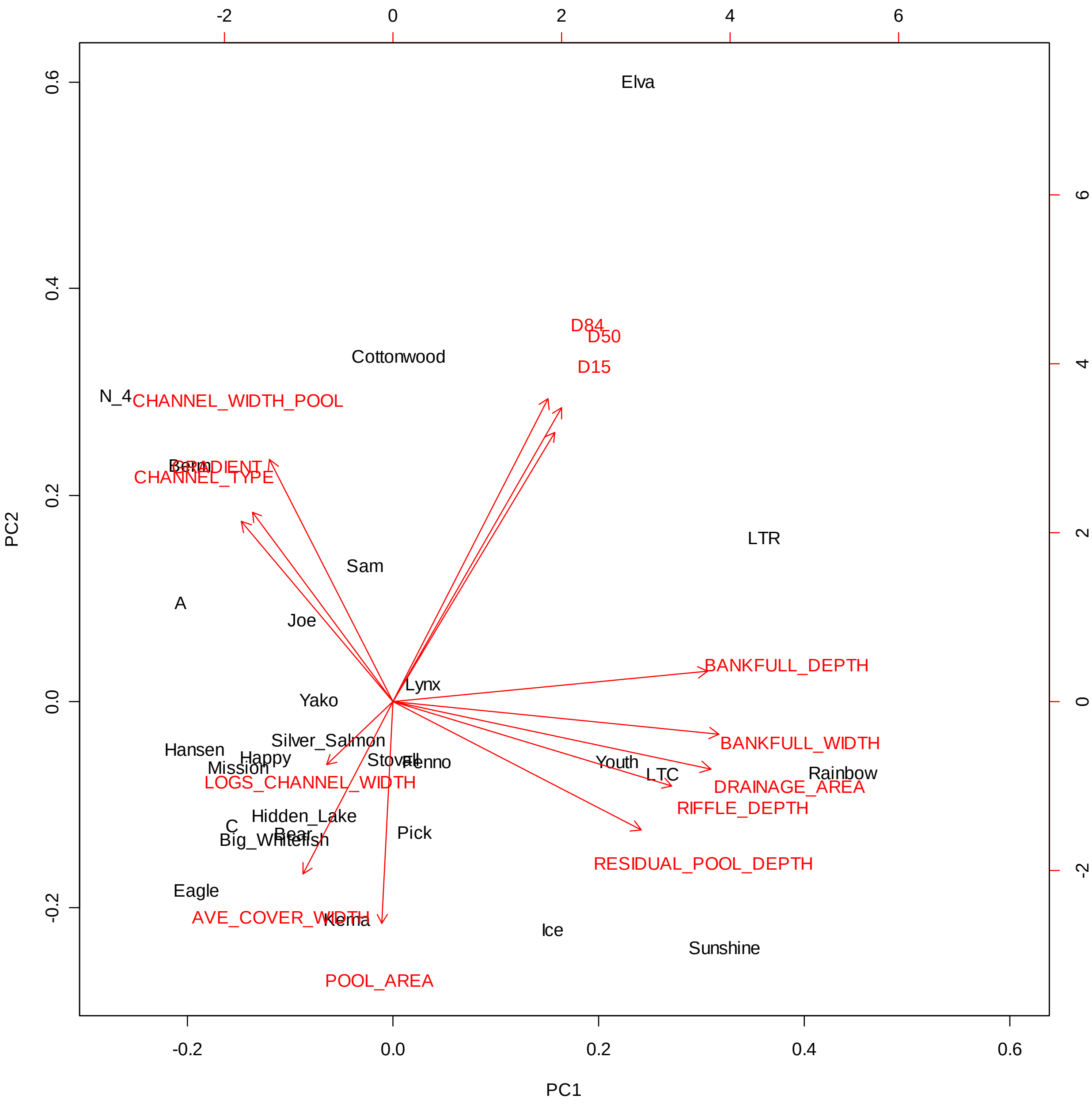

-2
0
2
4
6
0.6
0.4
0.2
0.0
-0.2
PC2
6
4
2
0
-2
Elva
D84
D50
D15
Cottonwood
N_4
CHANNEL_WIDTH_POOL
Bern
GRADIENT
CHANNEL_TYPE
LTR
Sam
A
Joe
BANKFULL_DEPTH
Lynx
Yako
Silver_Salmon
Hansen
Happy
Stovall
Fenno
BANKFULL_WIDTH
Youth
LTC
Rainbow
Mission
LOGS_CHANNEL_WIDTH
DRAINAGE_AREA
RIFFLE_DEPTH
Hidden_Lake
C
Bear
Big_Whitefish
Pick
RESIDUAL_POOL_DEPTH
Eagle
AVE_COVER_WIDTH
Kerna
Ice
Sunshine
POOL_AREA
-0.2
0.0
0.2
0.4
0.6
PC1

Figure 6.

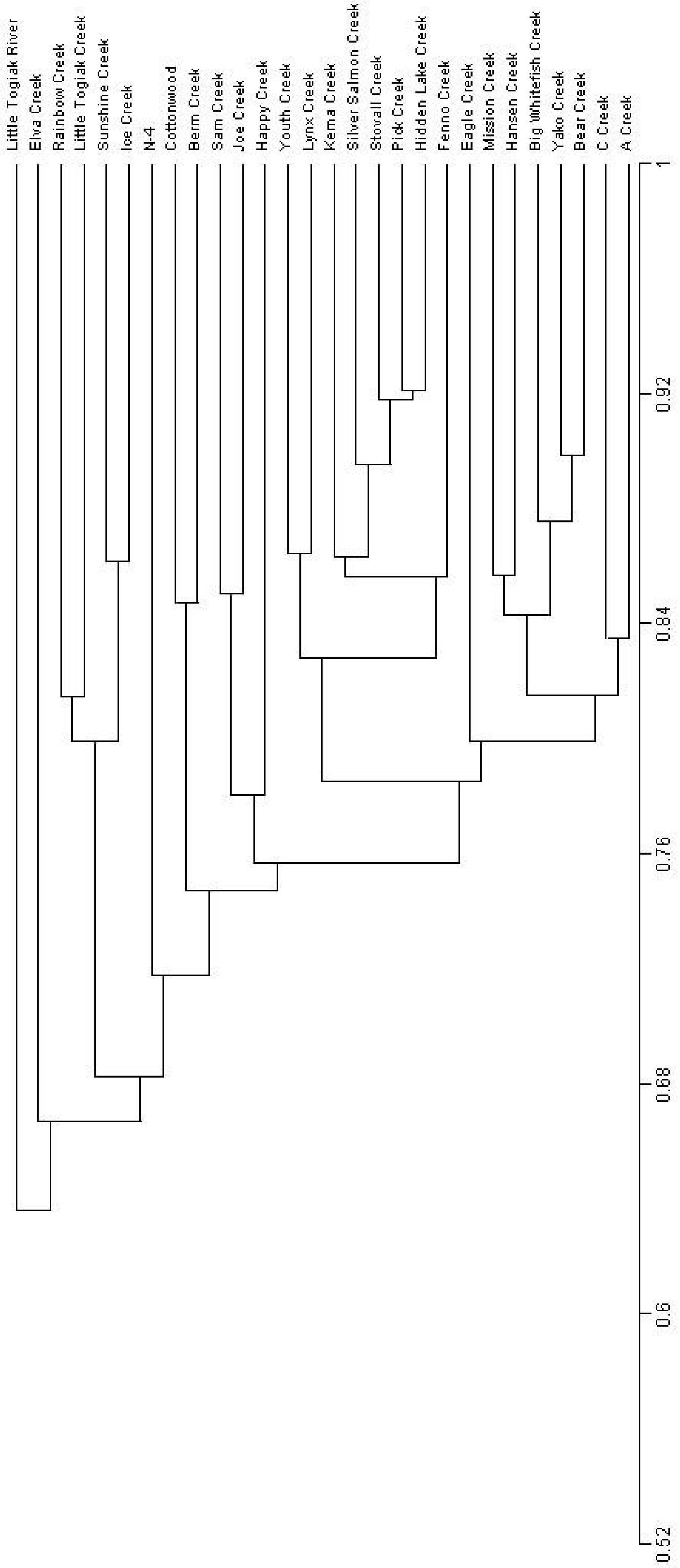

Little Togiak River
Elva Creek
Rainbow Creek
Little Togiak Creek
Sunshine Creek
Ice Creek
N-4
Cottonwood
Berm Creek
Sam Creek
Joe Creek
Happy Creek
Youth Creek
Lynx Creek
Kema Creek
Silver Salmon Creek
Stovall Creek
Pick Creek
Hidden Lake Creek
Fenno Creek
Eagle Creek
Mission Creek
Hansen Creek
Big Whitefish Creek
Yako Creek
Bear Creek
C Creek
A Creek
1
0.92
0.84
0.76
0.68
0.6
0.52

Figure 7.

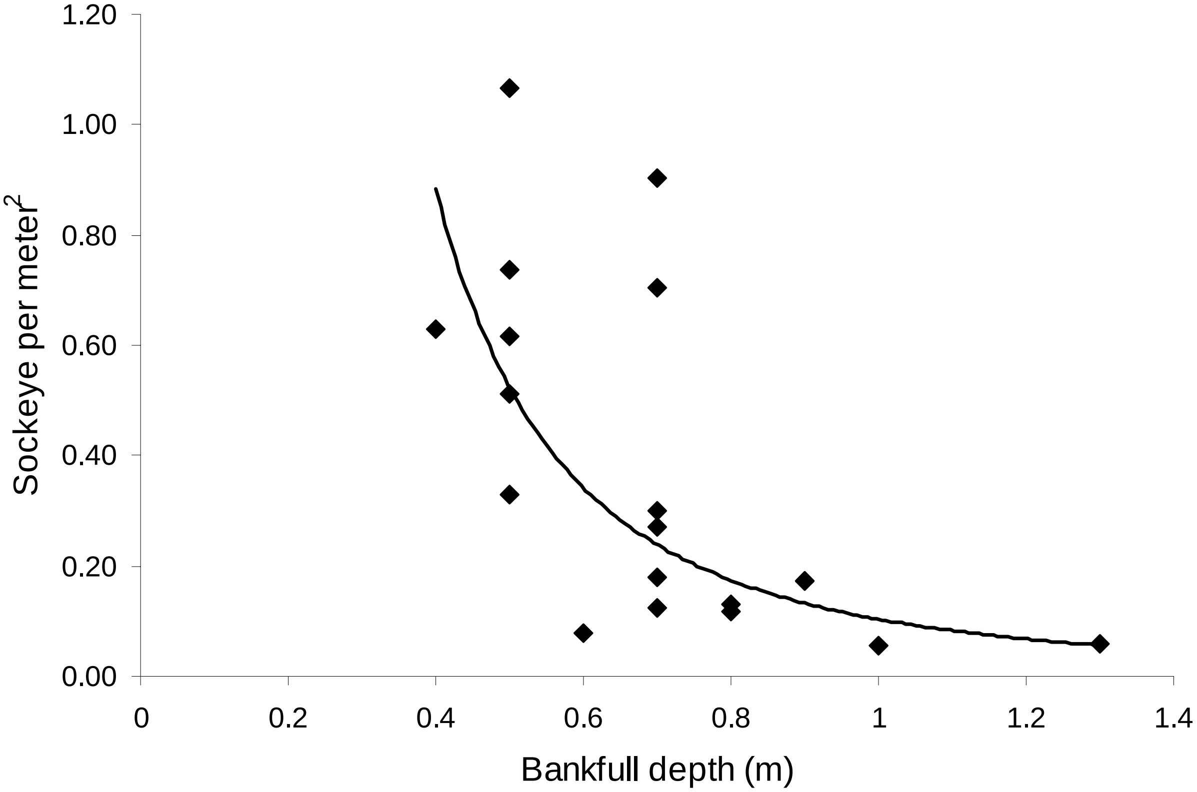

1.20
1.00
0.80
0.60
0.40
0.20
0.00
Sockeye per meter^2
0
0.2
0.4
0.6
0.8
1
1.2
1.4
Bankfull depth (m)

Figure 8.

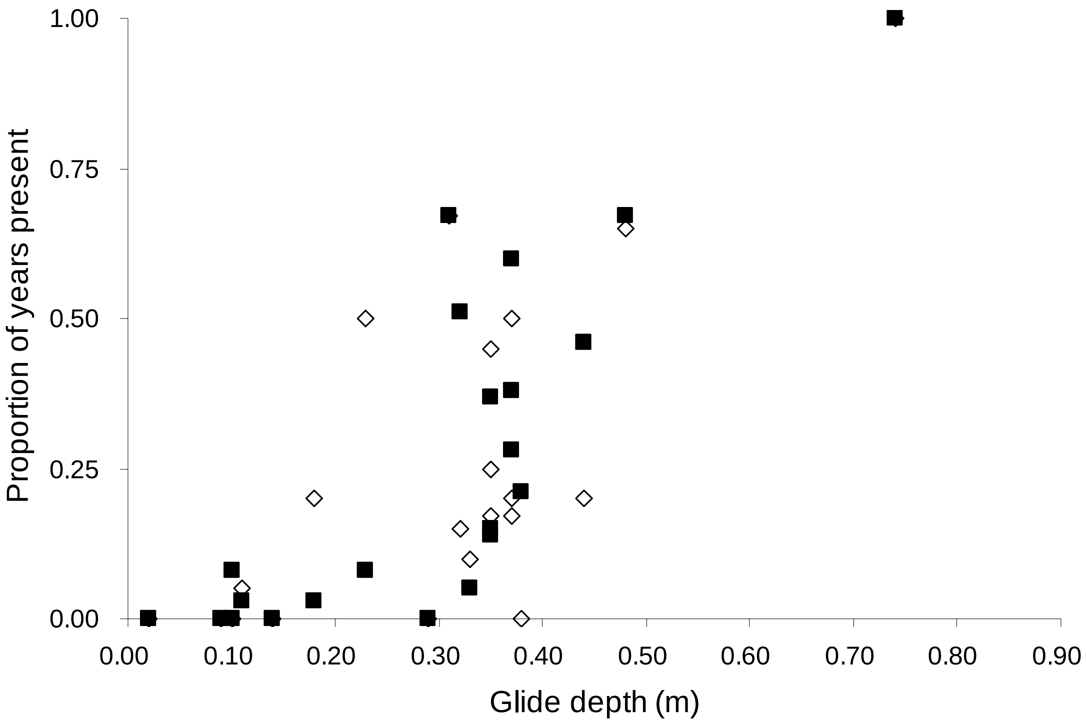

1.00
0.75
0.50
0.25
0.00
Proportion of years present
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
Glide depth (m)

Figure 9.

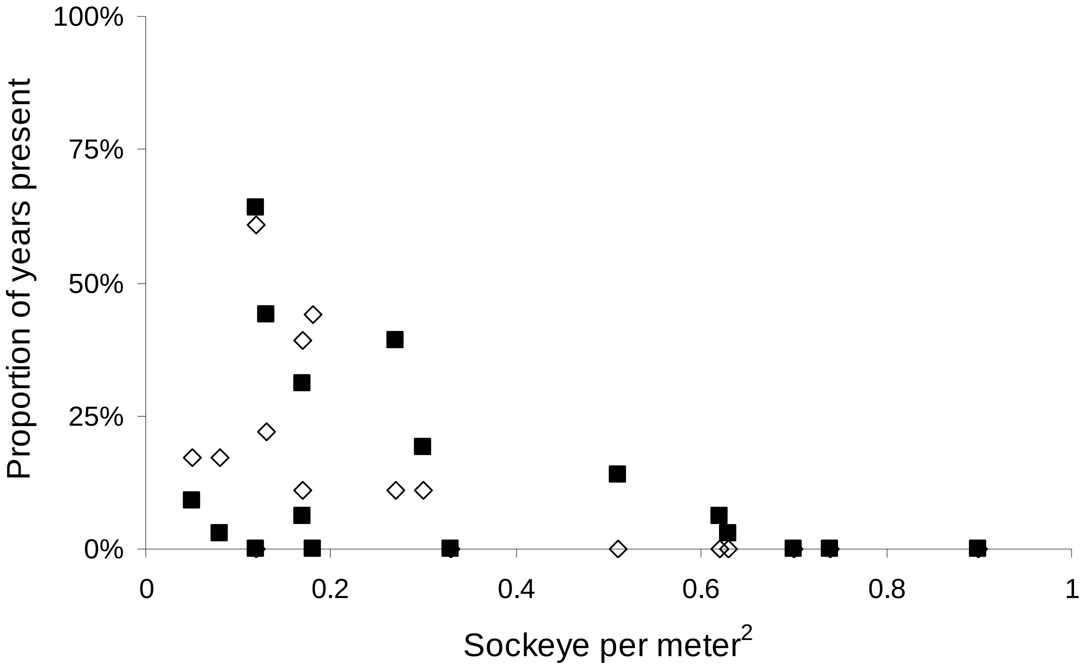

100%
75%
50%
25%
0%
Proportion of years present
0
0.2
0.4
0.6
0.8
1
Sockeye per meter^2

Figure 10.

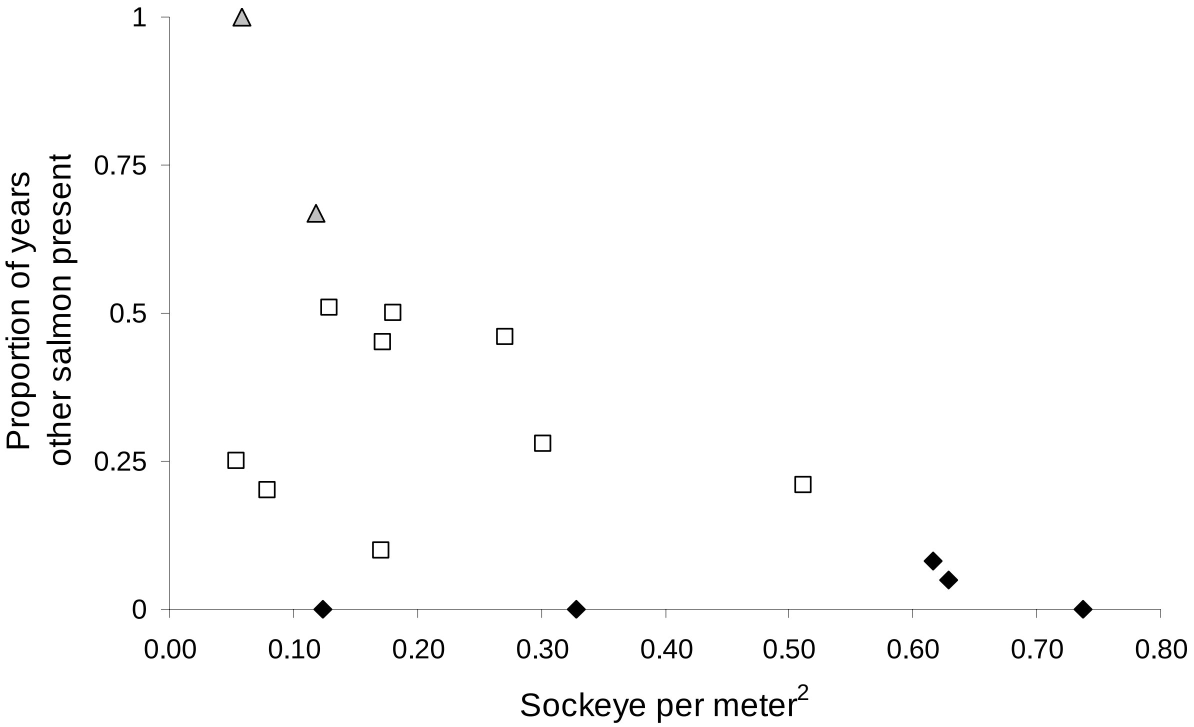

Proportion of years
other salmon present
1
0.75
0.5
0.25
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
Sockeye per meter²

Figure 11.

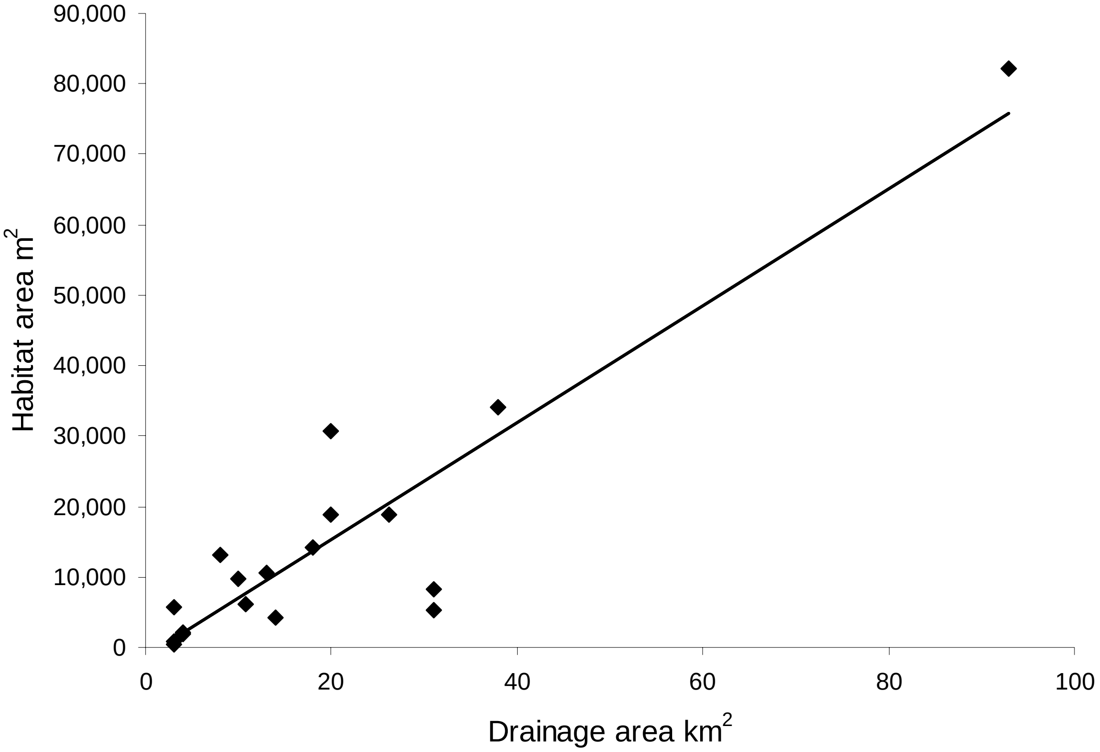

90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
Habitat area m^2
0
20
40
60
80
100
Drainage area km^2

Figure 12.

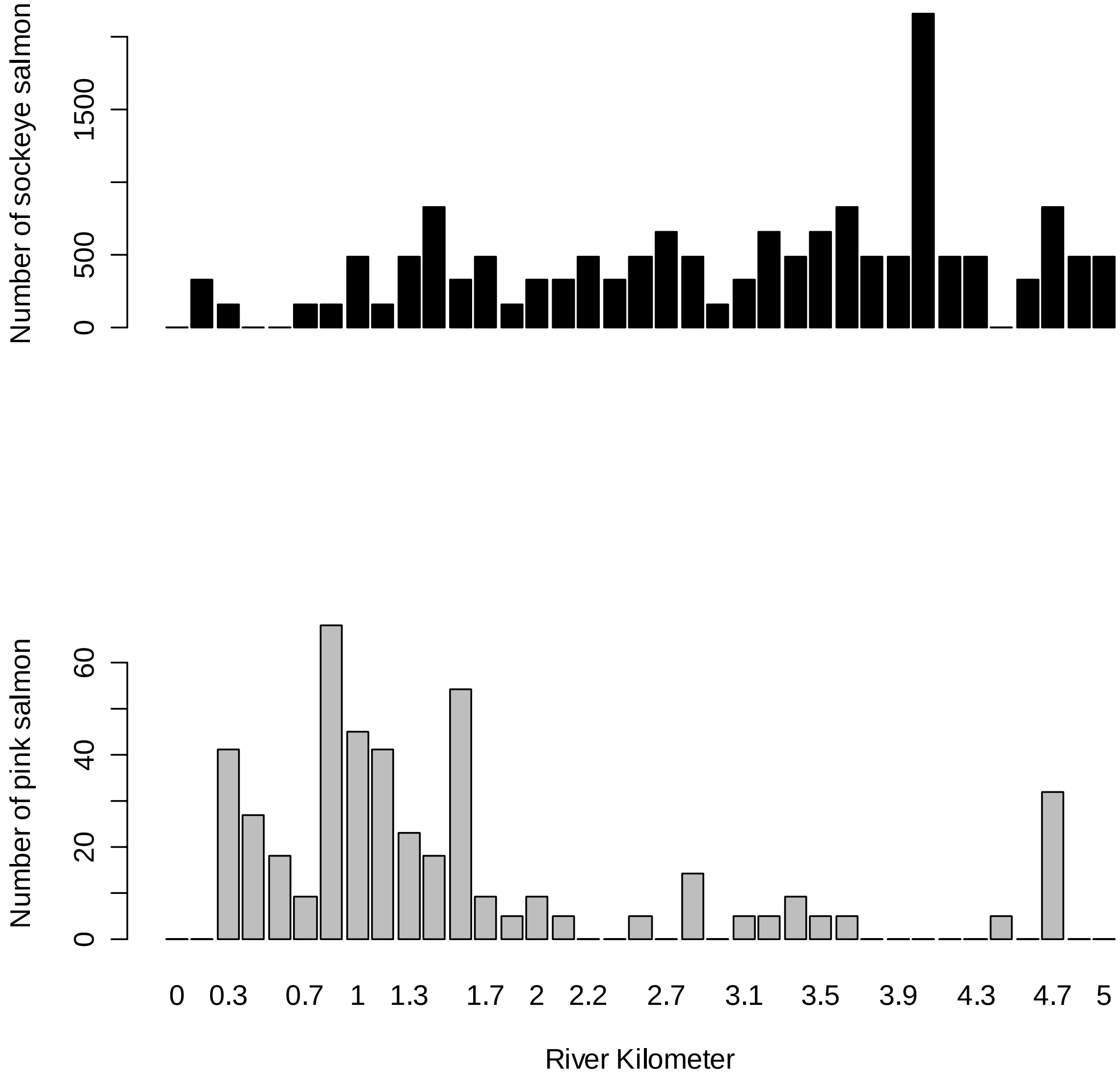

Number of sockeye salmon
0
500
1500
Number of pink salmon
0
20
40
60
0
0.3
0.7
1
1.3
1.7
2
2.2
2.7
3.1
3.5
3.9
4.3
4.7
5
River Kilometer

Figure 13.

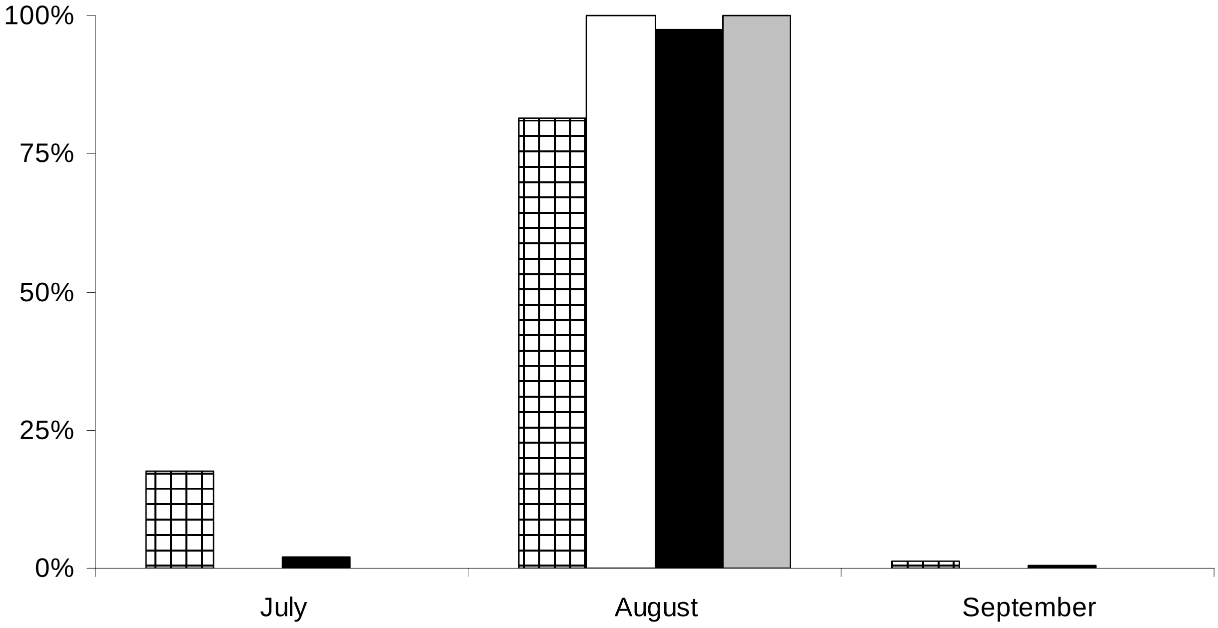


Figure 14.

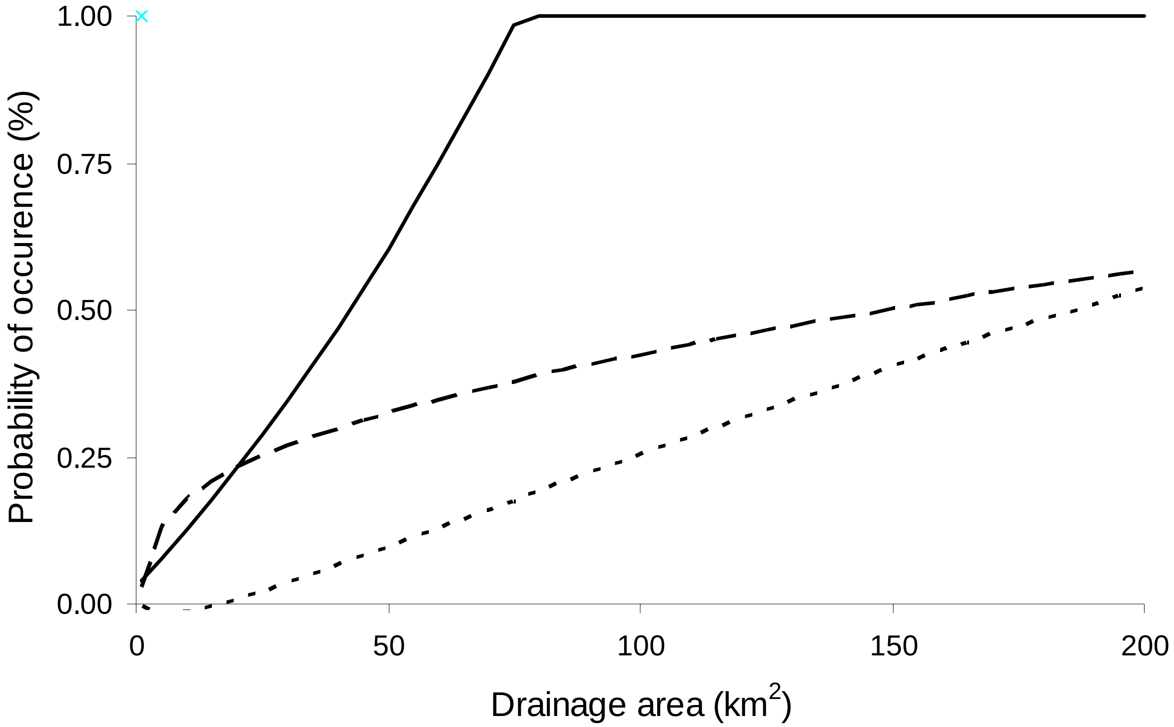

1.00
0.75
0.50
0.25
0.00
Probability of occurence (%)
0
50
100
150
200
Drainage area (km^2)

Figure 15.

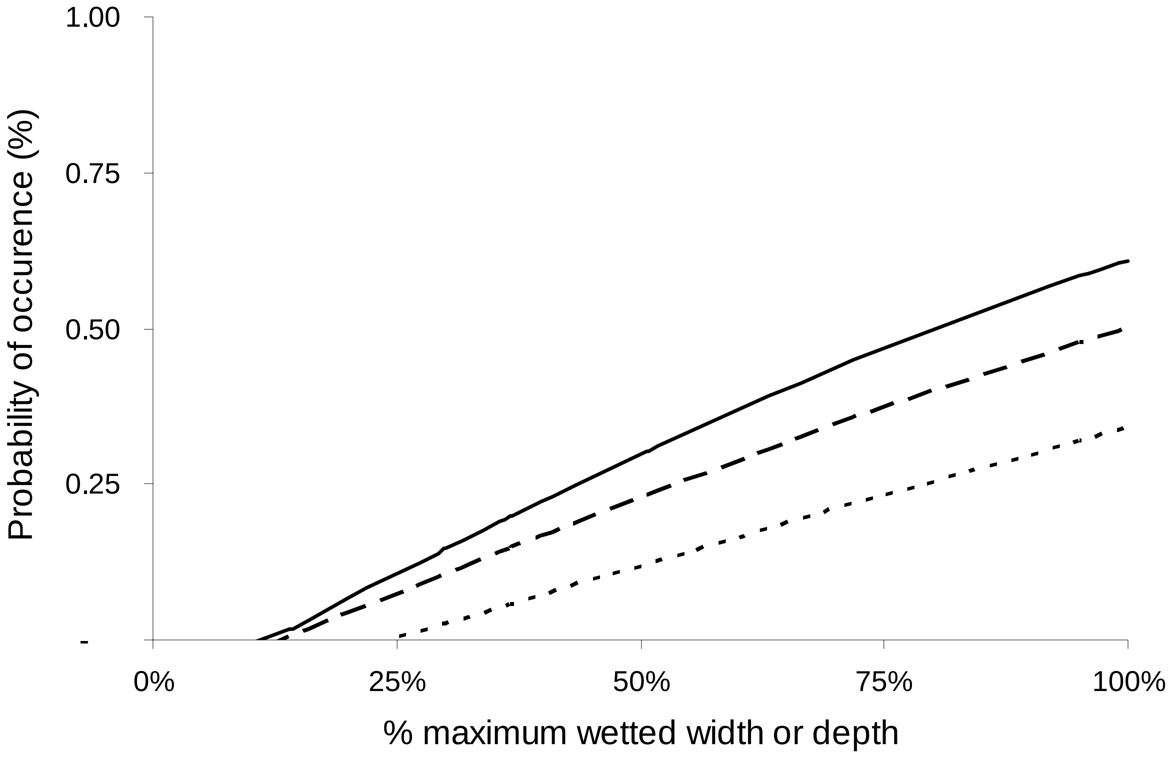
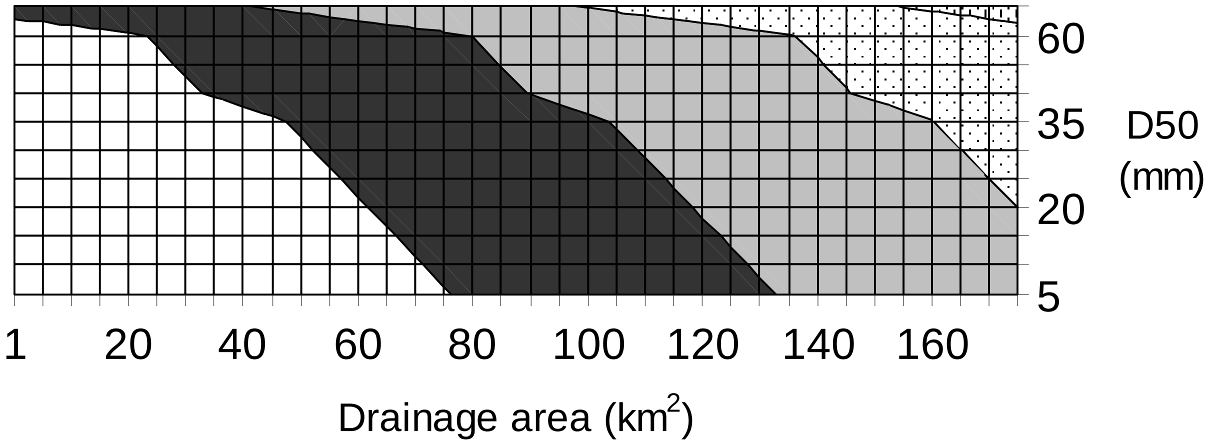

1.00
0.75
0.50
0.25
-
0%
25%
50%
75%
100%
Probability of occurence (%)
% maximum wetted width or depth

Figure 16.



Appendix A: Model selection results from correlating salmon occurrence and abundance with habitat characteristics

Model selection results for factors that affected pink, chum, and Chinook salmon occurrence in the Wood River system 1968 to 2007 including drainage area. Models are ranked from most plausible (ΔAIC*c*=0) to least plausible; p is the number of parameters. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i).

Species	Model	Log Likelihood	p	ΔAIC*c*	Akaike weight (w_i)	R^2	w_I / w_i
Pink	Drainage area	10.815	2	0.000	0.475	0.771	1.000
	Drainage area, cover width	11.287	3	2.232	0.156	0.783	3.052
	Drainage area, sockeye density	11.168	3	2.471	0.138	0.780	3.439
	Drainage area, glide depth	11.111	3	2.584	0.130	0.779	3.640
Chum	Drainage area, glide depth	13.805	3	0.000	0.272	0.846	1.000
	Wetted depth, glide depth	13.065	3	1.480	0.130	0.832	2.095
	Drainage area, glide depth, D50	14.860	4	1.594	0.123	0.864	2.218
	Glide depth	11.384	2	1.666	0.118	0.796	2.300
Chinook	Drainage area, glide depth	27.411	3	0.000	0.356	0.961	1.000
	Drainage are, glide depth, sockeye density	28.948	4	0.633	0.259	0.967	1.372
	Drainage area	25.119	2	1.409	0.176	0.949	2.023
	Drainage area, sockeye density	26.054	3	2.714	0.092	0.954	3.884

Model selection results for factors that affected pink, chum, and Chinook salmon occurrence in the Wood River system 1968 to 2007 excluding drainage area. Models are ranked from most plausible ($\Delta AICc=0$) to least plausible; p is the number of parameters. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i).

Species	Model	Log Likelihood	p	$\Delta AICc$	Akaike weight (w_i)	R^2	w_I / w_i
Pink	Wetted width	8.123	2	0.000	0.429	0.686	1.000
	Wetted width, D50	9.215	3	0.991	0.261	0.724	1.642
	Wetted width, glide depth	8.454	3	2.513	0.122	0.698	3.514
	Wetted width, cover width	8.251	3	2.921	0.100	0.690	4.308
Chum	Wetted depth, glide depth	13.065	3	0.000	0.274	0.832	1.000
	Glide depth	11.384	2	0.186	0.250	0.796	1.098
	Glide depth, D50	12.521	3	1.087	0.159	0.821	1.722
Chinook	Wetted depth	7.817	2	0.000	0.321	0.609	1.000
	Wetted depth, glide depth	8.255	3	2.299	0.102	0.628	3.156

Model selection results for factors that affected pink, chum, and Chinook salmon abundance in the Wood River system 2004 to 2007. Models are ranked from most plausible ($\Delta AICc=0$) to least plausible; p is the number of parameters. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i).

Species	Model	Log Likelihood	p	$\Delta AICc$	Akaike weight (w_i)	R^2	w_I / w_i
Pink	Drainage area, D50	-77.072	3	0.000	0.514	0.931	1.000
	Drainage area, cover width, D50	-75.781	4	1.124	0.293	0.941	1.754
	Drainage area, glide depth, D50	-76.196	4	1.955	0.193	0.938	2.658
Chum	Drainage area	-44.682	2	0.000	0.473	0.854	1.000
	Drainage area, D50	-43.842	3	1.497	0.224	0.868	2.114
	Drainage area, cover width	-44.475	3	2.763	0.119	0.858	3.980
	Drainage area, glide depth	-44.531	3	2.874	0.112	0.857	4.209
Chinook	Wetted width, cover width	-46.019	3	0.000	0.164	0.406	1.000
	Bankfull width, cover width	-46.494	3	0.951	0.102	0.372	1.609

The influence of population dynamics and environmental conditions on pink salmon re-colonization after release of a large-scale, press disturbance

Abstract

The transition from dispersal into unoccupied habitat to the establishment of a self-sustaining new population depends on the dynamics of the source and recipient populations, and the environmental conditions that facilitate or hinder exchange and successful reproduction. We used population growth rate, interannual population variability estimates, flow data, and an estimated dispersal effect to determine when colonizing pink salmon (*Oncorhynchus gorbuscha*) spawning populations became self-sustaining after a long-term migration blockage (Hell's Gate) was mitigated in the Fraser River, British Columbia, Canada. We used pink salmon spawning data from 1947 to 1987 in 66 streams to define populations, population growth rates, and the level of dispersal to newly accessible habitats. We also quantified the distance from source populations, the amount of newly accessible habitat, and determined whether stream flow conditions impeded fish passage at Hell's Gate. Population dynamics models fit to observed data indicated that the combination of an initially large source population in the Fraser River below Hell's Gate, high intrinsic growth rates linked to favorable climate-driven conditions, a constant supply of dispersers, and large amounts of newly available habitat resulted in the development of self-sustaining Fraser River pink salmon populations upstream of the historic barrier. Self-sustaining populations were developed within tens of years of barrier removal and have continued to help expand the overall population of Fraser River pink salmon. However, not all locations had the same productivity and the magnitude of exchange among them is partly mediated by river conditions that permit or

impede passage. Both re-colonized abundance levels were reduced and population spatial structure shifted relative to historic population abundance and spatial structure estimates.

Introduction

In ecological systems, chronic and sustained (press) disturbances or acute and short-term (pulse) disturbances can produce new environmental conditions and dramatically reduce or extirpate local animal populations (Pimm and Pimm 1982; Underwood 1994; and Knapp et al. 2001). The population response will vary according to perturbation type and extent, population characteristics, competition, and habitat condition. Perturbations, regardless of type, are often eventually alleviated, so the question is, “How do populations respond to the release of perturbations, and what biotic and abiotic factors allow for the re-establishment and persistence of populations?”

Some of the most important factors that determine the establishment or re-establishment, and persistence of populations have been captured in several key ecological concepts; island biogeography, metapopulations, source-sink dynamics, and habitat connectivity. Island biogeography identifies the importance of source populations, their proximity to newly available habitats, and the relative size of the new habitats (MacArthur and Wilson 1963; 1967; Pulliam 1988). Metapopulation structure and dynamics focuses on the importance of groups of populations, their overall abundance, and the importance of dispersal and exchange among the component populations (Hanski 1999; Cooper & Mangel 1999). Dispersal may reduce density dependence in source habitats, and allow for “stepping stone” colonization of other habitats (MacArthur and Wilson 1967). The “interplay” between dispersal and occupancy of new habitats is metered through the degree of connectivity, which can profoundly influence on metapopulation persistence (Fagan 2002; Isaak et al. 2007). These concepts allow for the identification of key variables which determine the establishment or re-establishment of self-sustaining populations including distance between the newly opened habitat and the source population, newly opened habitat extent and suitability, source population size, dispersal rate, the presence of barriers to connectivity, environmental conditions, and the life history needs of the animal.

Notwithstanding their well-known homing ability, salmonid fishes can quickly colonize new habitats and establish self-sustaining populations soon after disturbances are released (Hendry et al., 2004). They have done so repeatedly over the evolution of the species (Hendry et al., 2004; Waples et al. 2008). However, there are many rivers within the native range of salmon that are devoid of one or more species, and transplants within the natural range of salmon have virtually never succeeded in establishing self-sustaining populations (Quinn 2005). This indicates that most of the accessible habitat is already occupied by the species adapted to it, and expansion depends on access to previously inaccessible habitat, or sufficient changes in environmental conditions that previously unsuitable habitat becomes suitable. This perspective leads to the questions, when does a colonizing salmon population become self-sustaining, and what are the key variables that determine colonization success? While there are theoretical and modeled examples of salmon colonization (Cooper and Mangel 1998; Schick and Lindley 2007), there are few actual examples where we can quantitatively identify when a colonizing salmonid population becomes self-sustaining. Furthermore, there are no examples that have identified the relative importance of source populations and newly opened habitat characteristics to self-sustaining colonizing salmonid populations.

In this paper we focus on pink salmon (*Oncorhynchus gorbuscha*) spawning populations within a large watershed in British Columbia to quantify key variables that determined the success of colonizing salmon after recovery from a migration barrier that prevented dispersal into the vast majority of the watershed. Pink salmon are anadromous and semelparous; adults lay their eggs in the gravel of streams and rivers during late summer and fall (Heard 1991; Quinn 2005). Fry emerge from the gravels the following winter - spring and immediately migrate downstream to salt water where they spend a year feeding and growing. Adults migrate back into freshwater during early summer, complete maturation, and then make the final upstream migration to their natal sites during the late summer and fall where they breed and inevitably die. Virtually without exception, pink salmon spawn at age two and so those spawning in odd or even numbered years are isolated. For reasons that are not entirely clear, pink salmon populations in the southern portion of their overall range typically spawn in large numbers during odd years, whereas northern populations are dominated by even-year spawners (Heard 1991).

Pink salmon were abundant in the Fraser River system of British Columbia until a rockslide in a canyon known as Hell’s Gate created a hydraulic barrier to migration in 1913 (Ricker 1989; Roos 1996). For over three decades the species was absent from the river above the site of the slide until fishways were completed in 1947. Pink salmon were once again recorded in its former habitat immediately thereafter (Withler 1982; Ricker 1989). However, the presence of large numbers of pink salmon in the river below Hell’s Gate raised the question of whether all or any of the new populations were actually self-sustaining or merely dispersers (i.e. “strays”) forming sink population supported by individuals from the larger, productive populations downriver. Accordingly, our first goal was to identify and quantify key variables that determined pink salmon population establishment including the source population's size, distance, dispersal rate, quantity and quality of the newly available habitat, barriers to connectivity, and environmental conditions. We then determined which pink salmon populations were in fact self-sustaining and which were "sinks" for larger populations. We defined pink salmon spawning populations as self-sustaining when the estimated population growth rate (e.g., recruits per spawner) exceeded 1.0. Lastly, we compared current and historic population abundance and spatial structure to determine if the Fraser River pink salmon populations have returned to pre-rockslide conditions.

Materials and Methods

Study area

The Fraser River is the fourth largest watershed in the Pacific Rim behind the Amur, Yukon, and Columbia Rivers (Figure 1). It has a drainage area of 231,313 km^2, and 1,370 km of riverine habitat. The Fraser River has many salmonids including the five semelparous Pacific salmon species: Chinook (*O. tshawytscha*), sockeye (*O. nerka*) coho (*O. kisutch*), chum (*O. keta*), pink, and the iteroparous steelhead/rainbow trout (*O. mykiss*), cutthroat trout (*O. clarki*), and char (*Salvelinus malma and S. confluentus*). The populations of sockeye, Chinook, and pink salmon are the largest in Canada (Parken et al. 2008).

The total Fraser River pink salmon adult return averaged 11,500,000 (S.D. +/- 6,218,360) adults from 1947 to 1987, with an average of 2,241,342 (S.D. +/- 1,451,741) adults escaping the fisheries and spawn in the watershed. Pink salmon were cut off from most of the watershed between 1913 and the late 1940s due to a railroad construction induced rockslide at Rkm 209 (Hell's Gate) that altered flow conditions and made adult fish passage impossible (Roos 1996). Main stem and tributary pink salmon spawning populations above the slide area disappeared. The majority of rock was removed by 1915 and members of other species persisted, albeit at low levels of abundance, above Hell's Gate but pink salmon were apparently extirpated (Ricker 1987; Roos 1996).

A joint Canadian-United States "convention" was signed in 1930 to "protect, preserve, and extend" sockeye salmon (the most important commercial species), and other salmonids such as pink salmon, in the Fraser River system above Hell's Gate (Roos 1996). Another rockslide occurred in 1941 and the Commission recommended in 1944 the construction of fishways which were completed in 1947 (Roos 1996). After fish passage facilities were constructed, adult pink salmon migrated past the flow barrier and re-colonized the upper Fraser River, establishing populations above Hell's Gate in one to two decades (Withler 1982; Roos 1996).

Data

Pink salmon population estimates were developed for the Fraser River using mark-recapture techniques and foot surveys (Canada Department of Fisheries and Oceans (DFO)). From 1957 to 1987 foot surveys were conducted in 66 streams distributed throughout the Fraser River basin (Appendix A). Surveys were conducted every 7 to 10 days from August through October, the spawning period for this species in this system. Each of the 70 spawner survey reaches (more than one reach surveyed in several of the 66 streams) was identified as a primary (21) or supplemental (49) reach and the typical survey method (e.g., foot survey v. mark and recapture) was noted. Primary reaches were consistently surveyed on an annual basis, whereas supplemental reaches were periodically, but not consistently, surveyed from 1957 to 1987. The survey reach locations were verified on maps by the individuals who conducted the majority of the spawner surveys for Canada Department of Fisheries and Oceans (DFO) over the 30 year time period. The 70 survey reaches fall into several watersheds designated "spawning population complexes" including the Lower Fraser River, the Fraser River Canyon, the Seton-Anderson, the Thompson River, and the Upper Fraser River (Figure 1). Each of the watersheds included more than one breeding location. These data were then used to estimate the number of adult pink salmon returning to spawn to each complex (i.e., after fishing had occurred). Methods for estimating the number of returning pink salmon changed after 1987; spawner surveys were terminated and the only approach was mark-recapture in the Lower Fraser River below Hell's Gate (Schubert et al. 1997).

Pink salmon population estimates were also developed for from 1947 to 1955 by Ricker (1989) and Beamish (2002) (Table 1) for the Lower Fraser River, and by Withler (1982) for the Upper Fraser River (Table 1). Data from 1947 to 1955 do not include watershed-specific population estimates, but estimates were identified as below and above Hell's Gate. The effect of fishing was also incorporated into our pink salmon population estimates using data gathered and compiled by the Pacific Salmon Commission (http://www.psc.org/publications_annual_fraserreport.htm).

We used Geographic Information Systems (GIS) to help quantify and interpret available pink salmon population data relative to the colonization of the Fraser River above Hell's Gate. Distance measurements were generated by creating routes from an existing DFO 1:50,000 scale hydrography polyline layer and were expressed in river kilometers (Rkm). The hydrography route layer was used to quantify the distance of each river and spawner survey reach to the confluence with the main stem Fraser River and to Hell’s Gate. Watershed boundaries distinct to Fraser River pink salmon populations were delineated by dissolving sub-basins defined by an existing 1:50,000 scale watershed polygon layer.

Approach and Analysis

We developed a metapopulation model which was fit to observed spawning population size for each watershed. In the years 1947 to 1955 the data consisted only of counts below and above Hell’s Gate but from 1957 onwards the spawning counts were by major complex and the data were fit to those data. The assumptions of the model were:

1. The number of fish produced from each population was a population specific rate of increase times the number of spawners as modified by density dependence (using the Ricker model formulation 1954) and as modified by either a year specific survival effect, or a flow specific survival effect.
2. A fraction of the returning fish was harvested and this fraction changed from year to year and is known.
3. Of those surviving harvest, all returned to their natal site except a constant fraction that disperse to other sites.
4. The fraction of dispersers straying to other sites is a decreasing function of the distance between the natal site and the place of actual spawning times a site specific probability of straying to a site.

This model can be written as:

$$\hat{N}_{j,t+2} = \left(\alpha_j N_{j,t} e^{\frac{-N_{j,t}}{K_j}} y_{t+2}(1-\mu_{t+2}) \right) - E_{j.t+2} + I_{j,t+2} \qquad \text{(Eq. 1)}$$

$$E_{j.t+2} = \alpha_j N_{j,t} e^{\frac{-N_{j,t}}{K_j}} y_{t+2}(1-\mu_{t+2})s$$

Where $N_{j,t}$ is the escapement in area *j* at time t, *t* is time, K_j is habitat capacity for population *j*, α_j is the population growth rate for population j, μ_t is the harvest rate in year *t*, y_{t+2} is the year effect on survival (see Eq. 3), $E_{j,t+2}$ is the number of that will return to the system but potentially stray, *s* is the straying rate, and $I_{j,t+2}$ is the number of immigrants to population *j* at time *t* (Table 3). Some fraction of the immigrants will be potential strays from the same site. We defined habitat capacity as the total amount of habitat area under flow conditions at the time of spawning, irrespective of habitat preference or quality. The allocation of immigrants to each population was calculated with a distance-dependent dispersal equation:

$$I_{j,t} = \sum_{i=1}^{n} E_{i,t} p_{i,j}$$

$$p_{i,j} = \frac{\exp(-cd_{i,j})g_j}{\sum_{j=1}^{n}\left(\exp(-cd_{i,j})g_j\right)} \qquad \text{(Eq. 2)}$$

Where $I_{j,t}$ is the number of fish from the “stray” pool that return to spawn in area j. While we call these fish strays, some strays may return to their area of birth. $p_{i,j}$ is the proportion of emigrants from area *i* that return and spawn in area *j*, $d_{i,j}$ is the distance from area *i* to area $_j$, *c* is a parameter describing how probability of colonization decreases with distance, and g_j is a parameter describing the relative desirability of site *j* as a straying destination.

Two other variables, a year effect and an annual flow effect, were estimated and multiplied to the population dynamics model. The year effect (*y*) can either be estimated directly as a free parameter or made a function of flow shown below as equation 3. The year effect was an indicator of other factors that can affect annual population size including initial survival in freshwater, estuarine, and ocean conditions. The annual flow effect multiplier (*F*) attempted to capture freshwater conditions affecting upriver migration of adult salmon at Hell's Gate. This is not only the site of historic barrier but, even with fishways, remains a site of very high water velocities and difficult passage (Crossin et al. 2003). These and other studies (Rand and Hinch 1998, Rand et al. 2006) led us to hypothesize that higher mean monthly flow during the adult spawning migration period (October) would delay and possibly inhibit passage of adult pink salmon above Hell's Gate and decrease the number of spawners above Hell's Gate.

To capture the effect of flow at Hell's Gate we used data from the Fraser River gage station at Hope (08MF005; national water data archive, hydrometric program, Water Survey of Canada, http://www.wsc.ec.gc.ca/products/hydat/main) to develop relationships between mean monthly flow in October and each spawning population complex. We estimated different relationships for spawning populations above and below Hell's Gate (Eq. 3) because while the fishways were designed to facilitate fish passage for the majority of flows, high discharges can still delay and even block migration for spawning population complexes above Hell's Gate. Mean October flow (cubic meters per second (cms)) was used as the returning freshwater condition because peak spawning typically occurred during mid to late October (DFO). We hypothesized that increased flow at Hell's Gate would be positively related to the number of pink salmon spawning in the Lower Fraser and Canyon population complexes but negatively related to the number of pink salmon spawning in the Thompson and Seton-Anderson watersheds (Figure 2).

$$\begin{aligned} Y_t &= \exp\left(-q\left[F_t - \overline{F}\right]\right) \text{ if the spawning population is above Hells Gate} \\ Y_t &= \exp\left(q\left[F_t - \overline{F}\right]\right) \text{ if the spawning population is below Hells Gate} \end{aligned} \quad \text{(Eq. 3)}$$

Where F_t is the mean October flow at Hells Gate at time *t*, $\overline{F}$ is the average mean October flow at Hells Gate from 1912 to 1987, and q is a parameter to be estimated which determines the intensity of the flow effect.

We calculated the model parameters for each spawning population within a likelihood framework where the best model fit for the years 1947 to 1987 for all the spawning populations was provided by minimizing the negative log likelihood of each population in each year (Hilborn and Mangel 1997). We assumed an observation error model with lognormally distributed errors about the counts. We calculated the negative log likelihood (l) of the predicted colonizing population size ($\hat{N}_{j,t}$) given the observed colonizing population size ($N_{j,t}$):

$$l(N_{j,t} \mid \hat{N}_{j,t}) = -\ln\left(\left[\frac{1}{\sigma\sqrt{2\pi}}\right]\right) + \left(\frac{\left(N_{j,t} - \hat{N}_{j,t}\right)^2}{2\sigma^2}\right) \quad \text{(Eq. 4)}$$

Where σ (0.36) is the standard deviation of the process error for all the spawning populations. We summed the individual negative log likelihoods generated for each spawning population in a given year to calculate the total log likelihood to represent how well the model fits the data, where smaller total negative log likelihood corresponds to a better fit.

We constructed a set of nested models based upon several competing hypotheses. The first main hypothesis was the null model, where we assumed only a population effect with no immigration, year, or flow effect. The second main hypothesis included a population effect and an effect from one of the three main variables - immigration, year, or flow. In this case we hypothesized that one of these variables alone dominated and aids in better predicting spawning population size over time. The third main hypothesis included a population effect and two additional effects from immigration, year, or flow. The third hypothesis was that a combination of two of the three main variables better predict spawning population size. The last main hypothesis included all four variables – population, immigration, year, and flow effect (i.e., all of the variables were important in predicting pink salmon spawning population size in the Fraser River).

We used Akaike's Information Criterion adjusted for small sample sizes (AIC*c*) to determine which model best fit the data (Burnham and Anderson 2002). The difference between the AIC*c* of a candidate model and the one with the lowest AIC*c* provided the ranking metric (ΔAIC*c*). Generally speaking, ΔAIC*c* between 0 and 2 indicates substantial support for a model being the best approximating model, ΔAIC*c* between 4 and 7 represents less support, and ΔAIC*c* of greater than 7 indicates very little support (Burnham and Anderson 2002). Akaike weights (w_i) were calculated, representing the strength of evidence in favor of model i being the best model. The ratio of Akaike weights (w_I/w_i) indicated the plausibility of the best-fitting model compared to other models (Burnham and Anderson 2002).

Results

As documented by Withler (1982), 1,525 adult pink salmon were estimated above Hell's Gate in 1947 with increases to 19,000 by 1951 and 129,000 in 1955, an increase of two orders of magnitude in four generations (Table 1). During this time period the total return of pink salmon to the Fraser River system was at eight to twelve million (Table 1). In addition to the numerical increase above Hell’s Gate, there was a spatial expansion pattern, particularly in the Thompson and Seton-Anderson watersheds, where spawner estimates were consistently increasing from 1957 to 1981 (Table 2). A reduction in the number of pink salmon in each of those watersheds occurred between 1983 and 1987, with an increase in the number of pink salmon below Hell’s Gate and found in the Lower Fraser and Canyon tributaries (Table 2).

Two models were most likely to predict pink salmon spawning population dynamics in recently colonized habitats (Table 4), and their parameter estimates were similar (Table 5). The best model included a dispersal effect, a year effect, and a flow effect on migration at Hell’s Gate (Figure 3). The model fit was 7 times more plausible than the next best candidate model which included all the same variables with the exception of a dispersal effect (Table 4). The models with only one of the three single parameters or a different combination of two of the three variables were less plausible than the models including year and flow, or year, flow, and dispersal (Table 4).

The two best model distinguished themselves from the next best model by capturing the downward trend in the overall population prior to the mid 1960’s and the large-scale population variation since 1985 (Figure 3). A large number of pink salmon that typically had spawned upstream of Hell’s Gate did not gain access to the upper areas in 1985 due to impassable flow conditions, and thus spawned below Hell’s Gate. The variation prior to 1977 was predominantly captured with the year effect, while the variation seen since 1977 was captured by the flow effect. The initial increase in

Thompson and Seton/Anderson populations since 1947 was captured with the dispersal effect in the best-fitting model (Figure 3).

The initial population size estimates were within 1% of the observed data for the two best fit models. However carrying capacity estimates were considerably larger than actual population sizes for the Lower Fraser River and Canyon stream populations (Table 5). Carrying capacity estimates were similar to actual spawning population sizes for the Thompson and Seton-Anderson populations (Table 5). The dispersal probability to a spawning population varied considerably ranging between none to almost 75% (Table 5). A continual source of dispersers from the source (~3%) combined with a large initial source population resulted in a large estimated number of dispersers (“strays”) (17,535 ± 4,100) to colonize newly opened habitats irrespective of model fit (Figure 4). Estimated recruits per spawners > 1.0 occurred consistently in each estimated spawning population complexes from 1957 to 1987 (Table 5, Figure 5). Estimated recruits per spawner were two times greater for the upriver spawning populations (Thompson and Seton-Anderson) than for the lower river spawning populations (Lower Fraser and Canyon streams) (Table 5, Figure 5).

Correlations in abundance between the five spawning population complexes varied. The greatest degree of correlation was between the Lower Fraser River and Canyon streams population complex (Table 6). The Seton-Anderson and Thompson River population complexes were also highly correlated, suggesting an exchange between the two populations. The Thompson River and Uppermost Fraser River spawning population complexes were also highly correlated, with the Thompson being a potential source population to the Uppermost Fraser, which could not be modeled as a population because the abundance estimates were zero for some years between 1957 and 1987. Spawning populations above and below Hell's Gate were not closely correlated in abundance, even though the initial source population complex for above Hell's Gate was the Lower Fraser River. This suggests that the populations above Hell's Gate became independent of their source and self-sustaining as a whole. In some cases there was a negative correlation between the spawning population complexes above and below Hell's Gate, which could be due to factors such as the opposite effects of flow conditions (Figure 2).

The average historic pink salmon population size in the Fraser River system prior to the 1915 slide was estimated to be ~48 (± 4.6) million with the majority spawning above Hell's Gate (~46 ± 3.6 million) versus below it (~2.4 ± 1.1 million) (Ricker 1989; Beamish 2002). During the 1980's there were ~1.2 million (± 212,693) above Hell's Gate in the Thompson and Seton-Anderson systems, a decrease of 97% from historic population estimates. Lower Fraser River pink salmon population size during the 1980's was ~2.7 million (± 690,854) which is a 12.5% increase compared to estimates prior to the slide. Almost 70% of Fraser River pink salmon now spawn in the lower river, with the remaining 30% spawning above Hell's Gate.

Discussion

The release of a multi-decadal disturbance in the form of a migration barrier in the Fraser River, British Columbia allowed for the natural re-establishment of self-sustaining spawning populations of pink salmon within one to two decades after construction of passage facilities. Compared to other species of Pacific salmon, pink salmon are 1) more numerous, 2) apparently more likely to stray (2% to 34%), 3) less variable in life history,

4) have a short period of freshwater residence, and have 5) a shorter generation time and 6) higher population productivity (e.g., recruits per spawner) (Heard 1991; Hendry et al. 2004; Quinn 2005; Myers et al 1995). All of these attributes make them likely to colonize new habitats and expand quickly. Consistent with this perspective, pink salmon were the first salmonid to colonize recently opened/created streams in southeast Alaska within one decade of glacial retreat (Milner and Bailey 1989). Pink salmon recolonized 25 streams that changed elevation by over 4 meters in Prince William Sound within 6 years of the 1964 earthquake (Roys 1971). Pink salmon in the Fraser River system are an excellent example of the establishment of self-sustaining tributary-specific spawning populations that responded to a release of a press disturbance due to their energy efficient migrations and overall swimming performance (Peters et al. 1983; Standen et al. 2002; Crossin et al. 2003; MacNutt et al. 2006). Fraser River pink salmon were able to colonize above a barrier and adapt to differences in source population distance, habitat characteristics, and competition from other salmonid species.

All estimated pink salmon spawning populations in the Fraser River consistently had population growth rates > 1.0, and two of those are above the historic barrier at Hell's Gate, thus by our definition these are all self-sustaining spawning populations. (Figure 5). The combination of large numbers of individuals, and relatively high and consistent population productivity is a primary foundation for potential colonization of newly opened habitats. Another critical attribute to recolonization by pink salmon in the Fraser River was a continual source of dispersers from highly productive spawning populations downriver. We estimated a relatively constant dispersal rate among populations and over time (2.5%) from a large initial source population in the lower river which resulted in persistently large numbers of colonizing pink salmon to the newly opened habitats (Figure 4). This estimate is quite plausible based on other estimates of pink salmon stray rates (Hendry et al. 2004) Lastly, the ability of pink salmon to migrate long distances efficiently (Standen et al. 2002; Crossin et al. 2003; MacNutt et al. 2006), their self-sustaining population dynamics, and large numbers of dispersers into newly opened habitats, led to rapid recolonization of the Fraser River above Hell's Gate.

Pink salmon abundance levels, while becoming large in the Upper Fraser River above Hell's Gate in a relatively short time period (e.g., decades), have not approached the estimated levels prior to the slide (Ricker 1989). In addition, the proportion of pink salmon above and below the slide has shifted since recolonization, with the majority of pink salmon now occurring below the slide. Shifts in the relative abundance between spawning salmon populations across a watershed or region over time have been documented elsewhere. For example, in Bristol Bay, Alaska the productivity and relative abundance of sockeye salmon populations shifted with climatic conditions that favored specific life history patterns and geographic regions (Hilborn et al. 2003).

Several hypotheses have been postulated regarding the difference in population size before and after the slide (Ricker 1989). One hypothesis was that the Upper Fraser River pink salmon populations (e.g., Thompson, Seton-Anderson, Uppermost Fraser River) were larger bodied fish and stronger swimmers relative to what is typically encountered with pinks, and these populations were lost after the slide (Ricker 1989). These populations were lost due to a combination of the selective removal of larger individuals from the population by gillnet and troll fisheries and the slide, and the resulting colonization was from smaller, lower Fraser River pink salmon populations

(Ricker 1989). The overall decrease in fish size has been hypothesized to make the migration through the canyon more difficult, thus fewer fish can make the migration (Williams 1986; Ricker 1989).

Several lines of evidence support this hypothesis, first was a decrease in Fraser River pink salmon body size from 1951 and 1987 of 23% (0.46 kg; Ricker 1989). This change in size may have been due to other factors besides selective harvest such as changing ocean conditions that effect growth rate and size (Beamish 2002). Second, even though the overall size of pink salmon may have declined over the last century, the Upper Fraser River fish are still relatively larger bodied fish than their Lower Fraser counterparts and have higher maximum swimming speeds, allowing them to negotiate the Hell's Gate rapids (Williams 1986; Ricker 1989). Other possible hypotheses put forth include longer migrations through more difficult rapids, regardless of the fish ladders, more severe Upper Fraser River habitat conditions during the egg to fry life stage due to higher flow events and more extreme cold temperature conditions, and human impacts to spawning grounds (Ricker 1989).

The persistence of self-sustaining populations in newly accessible habitat is related to the compatibility between specific life history adaptations and the physical and ecological characteristics of the new habitats (Quinn 1984; Allendorf and Waples 1996). The concept that self-sustaining populations can be established, or population size increased, when a sufficient number of colonists have life history traits or adaptations compatible with available habitats is important because it focuses on specific factors that can influence successful recolonization (Table 7). The potential effect of these variables on dispersal and recolonization will vary according to species, local adaptations within species (e.g. extent of freshwater use), and unique habitat characteristics that are compatible with both (Quinn 1984).

Island biogeography and recolonization

The theory of island biogeography (MacArthur and Wilson 1963) proposed that the distance from source population and size of newly opened habitat area are two important factors that can determine the likelihood of dispersal and colonization. This concept is relevant to the case at hand; distance from the source population and habitat area, defined as the relative desirability of a site as a straying destination (g_j), was important in determining the establishment of self-sustaining pink salmon populations above Hell's Gate. Correlation between the Lower Fraser River source population and spawning populations above Hell's Gate decreased exponentially with distance, as theory would predict. In addition, larger habitats such as the Thompson River system (~55,000 km^2 drainage area) had more pink salmon spawning from the initial pulse of upstream dispersers than other areas such as the Seton-Anderson (~1,700 km^2 drainage area).

Other animal populations show similar associations with source distance or habitat or patch area (Hill et al. 1996; Gaggiotti et al. 2002). However, area became less important and distance became more important once self-sustaining populations were established. For example, the Uppermost Fraser River, above the Seton-Anderson and Thompson systems, has the largest habitat area (~150,000 km^2 drainage area) but did not receive the initial colonists, nor did populations get established as self-sustaining in the 30 year time frame that was evident in smaller watersheds closer to the initial source. In addition, the correlation with the uppermost watersheds was greater with more recently established pink salmon spawning populations above Hell's Gate. This implies that recently colonized habitats may have become a “stepping-stone” for dispersers’ farther upstream (MacArthur and Wilson 1967; Sondgerath and Schroder 2002).

Metapopulation structure and dynamics

Metapopulations are considered to be assemblages of local populations that are connected to each other through periodic migration (Hanski 1998). Their persistence as a whole is thus, in part, due to the recolonization following the extinction of subunits (Hanski 1998). Three conditions need to be met in order to satisfy the metapopulation concept for salmonids; habitats must be discrete, asynchrony must be present in population dynamics, and dispersal is a key link between the populations (Schtickzelle and Quinn 2007). Fraser River pink salmon populations meet all three of these requirements. Salmon spawning habitats, in general, are typically considered discrete because; 1) there are numerous locations between the core spawning regions that are unsuitable for spawning due to depth, velocity, and substrate size, and 2) movement of individuals once spawned is minimal, resulting in use of only one general area (Quinn 2005). A second requirement is asynchrony in population dynamics. This is the case with Fraser River pink salmon due to their differences in run timing (early October and late October), population growth rates (Figure 5), and correlations over time (Table 6).

The final condition for metapopulations dynamics is that dispersal must link populations. While most salmonids home to their natal streams (Quinn 2005), evidence for dispersal exists with the fact that pink salmon were disconnected from the majority of the Fraser River watershed due to the rock slide at Hell’s Gate and recolonized newly opened habitats once the fishway was constructed (Roos 1996). This is corroborated by the genetic similarity of spawning populations above and below Hell’s Gate (Beacham et al. 1985, Beacham et al. 1988). The estimated dispersal rates (~2 to 3%) based on the population dynamics in this study were similar to dispersal rates associated with other naturally spawning pink salmon populations in the Pacific Northwest (5.1%: Thedinga et al. 2000).

Connectivity

For metapopulation dynamics to persist there must be connectivity between the populations. The interaction between dispersal and the degree of connectivity can therefore have a profound effect on population persistence, particularly in dendritic networks such as rivers (Fagan 2002; Isaak et al. 2007). A lack of connectivity between populations can lead to profound effects in population size, life history variation, and genetic diversity (Beechie et al. 2006; Waples et al. 2008). Barriers are a key factor in determining the ability of salmonid spawning complexes to connect and exchange individuals. Numerous large barriers can isolate salmonid populations in space and over time. Such is the case with many populations of salmonids throughout the Pacific Northwest due to large, impassable dams that have been in place for almost one century and resulted in extreme fragmentation (Waples et al. 2008). However, one or a few smaller or transient barriers will allow for the exchange of individuals within and between populations, allowing for greater potential spawning interactions and genetic interaction over time. Fraser River pink salmon populations were disconnected with one major barrier from their natural extent for a period of decades. The resulting removal of the barrier at Hell's Gate allowed for unimpeded connectivity between most habitats throughout the Fraser River system.

The importance of temporal effects

Larger scale ocean and climate processes have affected Fraser River pink salmon during the decadal time period of recolonization above Hell's Gate. Prior to 1976 the average annual Fraser River pink salmon run size (the number of spawners plus those caught in Pacific Coast fisheries) was 6.8 million (± 3.4 million) with the number of spawning pink salmon averaging 1.6 million (± 391,901). From 1977 to 2001 the Fraser River pink salmon run averaged 15.6 million (± 6.3 million), while the number of spawning pink salmon averaged 6.8 million (± 5.0 million). The over two-fold increase in run size in the Fraser River pre versus post 1976 is comparable to the overall increase across the Pacific Rim. Prior to 1976, the annual average was about 151 million adult pink salmon across the entire Pacific Ocean but from 1977 to 2001 the total population more than doubled to 323 million fish per year (Ruggerone and Nielsen 2004). The apparent shift to environmental conditions favoring pink salmon in general, including Fraser River pink salmon more than likely played a large role in the rapid recolonization of the upper Fraser River as it produced a large source population from which individuals might stray upriver, and it also provided high rates of survival and recruitment of the progeny of the strays. This phenomenon was, in part, captured with the year effect on population dynamics.

Higher flows and water temperatures increase energy use by migrating salmon in the Fraser River (Rand and Hinch 1998), and conditions at Hell's Gate can also delay migration or physically prevent passage (MacDonald and Williams 1998). Flows during the normal period of pink salmon migration can vary between 1,000 and 2,500 $m^3 * s^{-1}$, and can affect the timing of migration and spawning, and *en route* mortality of salmonids (Rand et al. 2006). We found that flows can affect the relative bi-annual abundance of pink salmon spawning complexes above and below Hell's Gate. Impassable flow conditions during migration can deter pink salmon that typically spawn above Hell's Gate, and result in these fish spawning in streams below Hell's Gate (Figure 3). Capturing this temporal effect is important in understanding the bi-annual variation displayed in the population dynamics of pink salmon in the Fraser River.

Summary

The combination of an initially large source population, high intrinsic growth rates linked to favorable climate-driven conditions, a constant supply of dispersers, and large amounts of newly available habitat resulted in the development of self-sustaining pink salmon populations in the Fraser River upstream of the historic barrier at Hell's Gate. Self-sustaining populations were developed within years to decades of barrier removal and have continued to help expand the overall population of pink salmon in the Fraser River, British Columbia, Canada. Analysis of the dynamics of the populations revealed that not all locations that have pink salmon are similar; with some populations have higher productivity with this complex of populations, and magnitude of exchange among them is mediated in part by river conditions that permit or impede passage. Lastly while re-colonization of the Upper Fraser occurred in a relatively short time frame, the population structure has shifted relative to its historic abundance and spatial structure, with the majority of Fraser river pink salmon spawning now occurring below the slide.

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Tables

Table 1. Data from Ricker (1989) and Beamish (2002) on estimated numbers of pink salmon returning to the Fraser River – 1947 to 1955, and data from Withler (1982) on estimated numbers of pink salmon returning to the Fraser River above Hell's Gate - 1947 to 1955

Year	Total Return to Fraser River (Ricker 1989, Beamish 2002)	Total Return above Hell's Gate (Withler 1982)
1947	12,290,000	1,525
1949	9,430,000	1,225
1951	7,970,000	19,000
1953	9,090,000	62,150
1955	8,820,000	129,000

Table 2. Estimated numbers of adult pink salmon spawning in regions of the Fraser River system, British Columbia, Canada.

Year	Lower Fraser	Canyon Streams	Thompson	Seton-Anderson	Uppermost Fraser
1957	1,073,904	12,660	269,332	60,820	263
1959	733,933	28,862	87,224	16,153	62
1961	547,850	15,290	69,411	62,175	83
1963	516,831	21,832	285,243	136,562	723
1965	543,757	7,798	233,100	125,458	3,180
1967	785,797	7,942	450,487	239,720	3,015
1969	848,532	4,894	248,900	212,980	0
1971	928,046	22,549	258,203	308,241	5,346
1973	766,053	18,237	283,504	249,058	0
1975	315,059	9,516	480.350	280,860	36
1977	775,016	9,276	978,325	435,341	3,444
1979	1,523,458	25,610	891,191	712,840	1,846
1981	2,255,753	43,234	1,166,348	626,402	5,532
1983	3,310,999	46,456	512,398	501,475	1,721
1985	5,254,163	164,437	193,448	274,120	530
1987	1,066,032	11,736	253,109	743,286	496

Table 3. Derivation of variables used in population dynamics model for Fraser River pink salmon 1947 to 1987. Bolder variables are model outputs.

Variable	Data and associated source	Estimated parameter
Initial population size (N_{1945})	Department of Fisheries & Oceans (DFO) spawner survey data (Tracy Cone, Tracy.Cone@dfo-mpo.gc.ca), Withler (1982), Ricker (1989), Beamish (2002)	Treated as known
Estimated population size ($\hat{N}_{j,t+2}$)		
Carrying capacity (K)		X
Population growth rate (α)		X
Year effect (y)		X
Flow (F)	Hope (08MF005) (National water data archive, Hydrometric program, Water Survey of Canada,http://www.wsc.ec.gc.ca/products/hydat/main)	Treated as known
Flow effect intensity (q)		X
Harvest rate (μ)	Pacific salmon commission Fraser River annual reports (http://www.psc.org/publications_annual_fraserreport.htm)	Treated as known
Number of emigrants ($E_{j,t+2}$)		
Straying rate (S)		X
Number of Immigrants ($I_{j,t}$)		
Probability matrix ($p_{i,j}$)		
Distance-dependent dispersal coefficient (c)		X
Relative desirability of site j as straying destination (g_j)		X
Distance between source & colonizing population (d_{j-y})	Department of Fisheries & Oceans (DFO) Fish and Stream Information Summary System (http://www-heb.pac.dfo-mpo.gc.ca/maps/fiss_e.htm)	Treated as known
Sigma (σ)		X

Table 4. Model selection results for factors that affected pink salmon recolonization of the Fraser River above Hell's Gate from 1957-1987. Models are ranked from most plausible (ΔAIC*c*=0) to least plausible; p is the number of parameters. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i).

Candidate models	Log likelihood	p	ΔAIC*c*	Akaike weight (w_i)	w_I / w_i
Year, dispersal, flow	29.87	40	0.00	0.874	1
Year, flow	35.82	36	3.9	0.124	7
Year	42.82	34	13.9	0.001	1,043
Year, dispersal	39.94	38	16.1	0.000	3,197
Flow	81.87	15	54.0	0.00	532,048,240,602
Flow, dispersal	78.83	19	55.9	0.00	1,389,548,513,671
Dispersal	81.66	17	57.6	0.00	3,186,677,646,907
Null	86.20	13	58.7	0.00	5,468,360,709,664

Table 5. Parameter estimates for the two most plausible pink salmon recolonization models.

	Year, Dispersal, Flow	Year, Flow
Initial population size (N_{1945})		
Lower Fraser	5,202,939	5,243,721
Canyon streams	54,198	13,275
Thompson	0	590
Seton-Anderson	5	225
Recruits per spawner (α)		
Lower Fraser	6.0	6.9
Canyon streams	5.9	5.8
Thompson	10.2	12.8
Seton-Anderson	10.6	11.8
Carrying Capacity (K)		
Lower Fraser	22,532,077	5,548,989
Canyon streams	517,653,643	8,651,919,684
Thompson	769,664	511,381
Seton-Anderson	712,352	551,076
Dispersal probability ($p_{i,j}$) it a spawning population		
Lower Fraser	0.74	
Canyon streams	0.00	
Thompson	0.21	
Seton-Anderson	0.05	
Straying rate (s)	2.47%	

Table 6. Correlation coefficients between numbers pink salmon spawning annually in regions of the Fraser River, British Columbia, Canada 1957-1987

	Lower Fraser	Canyon streams	Thompson	Seton-Anderson	Uppermost Fraser
Lower Fraser	1.00				
Canyon streams	0.92	1.00			
Thompson	0.12	-0.06	1.00		
Seton-Anderson	0.29	0.07	0.67	1.00	
Uppermost Fraser	0.05	-0.05	0.59	0.36	1.00

Table 7. Concept and associated factors that affect colonization. (adapted from Pess et. al 2008).

Concept	Factors	Increasing dispersal and recolonization	Decreasing dispersal and recolonization
Island biogeography and source-sink dynamics	Distance from source population	Near	Far
	Habitat area	Large	Small
	Habitat type	Similar	Different
	Habitat conditions	Good	Poor
Metapopulation structure & dynamics	Source population size	Large	Small
	Dispersal rate	High	Low
	Competition with existing species	Small	Large
Connectivity	Barriers to movement	Few, small	Many, large

Figure Captions

Figure 1. Map of the Fraser River watershed, British Columbia, Canada.

Figure 2. Graphic representation of flow effect variable on estimated number of Fraser River pink salmon population complexes above and below Hell's Gate. High flows can deter upriver pink salmon migration and potentially increase the number of pink salmon counted on spawning sites below Hell's Gate. The dashed line represents the flow effect on pink salmon populations that spawn upstream of Hell's Gate and the solid dark line represents pink salmon populations that spawn below Hell's Gate.

Figure 3. Observed (circles) and modeled (heavy black line) data of pink salmon spawning populations 1947 to 1987 in the Fraser River, British Columbia, Canada following removal of a flow barrier at Hell's Gate. Modeled data is from the best fitting candidate model and includes dispersal, year, and a flow effect. a. Lower Fraser. b. Canyon streams. c. Thompson. d. Seton-Anderson. e. Fraser below Hell's Gate. f. Fraser above Hell's Gate

Figure 4. Estimated number of pink salmon dispersers ("strays") from source population complexes below Hell's Gate to sites above Hell's Gate in the Fraser River, British Columbia, Canada 1957 to 1987. The dashed line represents straying rates of 2.5%.

Figure 5. Estimated population growth rates from1957 to 1987 for spawning populations of pink salmon in the Fraser River, British Columbia, Canada. Dark solid lines indicate

median population growth rate. Box indicates 25th and 75th percentile, while solid lines at the end of the hash marks perpendicular to the box are 5th and 95th percentile.

Figure 1.

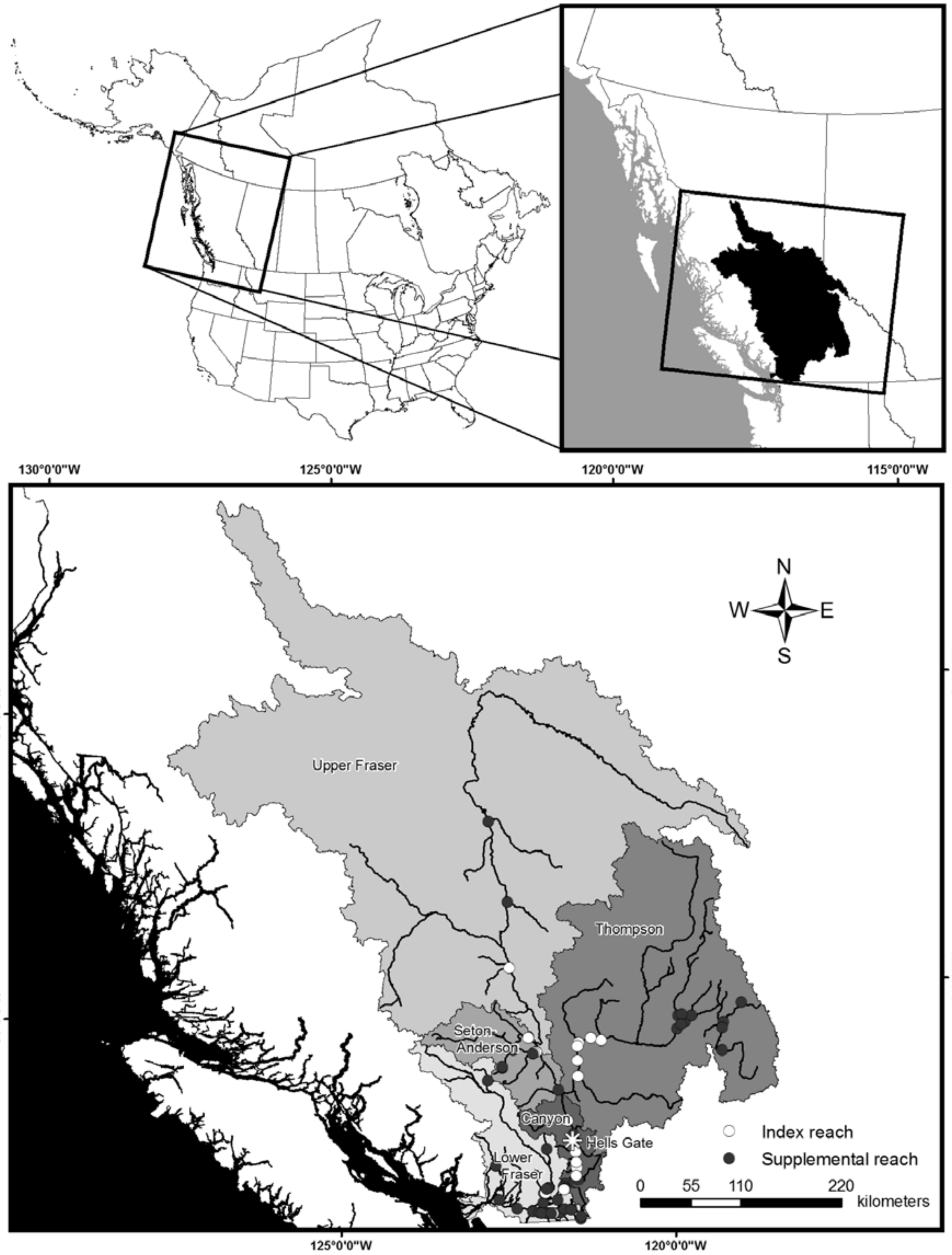

130°0'0"W
125°0'0"W
120°0'0"W
115°0'0"W
54°0'0"N
51°0'0"N
N
W
E
S
Upper Fraser
Thompson
Seton-Anderson
Canyon
Hells Gate
Lower Fraser
○ Index reach
● Supplemental reach
0
55
110
220
kilometers

Figure 2.

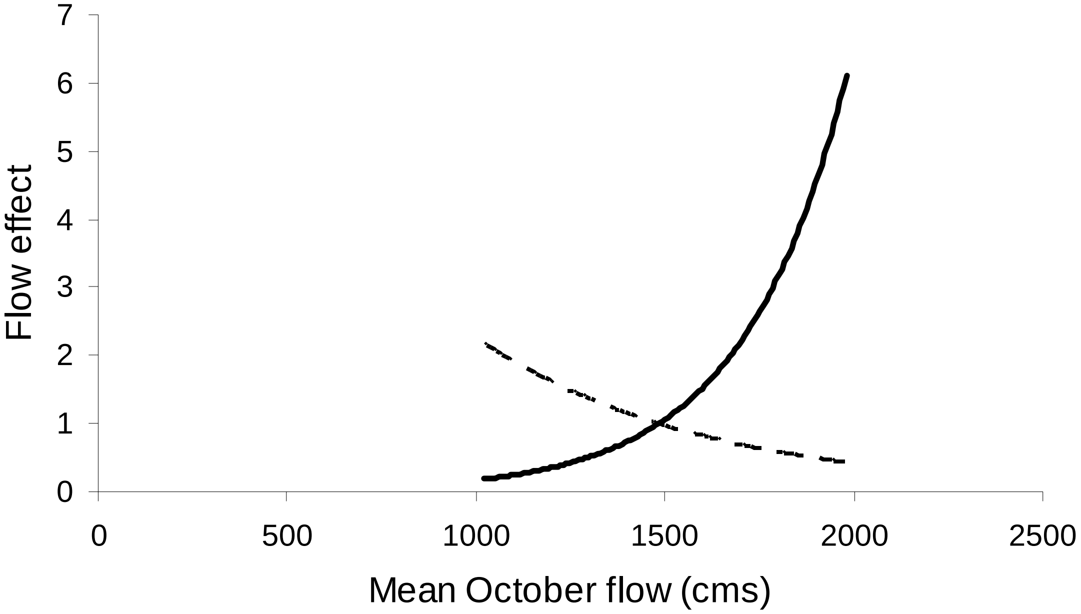

Flow effect
0
1
2
3
4
5
6
7
0
500
1000
1500
2000
2500
Mean October flow (cms)

Figure 3.

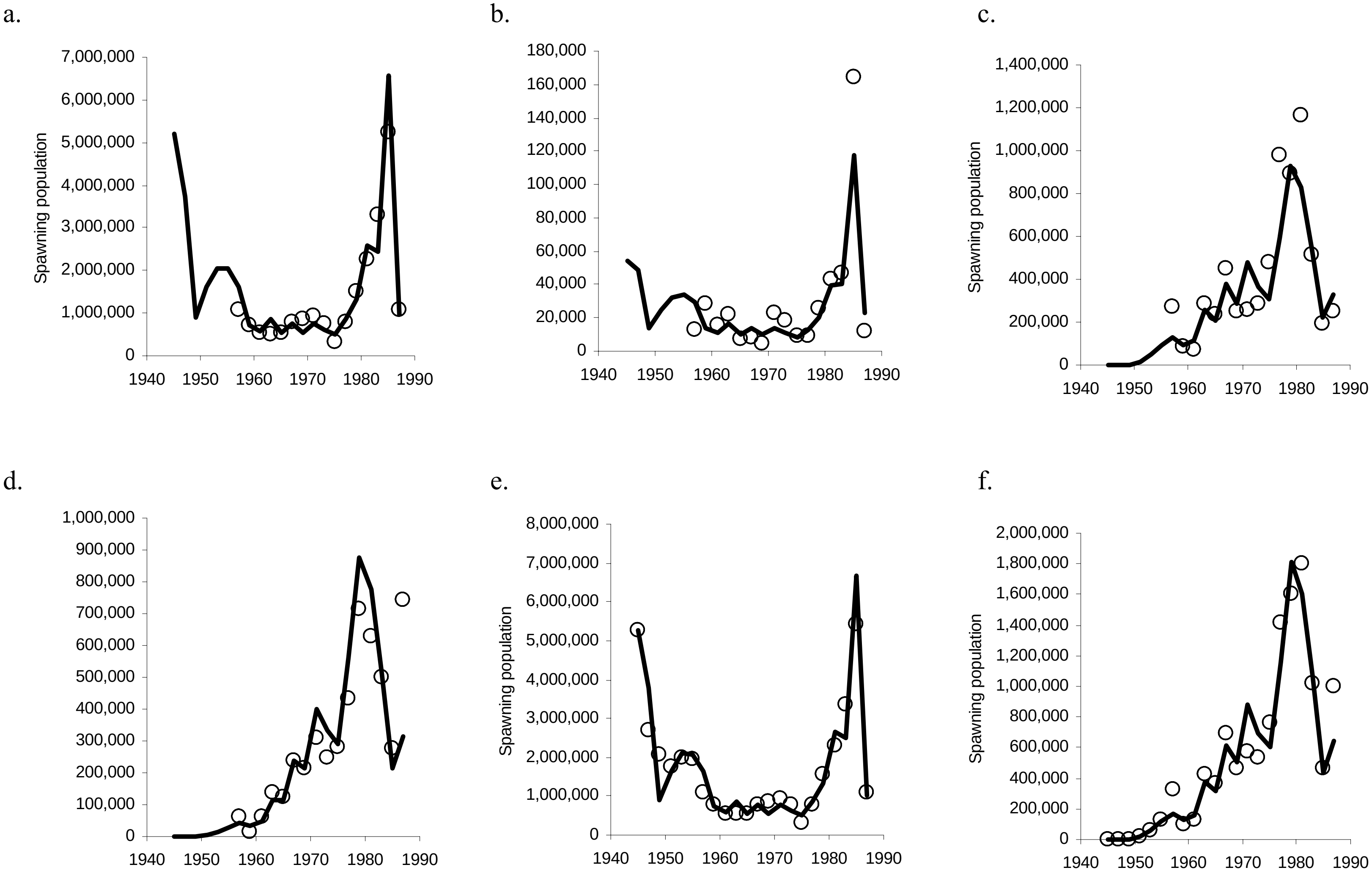
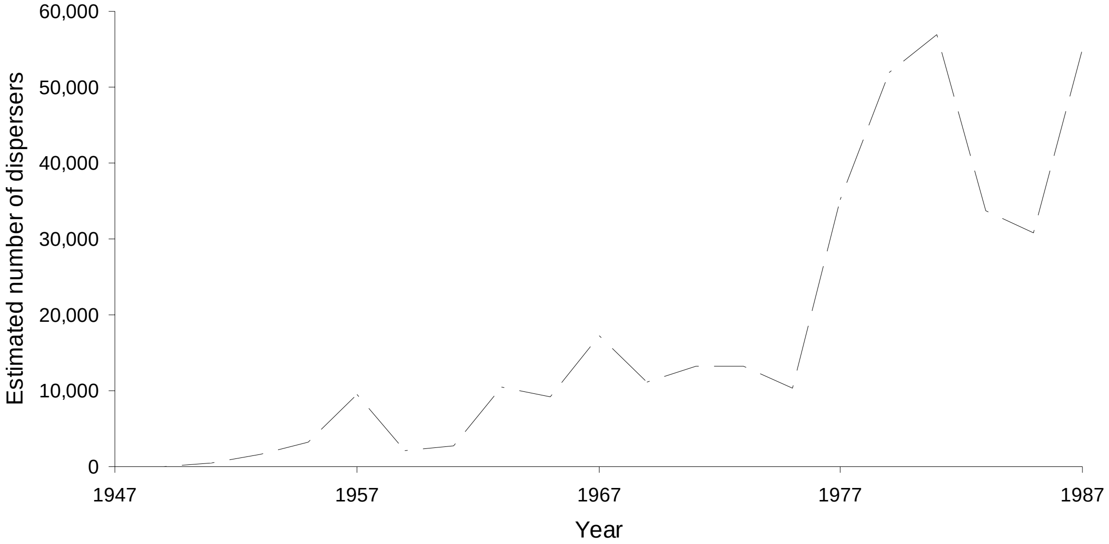
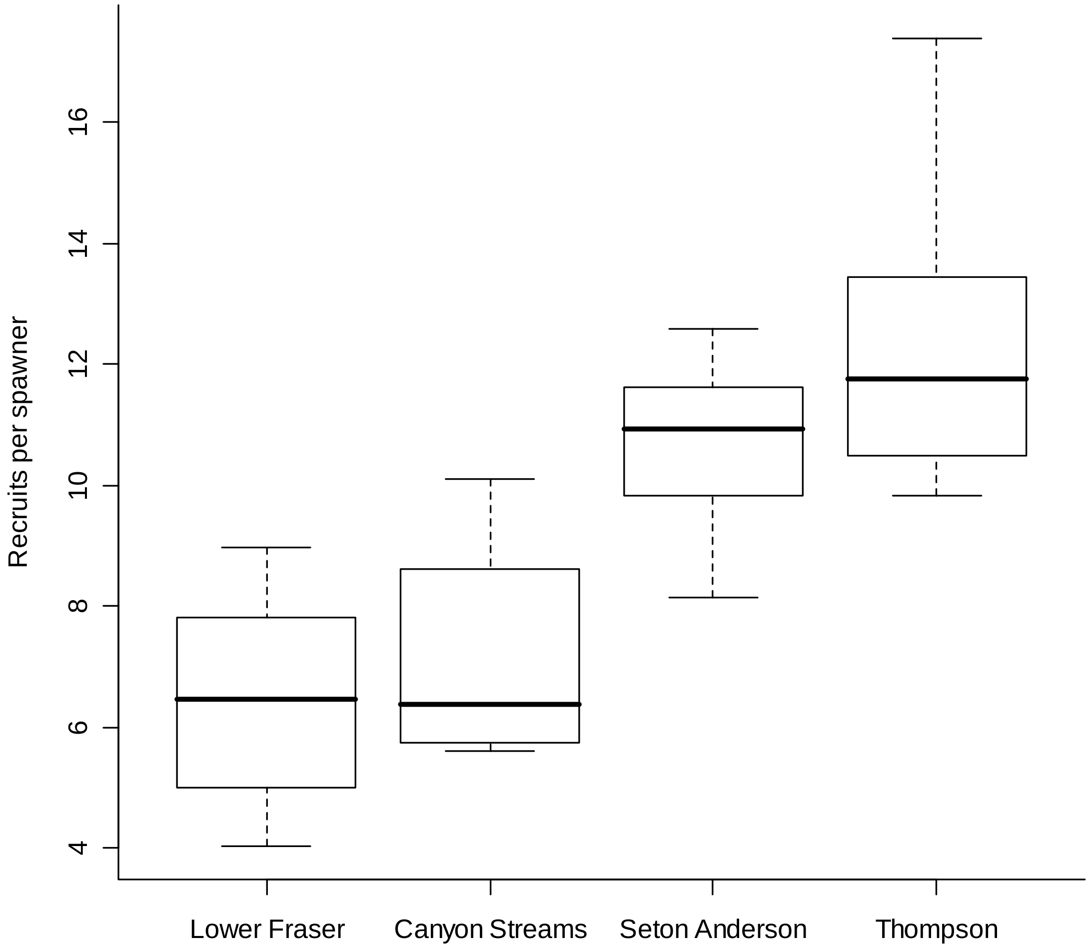

a.
Spawning population
7,000,000
6,000,000
5,000,000
4,000,000
3,000,000
2,000,000
1,000,000
0
1940
1950
1960
1970
1980
1990
b.
180,000
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
1940
1950
1960
1970
1980
1990
c.
Spawning population
1,400,000
1,200,000
1,000,000
800,000
600,000
400,000
200,000
0
1940
1950
1960
1970
1980
1990
d.
1,000,000
900,000
800,000
700,000
600,000
500,000
400,000
300,000
200,000
100,000
0
1940
1950
1960
1970
1980
1990
e.
Spawning population
8,000,000
7,000,000
6,000,000
5,000,000
4,000,000
3,000,000
2,000,000
1,000,000
0
1940
1950
1960
1970
1980
1990
f.
Spawning population
2,000,000
1,800,000
1,600,000
1,400,000
1,200,000
1,000,000
800,000
600,000
400,000
200,000
0
1940
1950
1960
1970
1980
1990

Figure 4.



60,000
50,000
40,000
30,000
20,000
10,000
0
Estimated number of dispersers
1947
1957
1967
1977
1987
Year

Figure 5.


Recruits per spawner
4
6
8
10
12
14
16
Lower Fraser
Canyon Streams
Seton Anderson
Thompson

Appendix A: Fraser River pink salmon survey streams 1957 to 1987

1. Streams surveyed for early-run (early October) pink salmon the in the Fraser River from 1957 to 1987 below and above Hell’s Gate. 2. Streams surveyed for late-run (late October) pink salmon in the Fraser River from 1957 to 1987. These surveys occurred only below Hell’s Gate. Data from Canada Department of Fisheries and Oceans (DFO).

1.

Below Hell’s Gate		Above Hell’s Gate			
Lower Fraser	Fraser Canyon	Fraser Canyon	Thompson	Seton-Anderson	Upper Fraser
Main stem	American Creek	Nahatlatch River	Adams River	Bridge River	Churn river
Johnson Slough	Anderson Creek		Bonaparte River	Cayoosh Creek	Gaspard Creek
Ruby Creek	Coquihalla River		Deadman Creek	Gates Creek	Hawkes Creek
	Emory Creek		Eagle River	Seton Creek	Lower Chilcotin River
	Flood Creek		Little River	Lower Seton Channel	Quesnel River
	Hunter Creek		Lower Shuswap River	Upper Seton Channel	Stein River
	Jones Creek		Nicoamen Creek	Portage Creek	Watson Bar Creek
	Jones Creek channel		Nicola River	Yalakum River	Williams Lake Creek
	Kawawa Creek		Thompson River		
	Lorenzetti Creek		North Thompson River		
	Nine mile Creek		South Thompson River		
	Popkum Creek				
	Ruby Creek				
	Sawmill Creek				
	Spuzzum Creek				
	Stoyama Creek				
	Texas Creek				
	Yale Creek				

2.

Below Hell’s Gate Lower Fraser
Main stem
Big Silver Creek
Birkenhead River
Border Creek
Brown Creek
Center Creek
Chilliwack-Vedder River
Chipmunk
Coquitlam River
Depot Creek
Foley Creek
Harrison River
Johnson Slough
Kanaka Creek
Little Chilliwack River
Liumchen Creek
Maria Slough
Middle Creek
N.Alouette River
Paleface Creek
Ryder Creek
S.Alouette River
Silver Cr.(Pitt River)
Silverdale Creek
Slesse Creek
Squakum Creek
Stave River
Steelhead Creek
Suicide Creek
Sweltzer Creek
Tamihi Creek
Upper Chilliwack River
Weaver Channel A.S.C.
Weaver Creek
Whonnock Creek

The influences of body size, habitat quality, and competition on the movement and survival of juvenile coho salmon during the early stages of stream re-colonization

Abstract

Adult salmon are known for their ability to home to natal sites for spawning yet they also stray and can quickly colonize newly opened or created habitats and establish self-sustaining populations. However, new salmonid populations can only become self-sustaining if habitats are also suitable for juvenile salmonids to survive until they emigrate as smolts. We studied the factors associated with growth and survival during the early stages of colonization and population establishment of juvenile coho salmon *Oncorhynchus kisutch* in Rock Creek, a tributary of the upper Cedar River in the Lake Washington basin of Puget Sound. The stream was occupied by rainbow trout *Oncorhynchus mykiss*, cutthroat trout *O. clarki*, speckled dace *Rhinichthys osculus*, and several sculpin species *Cottus spp.*. We hypothesized that smaller coho salmon, and those in pools with higher densities of competitors and poor quality habitat would have a lower survival rate than larger individuals and those in habitats of higher intrinsic quality and lower density. We found that juvenile coho salmon established a population and outnumbered resident trout species in Rock Creek within five years. Survival from late summer to spring smolt migration varied among years and was significantly higher within Rock Creek than it was in the Cedar River and Lake Washington during seaward migration. Juvenile coho salmon that migrated in the spring from Rock Creek,

rather than fall or winter contributed to over two-thirds of all Rock Creek coho salmon detected as smolts entering Puget Sound. Body size was positively correlated with survival, and larger fish tended to be found farther upstream in Rock Creek, in less densely populated habitat units. These results suggest that juvenile coho salmon can establish populations within years of initial colonization and that the annual body size is important in determining survival rate.

Introduction

Many factors such as fishing, poor hatchery practices, and especially habitat loss and degradation have caused the decline of Atlantic *Salmo salar* and Pacific *Oncorhynchus spp*. salmon populations (Nehlsen et al. 1991; NRC 1996, Montgomery 2003). Habitat loss is largely caused by barriers to migration such as road crossings, levees, and dams that block access to upstream and floodplain habitats. Lack of fish passage has been documented throughout North America (e.g., USGAO 2001; Langill and Zomora 2002; Kiffney et al. In press) and Europe (Yanes et al. 1995; Glen 2002), despite regulations requiring passage (Roni et al. 2002). As a result, many salmon populations in the United States occupy truncated and fragmented river systems, and their precipitously low abundances have warranted listing as threatened or endangered under the United States Endangered Species Act (ESA) (NRC 1996; Montgomery 2003). Removal of a blockage, whether it is a small culvert or a series of dams in a large watershed, is considered a key restoration action to aid in the recovery of listed salmon. These actions are currently being implemented across North America and will likely become more prevalent in the next five to ten years (Roni et al. 2002).

Although famous for their homing ability, salmon also display a low but important level of straying (Hendry et al., 2004). For example, in deglaciated streams of southeast Alaska, many salmonid populations have established themselves within decades of glacial retreat (Milner and Bailey 1989; Milner and York 2001). Where fish ladders have been installed or culverts removed, streams have experienced natural colonization of upstream habitats, and self-sustaining populations became established within a 5 year period (Bryant et al. 1999; Pess et al. 2003; Pess et al. 2005). Expansion of habitat area can thus allow salmonids to utilize a greater diversity of habitat types and conditions for multiple life stages. These conditions may allow rapid growth and high survival rates of juveniles and adults, leading to self-sustaining populations (Withler 1982; Milner and Bailey 1989). Colonization can also lead to divergence of life history traits in decades (Hendry et al. 2000; Quinn et al. 2001; Kinnison et al. 2001), and this enhanced diversity may build population resilience and local adaptation.

However, the success of colonization is never certain because newly accessible areas vary in suitability. Indeed, most transplants of anadromous salmonids within their native range have failed (Withler 1982) so presumably most salmon that stray do not form new populations. What are the key attributes of the fish and the environment that determine the success or failure of a colonization effort? Salmonid populations can only become self-sustaining in newly opened habitat if conditions are suitable for adults to spawn and juveniles to survive to the point where they can leave as smolts.

Low densities may result in high growth if competition is minimal but if mortality is depensatory the population may never establish (Liermann and Hilborn 2001).

Much of the work related to salmonid colonization has focused on the need for adult salmonids to access new habitats (Bryant et al. 1999; Pess et al. 2003). The occurrence, distribution, and success of juvenile salmonids are seldom examined in colonization. Juvenile salmonids may be found in newly accessible streams where adults spawned (Milner and Bailey 1989) but dispersal by juveniles can also facilitate colonization (Anderson et al. 2008). Once dispersed into newly available habitats, juvenile anadromous salmonids typically must interact and compete with existing resident species. In Pacific Northwest watersheds these species may include rainbow trout *Oncorhynchus mykiss*, cutthroat trout *O. clarki*, speckled dace *Rhinichthys osculus*, and several sculpin species *Cottus spp*. that are often numerically dominant.

There are several key questions related to the ecology of juvenile salmon and the establishment of new populations including, 1) How do colonizing juvenile salmon interact and compete at the early stages of population establishment with existing, numerically dominant resident species? 2) How do they use existing habitat at the initially low densities? 3) What is the relative role of fish condition (i.e., length and weight), competition with conspecifics and heterospecifics, and physical habitat on survival? And 4) how do these factors change from year to year as the salmon densities increase?

We addressed these questions by examining the early stages of population establishment by juvenile coho salmon *O. kisutch* in a river system where an impassable dam was modified to allow salmon recolonization. We hypothesized that the fish's condition, local competition, and local habitat quality would control growth and subsequent survival. Specifically, we predicted smaller coho salmon, and those in pools with higher densities of competitors and poor quality habitat (smaller, shallower pools) would show lower survival rates than larger individuals and those in habitat units of higher intrinsic quality and lower fish density.

Our hypotheses are based on the rationale that differences in the intensity of intra- and inter-specific competition, habitat use, food resources, or the interactions among these variables can cause differences in condition factor, growth, and survival of juvenile salmonids (Lonzarich and Quinn 1995; Rosenfeld et al. 2005). Larger body size and condition factor within a given cohort have been positively correlated to survival rates (Hartman et al. 1987; Lonzarich and Quinn 1995; Quinn and Petersen 1996; Bilby et al. 1996; Zabel and Achord 2004; Ebersole et al. 2006). Growth is affected by interactions between competition and habitat quality (Keeley 2001; Harvey et al. 2005; Rosenfeld and Boss 2001; Rosenfeld et al. 2005), and competitive dominance varies among species (Glova 1984, 1987; Sabo and Pauley 1997). Increased competition due to higher fish densities can lead to higher mortality and more variable growth rates (Keeley 2001) but density and survival can also be related to habitat quality (Kahler et al. 2001). We assessed two environmental variables, residual pool depth and distance upstream from source of the colonizing fish, for effects on survival. Residual pool depth (maximum depth minus the pool tailout depth (Lisle 1987)) was hypothesized to be important because juvenile coho salmon prefer pool habitats (e.g., Bisson et al. 1988; Sharma and Hilborn 2001; Roni and Quinn 2001; Harvey et al. 2005; Rosenfeld et al. 2005). Larger habitat volumes may allow for additional rearing environments thereby reducing competition, increasing opportunities for potential food resources, and ultimately leading to greater juvenile coho survival. Upstream distance was hypothesized to be important because adult coho salmon did not spawn in the study stream but instead spawned in the larger river to which the study stream was tributary, thus upstream colonization by juveniles is a critical process (Anderson and Quinn 2007; Anderson et al. 2008). We hypothesized that the greater the distance upstream, the greater the likelihood of mortality.

Materials and Methods

Study area

The Cedar River is a 487-km^2 watershed in Washington State that drains westward from the crest of the Cascade Mountains into Lake Washington, and ultimately Puget Sound (Figure 1). In 1901, the City of Seattle constructed a low-head, run-of-the-river water diversion facility (Landsburg Diversion Dam) at Rkm (river kilometer) 35 to supply water to the city. The diversion dam blocked 20 km of main stem habitat up to a natural fish migration barrier at Cedar Falls (Rkm 53.1) and 13 km of tributary habitat (Anderson et al. 2007). In September of 2003 a ladder was installed at the dam (Figure 1), giving coho and Chinook *O. tshawytscha* salmon access to the Cedar River and its tributaries as far as Cedar Falls (Anderson and Quinn 2007; Kiffney et al. 2009). There are four tributaries between Cedar Falls and the Landsburg Diversion dam (Williams, Steele, Rock, and Taylor creeks) but Rock Creek, the first tributary upriver of the diversion dam (Rkm 38.4), has the majority of habitat accessible to anadromous fish (~10.0 km). The other tributaries have natural migration barriers within 0.5 km of the stream mouth (Anderson et al. 2008). The Cedar River above the Landsburg Diversion Dam and below Cedar Falls is inhabited by anadromous Chinook and coho salmon, and resident rainbow trout, mountain whitefish, cutthroat trout, speckled dace, and several sculpins including torrent *Cottus rhotheus* and reticulate *C. perlexus*. Rock Creek had a similar species composition, however there are no mountain whitefish, more cutthroat than rainbow trout, and a larger proportion of dace in some habitats.

Data collection

Movement and survival of juvenile coho salmon were assessed by mark and recapture in Rock Creek from the fall of 2005 to the summer of 2008. We sampled 19 to 52 pools in the lower 2.5 km of Rock Creek (wetted width = 4.5 ± 1.6 m, residual pool depth 0.35 ± 0.19 m, velocity 0.33 ± 0.20 m/sec) in three separate reaches that were distinguished by stream channel slope and confinement (Anderson et al. 2008, Kiffney et al. In press.). Each pool was separated from the adjacent unit by a minimum of one habitat unit and electrofishing was performed in an upstream direction (unpulsed direct current at 500 V) on ten separate occasions of three to five days duration in each of the four seasons (Table 1).

Upon capture, all fishes were identified to species except sculpin, anesthetized (MS-222), weighed (± 0.1 g), measured (± 1 mm), and checked for 12.5 mm long x 2.1 mm diameter PIT (Passive Integrated Transponder PIT tags (Digital Angel, St Paul, MN, U.S.A.). All untagged salmonids, coho > 55 mm and 2.0 g and trout > 60 mm and 2.0g, received a PIT tag in the peritoneal cavity (Prentice et al. 1990). The PIT tag is a unique identifier that was detected in recapture events when pools were sampled again, or at stationary receivers. The number was recorded for any fish that had been tagged previously (Carlson et al. 2007). The fish were retained until they had recovered, and then released into the same habitat unit where they were captured. If fish had previously been tagged the tag number and location were recorded. Additional coho salmon were collected and tagged each spring at the Landsburg diversion facility, when routine annual "drawdown" of the pool above the dam for cleaning operations concentrated large numbers of fishes (Table 1). Wetted length and width, maximum depth, tail out depth, and the velocity at the tail out of each pool were measured at the same time or prior to electrofishing to quantify habitat characteristics and environmental conditions. A GPS coordinate was also recorded at each pool sampled (Table 2).

We installed a multiplex transceiver unit (MUX) with a six antenna array at the mouth of Rock Creek in October of 2005 to continuously monitor fish movement between Rock Creek and the Cedar River. Three pairs of antennas spanned the stream in each location, allowing us to identify the direction of movement by individual fish based on the sequence of the associated "hits" as the fish passed the antennas (Connelly et al. 2008). In stream systems that have a wetted channel width of < 15 m, PIT tag arrays like ours typically produce average up and downstream detection efficiencies > 95% (60% to 100%) during both low and high flow events (Connelly et al. 2008). Another PIT tag reader array at the outlet of the Lake Washington system at the Hiram Chittenden ("Ballard") Locks, detected coho salmon smolts migrating into Puget Sound (Figure 2) (Devries et al. 2004; Devries 2007).

Habitat use and apparent survival

We first quantified general spatial and temporal patterns of abundance and habitat use by juvenile coho salmon and resident fish species in Rock Creek. Population size was estimated using a maximum likelihood procedure adapted to a three-pass electrofishing depletion method (Schnute 1983; Rosenfeld et al. 2000). We then used our population estimates to determine the change in species composition over time.

To estimate survival of the juvenile coho salmon we developed individual capture histories for each tagged fish based on whether or not it was detected at one of the two PIT tag arrays, which included the mouth of Rock Creek and the Ballard Locks (Figure 2). Detection efficiencies for each PIT tag array were developed by tagging event and brood year to correct for individuals that were not detected at one of the arrays, but survived as indicated by their detection at the Ballard Locks. Ballard Locks detection efficiencies could not be determined by subsequent detections because this was the last PIT tag array in the system. As a result detection efficiencies were developed using a "fish-like" float with a PIT tag at different flows and times of year in order to generate detection efficiency curves (Devries et al. 2004; Devries 2007).

The detection efficiency estimate for all brood years and the two readers combined was 92% (±10%). Brood year (BY) 2005 had the lowest reader efficiency (73% to 80%)

due to technical difficulties during smolt migration from Rock Creek in May 2007. Only four juvenile coho salmon were undetected at Rock Creek from BY 2004 and only two from BY 2006. Brood year 2006 had the highest reader efficiency estimate (99% to 100%) even though the estimated Ballard Lock reader efficiency estimate was 30% less than the previous two brood year estimates due to unusually high flows during June 2008. Corrected survival estimates for each tagging event and brood year were calculated once detection efficiencies were estimated. It is important to note that our estimated survival rates are apparent rather than actual because we could not always distinguish between death and undetected emigration (Burnham et al. 1987).

Analysis

Several approaches were used to examine differences between recaptured (surviving) and non-recaptured juvenile coho salmon (presumed mortalities) to determine the relative importance of the factors hypothesized to affect survival. First, we compared length, weight, and condition factor between coho salmon that were detected and not detected (i.e., in subsequent tagging events or by readers) with t-tests. In the case of unequal variances (i.e., Levene's test for equality of variances; Zar 1999), means were compared using Welch's approximate t (Zar 1999). Length, weight, and condition factor were then compared with analysis of covariance (ANCOVA), where the dependent variable was length, weight, or condition factor at the date of capture and the independent variable was date captured by brood year. We concluded that the survivors differed in growth from the presumed mortalities if the slopes of the regression lines of size did not overlap and were consistently different (Carlson et al. 2007).

Lastly, we developed multiple logistic regressions and used a model selection approach with a predetermined set of independent variables to determine the relative importance of fish size, competition, and habitat quality on juvenile coho salmon apparent survival. Survival had a binomial distribution (i.e., yes or no) as the response variable, necessitating logistic regression (Agresti 1996). Independent variables included brood year, environmental condition (residual habitat depth, distance from mouth of Rock Creek), biological condition (length, weight, condition factor, and length^3), metrics which represent competition effects (relative length at tagging, density or biomass density of coho, total salmonids, total non salmonids, or total all fish), and the number of days in Rock Creek. This estimate of residency in Rock Creek provided an indication of what habitat was used (tributary vs. main stem or lake) for the majority of an individual's freshwater residence time (Table 3). Relative length at tagging is the length of a fish at capture minus the mean length for all fish of the same species captured in that habitat during the same sampling event, divided by the that mean length (Table 3). Weight at the time of capture can be difficult to measure precisely for small fish, and can be biased by recent food consumption and observation error. Therefore, length^3 was used as a metric of body size and is considered to be an indicator of absolute growth in weight and volume (Fulton 1902; Arslan et al. 2004). To determine which model best fit the data, model selection was conducted using an information-theoretic and Akaike's Information Criterion, adjusted for small sample sizes (AIC*c*) (Burnham and Anderson 2002). The difference between the AIC*c* of a candidate model and the one with the lowest AICc provided the ranking metric (ΔAIC*c*). A ΔAIC*c* between 0 and 3 generally indicate substantial support for a model being as good as the best approximating model, ΔAIC*c* between 4 and 7 represents less support, and ΔAIC*c* of greater than 7 indicates very little support for a candidate model relative to the best model (Burnham and Anderson 2002). Akaike weights (w_I) were calculated, representing the strength of evidence in favor of model *i* being the best model. The ratio of Akaike weights (w_I / w_j) indicates the plausibility of the best-fitting model compared to other models (Burnham and Anderson 2002). Models with evidence ratios of 10 or less were considered plausible (Burnham and Anderson 2002). If models were not clearly the "best" model based on the preceding criteria, then models having a score of three AIC*c* or less were considered the best suite of models. Each model was limited to three independent variables and all subsets were examined during model selection. Lastly, we compared predicted to observed survival by tagging event and stream reach in order to gain a better quantitative understanding of the difference between the predicted and observed survival estimates.

Results

Demographic changes and habitat use patterns

The number of juvenile coho salmon captured increased seven fold from 2005 to 2007 (Table 4). An increase of almost 2.5 fold occurred between 2005 and 2006 and 2.8 fold between 2006 and 2007. During that time the number of trout captured increased by 1.5 fold, while non-salmonids (chiefly sculpins) increased 2.5 fold (Table

4). The overall stream fish population increased 2.6 fold between 2005 and 2007 (Table 4). The percentage of juvenile coho salmon increased from < 10% to almost 50%, whereas the percentage of trout was reduced from almost half to < 25% of all fish captured (Table 4). Coho salmon habitat use patterns became more apparent as overall population size increased (Figure 3). The proportion of coho captured at each pool sampled in Rock Creek in 2007 increased with residual habitat depth (Figure 3, $r^2 = 0.15$, $p < 0.001$). Residual habitat depth was similar throughout the entire area sampled in Rock Creek and did not change with distance from the mouth of Rock Creek ($p = 0.31$); however juvenile coho salmon biomass density (g/m^2) decreased with distance from the mouth of Rock Creek (Figure 4, $p < 0.01$).

Movement and apparent survival of juvenile coho salmon

Movement from Rock Creek occurred in every month of the year, except July and August, for each brood year (Figure 5). More fish left in May than any other month, followed by November, December, and October (Figure 5). These four months comprised 80% of the permanent movement (i.e., without return) from Rock Creek. These movements were not in response to tagging efforts because 92% of the tagging occurred between one and three months prior to the first major movements observed in October (Table 1).

Movement was correlated, in part, with several factors including fish size and location within Rock Creek (Figures 6a, 6b, and 6c). Larger coho salmon left Rock Creek later during the spring for BY 2005 and 2006, but not BY 2004 ($p < 0.01$, $p < 0.001$, $p = 0.31$, Figure 6a). Juvenile coho salmon were also significantly larger above than below Rkm 1.5 in Rock Creek in all three brood years (BY 2004 $p = 0.007$, BY 2005 $p < 0.001$, BY 2006 $p < 0.001$, Figure 6b). Larger fish did not typically leave through the Ballard Locks earlier than smaller fish (BY 2004: $p = 0.16$, BY 2006: $p = 0.18$). However, BY 2005 coho salmon from above Rkm 1.5, were larger than those below Rkm 1.5, exited the Ballard Locks earlier ($p = 0.001$, Figure 6c); thus minimizing their time in habitats outside of Rock Creek such as the Cedar River and Lake Washington.

The average survival from the time of tagging in late summer to detection during smolt migration over all three brood years was 27% (±11%) (Table 5). Over one-third of all coho salmon tagged from BY 2004 and BY 2005 were estimated to have survived (Figure 7a). Estimated survival from tagging to Rock Creek outmigration was almost two times greater (73% ±11%) than estimated survival from Rock Creek to the Ballard Locks (38% ±14%), regardless of brood year (Figure 7b, Table 5). The number and survival of juvenile coho salmon migrants also varied by outmigration season from Rock Creek in all years (Figure 8). Over two-thirds of the coho salmon that successfully migrated into Puget Sound left Rock Creek in the spring, having spent the winter in Rock Creek rather than leave in the fall and spend the winter in the Cedar River or Lake Washington (Figure 8).

The relative importance of body size, competition, and habitat on survival

Length, weight, and condition factor differences among brood years were greater than the differences between detected and undetected coho salmon within a given brood year (Table 6), with larger, better conditioned juvenile coho salmon at tagging in the earlier years (BY 2004 and BY 2005) than BY 2006 (Table 6). Brood year 2005 juveniles were significantly larger in length and weight than BY 2004 ($p < 0.01$ for all comparisons). Condition factor was similar between BY 2004 and BY 2005 ($p = 0.30$), but higher in both BY 2004 and BY 2005 than BY 2006 ($p < 0.001$). Survivors were larger at tagging than those that were not subsequently detected for BY 2005 (Figures 9a, $p < 0.0001$ and 9b, $p < 0.001$) but not for BY 2004 and 2006 (length: $p = 0.71$, $p = 0.98$) or weight ($p = 0.72$, $p = 0.86$).

Survival from tagging to smolt migration varied among years and as a function of body size, habitat, and migration timing. AIC analysis revealed that brood year and body size (length^3) were important independent variables, present in all the best models (Tables 7 and 8). Non-salmonid biomass density, relative individual length at tagging, residual habitat depth, trout biomass density, the number of days in Rock Creek, and coho salmon biomass density added value to each of the potential models but inclusion of these variables did not appreciably change model metric scores. In contrast, there was a significant change in AIC*c* score when either length^3 or brood year was removed from the candidate model, indicating that both of these variables were important in explaining variation in survival of juvenile coho salmon from Rock Creek.

We over and underestimated survival in BY 2004 and 2006 by stream reach and tagging event based on our best candidate model which included brood year, length^3, and non-salmonid density. Brood year 2005 survival estimates were consistently underestimated by the model (5 of the 7 tagging event x stream reaches) (Table 9). Survival in Rkm 0.0 to 0.5 and Rkm 2.2 to 2.5 was consistently overestimated in BY

2004, while survival in Rkm 1.6 to 1.9 was consistently underestimated (Table 9). Conversely, survival in Rkm 0.0 to 0.5 was consistently underestimated in BY 2005, while Rkm 1.6 to 1.9 and 2.2 to 2.5 were mixed evenly between being over and underestimated (Table 9). Differences in estimated average observed and predicted survival was -1% (S.E. ±2%) for Rkm 0.0 to 0.5 and Rkm 1.6 to 1.9, and 6% (S.E. ±3%) for Rkm 2.2 to 2.5.

Discussion

This study yielded several important results that provide insight into coho salmon colonization and survivorship. Overall, we found that juvenile coho salmon can colonize and establish a population within years of initial colonization, and that fish size had a larger effect on survival than physical habitat and competition. Juvenile coho salmon successfully interacted with resident species in Rock Creek, quickly becoming the numerically dominant salmonids species. It is also important to note that during the early stages of colonization, adult coho salmon spawned exclusively in the Cedar River and occupancy of Rock Creek resulted from upstream movement by juveniles (Anderson et al. 2008). In subsequent years adult coho salmon have been observed spawning in Rock Creek, so juvenile densities may increase even further.

Higher juvenile coho salmon population levels have been observed after an increase in the amount of available habitat (Solazzi et al. 2000). This was the case in Rock Creek with the type of habitat that was “opened” with the introduction of a fish ladder at the Landsburg diversion - small (bankfull width of less than 10 m, wetted width of ~ 5 m), low gradient (0 to 2%), gravel/cobbled dominated stream channels with a preponderance of pool-riffle and forced pool-riffle channel types. These channel types are very suitable for cutthroat trout and coho salmon in coastal watersheds (Bustard and Narver 1975; Nickelson et al. 1992; Montgomery et al. 1999; Rosenfeld et al. 2000; Roni and Quinn 2001; Pess et al. 2003; Ebersole et al. 2006). Rock Creek also has other features such as an upstream wetland complex that attenuates high flows during the winter and enhances low flows during the summer and fall, a feature that also has been correlated with coho salmon productivity (Reeves et al. 1989; Nickelson et al. 1992; Pess et al. 2002). However, it has been unclear from these studies if tributaries were important because they provide more abundant spawning substrate and lower extreme flows or more summer and winter juvenile rearing habitat, as both have been previously documented (Montgomery et al. 1999; Solazzi et al. 2000; Rosenfeld et al. 2000). Because there were few if any adult coho spawning in Rock Creek during this study, we found that the rearing rather than the spawning component in Rock Creek was critical to continued colonization, survival, and increased overall abundance of juvenile coho seen in the Cedar River above Landsburg.

The increased relative abundance of juvenile coho salmon compared to resident salmonids (chiefly cutthroat trout) is consistent with other studies reporting that juvenile coho salmon are competitively superior to cutthroat trout, particularly if the coho salmon have a size advantage due differences in emergence timing and initial size (Glova 1984; Glova 1987; Sabo and Pauley 1997). In addition, the depth of pool habitat units surveyed between 2005 and 2008 (0.37 m ± 0.06) provided preferred conditions for larger juvenile coho salmon, relative to smaller cutthroat trout (Glova

1984; Bisson et al. 1988; Lonzarich and Quinn 1995; Roni and Quinn 2001; Harvey et al. 2005). Larger fish, of the same or different species, have bioenergetic requirements that result in the use of deeper water habitats (Rosenfeld and Boss 2001). Juvenile coho are typically larger than cutthroat of the same cohort (they emerge earlier in the spring and are larger at emergence because of differences in egg size) and now occur in Rock Creek at higher densities in deeper pools when instream cover is abundant (Glova 1986; Nickleson et al. 1992). The increase in the density of coho salmon from 2005 to 2007 in Rock Creek (0.03, 0.11, and 0.40 fish/m^2) resulted in end of summer coho densities that were, on average, quite similar to other studies across the Pacific Northwest (0.39 ± 0.16), even though densities in 2005 started well below the average densities (Harvey and Nakamoto 1996; Burnett 2001; Rodgers et al. 1992; Ebersole et al. 2006; Cederholm 1984; Fransen et al 1993; Roni and Quinn 2001; Kahler et al. 2001; Hotlby 1988; Rosenfeld et al. 2000; Murphy et al. 1989; and Brakensiek and Hankin 2007).

Movement from Rock Creek took place almost year-round but the primary seasons of juvenile coho salmon migration were in fall as parr and spring as smolts (Figure 5), consistent with other studies of this species (Crone and Bond 1976; Solazzi et al. 2000; Miller and Sadro 2003; Quinn 2005). Many mechanisms have been hypothesized for this movement including competition and subsequent displacement, physical displacement by high flows, or physiological adaptation to marine waters prior to ocean entrance (Chapman 1962; Quinn and Petersen 1996; Miller and Sadro 2003).

Larger coho salmon were consistently found farther upstream regardless of season and brood year, and in some instances, these fish left Rock Creek later within the spring than smaller juvenile coho salmon found in lower sections. A number of studies have shown that juvenile coho salmon size and outmigration patterns vary as a function of coarse scale habitat types (e.g., main stem vs. tributary vs. lake) (Rogers et al. 1992; Quinn and Petersen 1996; Ebersole et al. 2006), but there is little, if any, literature that suggests differences in size and movement as a function of upstream direction. It is likely that the differences in size within Rock Creek resulted from the lower densities farther upstream, and this pattern may not prevail in the future if densities become more uniformly high throughout the stream. In addition, we found inter-annual variation in the relationship between juvenile size and migration timing, as has been seen in other studies (Irvine and Ward 1989; Bohlin et al. 1993; Quinn and Petersen 1996).

Survival from tagging to smolt migration varied by year; BY 2004 and 2005 had higher apparent survival than BY 2006 (Figure 7a). The range in survival (16% to 38%) was quite similar to other over-winter survival rates in California, Oregon, Washington, British Columbia, and Alaska (Bustard and Narver 1975; Crone and Bond 1976; Petersen et al. 1994; Quinn and Petersen 1996; Solazzi et al. 2000; Ebersole et al. 2006; Brakensiek and Hankin 2007). Actual mechanisms for mortality are not known but presumably include some interaction between energetics and predation. Survival was significantly greater from tagging to Rock Creek outmigration than from Rock Creek to the Ballard Locks and into Puget Sound (Table 5, Figure 7b). Typically the difference in survival from tributary and main stem habitats and time periods (e.g., summer survival v. winter survival) was associated with differences due to season. Our estimates are similar to what others have found with respect to seasonal survival. For example our estimated survival from Rock Creek and into the main stem Cedar River/Lake Washington (73% ± 11%) is similar to summer survival (July - September) estimates in Washington (74%) and California (74%) (Spalding et al. 1995; Brakensiek and Hankin 2007), and our Rock Creek to Ballard Locks estimate of 38% (±14%) is similar to overwinter survival estimates in the preceding paragraph. However, survival estimates from Rock Creek to the Ballard Locks were consistently low, regardless of when the fish out migrated (Table 5). Thus even if residence time in the main stem and Lake Washington was relatively short, as was the case for Rock Creek spring migrants (30 ±24 days), the survival was similar to Rock Creek fall or winter migrants which spent a much larger proportion of their time in the main stem and Lake Washington (102 ± 26 days and 193 ± 33 days). Thus the majority of Rock Creek juvenile coho salmon post-tagging mortality consistently occurred in the main stem Cedar River and associated flood plain habitats, another downstream tributary, or Lake Washington. Coho salmon that migrated in the spring from Rock Creek as smolts rather than fall or winter as parr comprised over two-thirds of all coho salmon detected at the Ballard Locks, indicating the overall importance of tributary habitat for the establishment of the population. Coho salmon are eaten by non-native smallmouth bass *Micropterus dolomieui* and largemouth bass *M. salmoides*, and native northern pikeminnow

Ptychocheilus oregonensis primarily during the month of June when they travel between Lake Washington and the Ballard Locks (Tabor et al. 2004).

Tributary habitat is generally not considered as important in winter for juvenile salmon and trout compared to slow water environments such as floodplain channels connected to main stem rivers (Petersen 1982; Solazzi et al. 2000). Tributaries are important for spawning and summer rearing by coho salmon (Rosenfeld et al. 2000; Pess et al. 2002; Ebersole et al. 2006). The relative importance of tributary habitat for juvenile trout and salmon during winter increases if there is a lack of main stem off-channel habitat (Ebersole et al. 2006), and this is likely the case with the Cedar River above Landsburg, which has a lack of floodplain channels (Kiffney et al. in press).

Variation in survival was related to a group of factors including annual variation (brood year), body size (length^3), competition (biomass density or relative length at tagging), and habitat condition (residual pool depth). Brood year and length^3 were always significantly correlated to juvenile coho salmon apparent survival, regardless of the model and explain more of the variation in individual juvenile coho salmon survival (Tables 7, 8, and 9). This is consistent with previous studies that demonstrated higher overwinter survival for larger juvenile coho salmon (Hartman et al. 1987; Holtby 1988; Quinn and Peterson 1996; Ebersole et al. 2006; Brakensiek and Hankin 2007). Findings from this and other studies collectively stress the importance of summer growth and fish size at the onset of winter conditions, particularly in streams that have limited winter growth opportunities (Bustard and Narver 1975; Reeves et al. 1989; Nickelson et al. 1992; Brakensiek and Hankin 2007).

Absolute body size (e.g., length^3) was a more consistent predictor of individual survival for juvenile coho salmon in Rock Creek than relative body size. The stronger correlation between survival and absolute rather than relative body size indicated that size dependent factors such as the amount of energy reserves or the ability to withstand physical stress in the form of high flow and low water temperature may be more important during the winter than size-related competitive advantage (Ebersole et al. 2006). This may be particularly important during initial colonization when intra-specific density is low and growth is not density dependent (Anderson et al. 2008). The importance of absolute size was also indicated by the significant differences in weight, length, and condition factor between fish detected and not detected at the Ballard Locks, particularly in BY 2005. Other studies that have examined the relationship between growth, movement, and survival of juvenile coho salmon have also observed that absolute size affected overwinter survival (Ebersole et al. 2006), especially in years when the fish were relatively small (Quinn and Peterson 1996).

Absolute body size was more important than relative body size, perhaps because densities of coho salmon were so low in BY 2004 and BY 2005. Survival was highest in these years, when densities were less than what is typically documented in Oregon, Washington, and British Columbia (Bustard and Narver 1975; Nickelson et al. 1992; Roni and Quinn 2001). The proposed mechanism for higher survival during BY 2004 and BY 2005 would be reduced competition due to low juvenile coho densities. Relative body size was also an important variable in our models and was included in the form of relative length at tagging as well as biomass density of intra and interspecific competitors. Relative body size can affect juvenile salmonid movement and survival, and may have been particularly important as densities increased from 0.11 to 0.4 coho/m^2 in just one brood year cycle (Chapman 1962; Zabel and Achord 2004). The proposed mechanism would be reduced subsequent growth from competition.

It was easier to discern the effects of habitat conditions on juvenile coho utilization than survival. Residual pool depth was positively associated with the proportion of coho salmon in particular habitats. Water depth is often positively related to salmonid density and distribution, especially in coho salmon (Lonzarich and Quinn 1995; Quinn 2005) and has been identified as a source of cover from wading and diving predators (Harvey et al. 2005). Deeper environments can positively affect fish by providing more energetically favorable habitats that allow for greater food acquisition or reduce the intensity of competition that occurs due to more space (Grant et al. 1998; Rosenfeld et al. 2005). These benefits can ultimately result in enhanced survival, particularly in habitat conditions where the residual habitat depths are large and related to large-scale landscape controls such as differences in parent geology and alluvial deposits (Lonzarich and Quinn 1995; May and Lee 2004).

Assumptions and caveats

There were several constraints to our study. First, one source of observation error that could have confounded our results is higher tag mortality in smaller individuals (Brakensiek and Hankin 2007). Brakensiek and Hankin (2007) found that initial tag groups had significantly lower estimated survival rates than proceeding tag groups within the same brood year and that if only one group is tagged per brood year, then estimated survival rates may not reveal the survival rates of untagged fish. Similar to Brakensiek and Hankin (2007) we had multiple tag groups within a given brood year and within one to two months of the initial tagging event in order to reduce the effect of PIT tag mortality on our survival estimates. Another limitation was loss of PIT tag reader capability during critical outmigration times, which occurred in BY 2005 at the Rock Creek reader. The loss or reduced detection efficiency of a reader can lower the number of fish detected and subsequently affect apparent survival estimates. Two readers in one system alleviated part of this issue because we were able to determine detection efficiencies. Specifically, we were able to detect individuals at the Ballard Locks, allowing us to reconstruct which individuals and the timing of those individuals as they migrated past the Rock Creek reader but were not detected. Another potential limitation is determining outmigration timing from the entire system. It is generally assumed that coho smolts migrate to sea during the spring, however, there is increasing evidence some form of migration occurs during the fall as well (Miller and Sadro 2003). The Ballard Locks reader was active through the month of October and only two coho were detected during the fall migrating from the Cedar/Lake Washington system for all years indicating that the vast majority migrated during the spring. Lastly, the potential for observed pattern of size dependent apparent survival could be biased by sampling that goes beyond the PIT tag effect. The fate of free-ranging fish for survival models is problematic, however we attempted to compensate for this with a large sample size (n = 1393) a consistent sampling effort (e.g., three times per year), and a consistent sampling location (e.g. the same habitat units) (Burnham et al 1987).

Summary

Juvenile coho salmon successfully colonized and established a population that is now the numerically dominant salmonids in Rock Creek within five years of initial entry by juveniles. End of summer juvenile coho salmon densities are now similar to other streams with established populations in Oregon, Washington, and British Columbia. Body size positively affected survival but overall rates varied among years. Competition and habitat conditions also affected individual survival and juvenile coho salmon population levels. Tributary habitats can play an important role in the establishment of anadromous populations during initial colonization, and the same variables that are important to the survival of individuals also determine the initial success of the colonizing population.

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Tables

Table 1. Juvenile coho salmon sampling in Rock Creek, Cedar River, Washington State from 2005 to 2007.

*Spring 2008 sampling was 6 weeks earlier than spring 2006 and spring 2007 and in Rock Creek rather than the Landsburg diversion facility. In addition, spring 2008 conditions were more similar to typical winter conditions of 2006 and 2007. +Samples taken from Landsburg diversion drawndown but were not used in the analysis.

Sample	Brood Year	Sampling season and year	Sites	Number of sampling locations	Total fish captured	Coho salmon captured	Mean length (mm) (±S.E)	Mean weight (g) ((±S.E)	Mean condition factor (K)
1	2004	Summer 2005	Rock Creek	36	353	42	72 ±1.18	4.40 ±0.19	1.14 ±0.02
2	2004	Fall 2005	Rock Creek	46	691	122	81 ±0.62	5.83 ±0.15	1.12 ±0.02
3	2004	Winter 2006	Rock Creek	35	139	26	80 ±2.16	6.23 ±0.42	1.17 ±0.03
4+	2004	Spring 2006	Cedar River – Landsburg	1	583	150	111 ±0.71	13.9 ±0.28	1.12 ±0.01
5	2005	Summer 2006	Rock Creek	51	793	180	66 ±0.80	3.63 ±0.14	1.14 ±0.01
6	2005	Fall 2006	Rock Creek	52	1016	227	81 ±0.69	6.31 ±0.15	1.15 ±0.01
7	2005	Winter 2007	Rock Creek	19	143	63	83 ±1.41	6.12 ±0.27	1.03 ±0.02
8+	2005	Spring 2007	Cedar River – Landsburg	1	229	41	115 ±1.68	15.97 ±0.77	1.02 ±0.02
9	2006	Summer 2007	Rock Creek, Cedar River	49	1247	539	68 ±0.39	3.74 ±0.07	1.14 ±0.01
10	2006	Fall 2007	Rock Creek, Cedar River	36	1532	715	77 ±0.31	4.97±0.06	1.04±0.003
11*	2006	Spring 2008	Rock Creek	30	318	77	84 ±0.81	6.65±0.18	1.14 ±0.02

Table 2. Habitat surveys associated with juvenile coho sampling in Rock Creek, Cedar River, Washington State from 2005 to 2007

Season/Year	Number of pools	Wetted length (m±S.E.)	Wetted width (m±S.E.)	Residual pool depth (m±S.E.)	Dominant substrate	Subdominant substrate	Dominant cover type	Avg. cover width (m±S.E.)	Velocity (m/sec±S.E.))
Summer 2005	36	8.64 ±0.76	3.80 ±0.21	0.37 ±0.02	Gravel	Cobble	Streambank vegetation	0.08±0.02	0.22±0.01
Fall 2005	46	8.58 ±0.67	4.53 ±0.25	0.31 ±0.03	Gravel	Cobble	Streambank vegetation	0.09 ±0.02	0.31 ±0.02
Winter 2006	35	8.05 ±0.67	4.55 ±0.26	0.30 ±0.03	Gravel	Cobble	Streambank vegetation	0.09 ±0.02	0.47 ±0.03
Summer 2006	51	9.75 ±0.86	4.36 ±0.28	0.33 ±0.02	Gravel	Cobble	Streambank vegetation, log jams	0.06 ±0.02	0.31 ±0.04
Fall 2006	52	10.06 ±0.83	3.91 ±0.21	0.29 ±0.02	Gravel	Cobble	Streambank vegetation, log jams	0.06 ±0.02	0.24 ±0.02
Winter 2007	19	10.22 ±0.79	5.17 ±0.25	0.52 ±0.05	Gravel	Cobble	Streambank vegetation, log jams	0.31 ±0.14	0.47 ±0.04
Summer 2007	49	11.21 ±0.84	4.45 ±0.24	0.35 ±0.04	Gravel	Cobble	Streambank vegetation, log jams	0.30 ±0.10	0.30 ±0.02
Fall 2007	36	12.36 ±1.00	5.00 ±0.45	0.36 ±0.04	Gravel	Cobble	Streambank vegetation, log jams	0.30 ±0.06	0.29 ±0.06
Spring 2008	30	11.97 ±0.93	5.26 ±0.28	0.39 ±0.03	Gravel	Cobble	Streambank vegetation, log jams	0.28 ±0.12	0.54 ±0.04

Table 3. Independent variables used to correlate to tagging to smolt apparent survival of juvenile coho salmon in Rock Creek, Cedar River, Washington State between 2005 and 2007.

Independent variable	Notation	Frequency of measurement
Environment condition		
Residual habitat depth (m)	$\left(depth_{\max imum} - depth_{tail}\right)$ (Lisle 1987)	2005 to 2008
Distance from Rock Creek mouth (m)	$\left(dis\tan ce_{habitatunit} - dis\tan ce_{mouth}\right)$	2005 to 2008
Biological condtion		
Tagging fork length (mm)	$\left(length_{tail} - length_{nose}\right)$	2005 to 2008 n = 1393
Tagging weight (gms)		2005 to 2008 n = 1393
Condition factor (K) (Weatherly & Rogers 1978)	$\left(\frac{W}{L^3}10^5\right)$	2005 to 2008 n = 1393
Condition factor (K) (Fulton 1902)	$\left(length_{tail} - length_{nose}\right)^3$	2005 to 2008 n = 1393
Relative length at tagging	$\left(\frac{L_{i,j} - \overline{L_j}}{\overline{L_j}}\right)$	2005 to 2008 n = 1393
Competition		
Coho density or coho biomass density (coho/m^2 or gms/m^2)	$\sum_{i=1}^{n}\left(\frac{(coho)}{(area(m^2))}\right)$ or $\sum_{i=1}^{n}\left(\frac{(coho(gms))}{(area(m^2))}\right)$	19 & 51 pools
Salmonid density or salmonid biomass density (salmonid/m^2 or gms/m^2)	$\sum_{i=1}^{n}\left(\frac{(salmon)}{(area(m^2))}\right)$ or $\sum_{i=1}^{n}\left(\frac{(salmon(gms))}{(area(m^2))}\right)$	19 & 51 pools
Total density or total biomass density (Total fish/m^2 or gms/m^2)	$\sum_{i=1}^{n}\left(\frac{(fish)}{(area(m^2))}\right)$ or $\sum_{i=1}^{n}\left(\frac{(fish(gms))}{(area(m^2))}\right)$	19 & 51 pools
Number of days in Rock Creek	$\left(date_{outmigration} - date_{tagging}\right)$	2005 to 2008

Table 4. Number of captured fish in Rock Creek, Cedar River, Washington State, USA from 2005 to 2007

	2005 (BY 2004)	2006 (BY 2005)	2007 (BY 2006)
Coho	190 (16%)	470 (22%)	1340 (44%)
Trout *spp*.	540 (46%)	741 (38%)	759 (25%)
Non-salmonids	452 (38%)	738 (38%)	972 (32%)
Total	1182	1949	3071

Table 5. Apparent survival, detection efficiency, and estimated mortality for juvenile coho salmon from Rock Creek, Cedar River, Washington. BY 2004 through 2006.

	BY 2004			BY 2005		BY 2006					
	Summer 2005	Fall 2005	winter 2006	summer 2006	Winter 2007	Summer 2007	Fall 2007	Spring 2008	Total or Average	S.D.	95% C.I.
Number of fish tagged & detected											
Coho tagged	49	101	18	298	51	686	131	59	1393		
Rock Creek reader	23	62	14	138	26	445	88	49	845		
Rock Creek reader - corrected for efficiency	27	72	17	200	36	459	88	50	949		
Ballard Locks reader	8	19	5	72	15	53	12	6	190		
Ballard Locks reader - corrected for efficiency	12	29	8	93	23	95	22	11	291		
Rock Creek and Ballard Locks readers	8	16	4	33	9	51	12	6	139		
Ballard Locks but not Rock Creek reader	0	3	1	40	6	2	0	0	52		
Reader efficiency estimates											
Rock Creek efficiency	100%	84%	80%	44%	60%	96%	100%	100%	83%	21%	15%
Ballard Locks efficiency	50%	50%	50%	50%	50%	20%	20%	20%	39%	16%	11%
Detected by one reader (%)	100%	92%	90%	73%	80%	99%	100%	100%	92%	10%	7%
Not detected by either reader (%)	0%	8%	10%	27%	20%	1%	0%	0%	8%	10%	7%
Apparent Survival											
Survival in Rock Creek	55%	71%	93%	72%	71%	67%	67%	83%	73%	11%	8%
Surivival from Rock Creek to Ballard Locks	44%	40%	45%	44%	62%	21%	25%	22%	38%	14%	10%
Overall survival	24%	28%	42%	31%	44%	14%	16%	18%	27%	11%	8%
Estimated Mortality											
Mortality in Rock Creek	45%	29%	7%	28%	29%	33%	33%	17%	27%	11%	8%
Mortality from Rock Creek to Ballard Locks	56%	60%	55%	56%	38%	79%	75%	78%	62%	14%	10%
Overall mortality	76%	72%	58%	69%	56%	86%	84%	82%	73%	11%	8%

Table 6. End of summer average length, weight, and condition factor (± 95%C.I.) by brood year

Brood year	Length (mm)	Weight (g)	Condition factor
2004	78.2 (±1.3)	5.5 (±0.3)	1.13 (±0.04)
2005	81.2 (±1.5)	6.4 (±0.3)	1.15 (±0.02)
2006	77.4 (±0.6)	5.0 (±0.1)	1.04 (±0.01)

Table 7. Model selection for estimating juvenile coho salmon apparent survival in Rock Creek BY 2004 to 2006.

Model Parameters	k	Log Likelihood	AIC*c*	ΔAIC*c*	*w*AIC*c*	Deviance	d.f.
BY, Length^3, Non salmonid biomass density	5	-484.48	979.01	0.00	0.30	969.0	1341
BY, Length^3, Relative length at tagging	5	-484.96	979.97	0.96	0.18	969.9	1341
BY, Length^3	4	-486.12	980.27	1.26	0.16	972.2	1342
BY, Length^3, Residual habitat depth	5	-485.17	980.38	1.37	0.15	970.3	1373
BY, Length^3, Trout biomass density	5	-485.78	981.60	2.59	0.08	971.6	1341
BY, Days in Rock Creek, Length^3	5	-485.95	981.94	2.93	0.07	971.9	1341
BY, Length^3, Coho biomass density	5	-486.02	982.07	3.07	0.06	972.0	1341
BY, Days in Rock Creek, Non salmonid biomass density	5	-491.00	992.04	13.04	0.00	982.0	1341

Table 8. Maximum-likelihood estimates of intercept and slope parameters for the "best approximating" models predicting juvenile coho apparent survival from Rock Creek. Standard errors are in parentheses.

Model	Intercept	BY2005	BY2006	Length_3	Non salmonid biomass density	Relative Length at tagging	RHD	Trout Biomass density	Number of days in Rock Creek	Coho Biomass density
BY, Length^3, Non salmonid biomass density	-2.502 (0.302)	0.143 (0.246)	-0.929 (0.243)	1.776e-06 (4.025e-07)	0.145 (0.078)					
BY, Length^3, Relative length at tagging	2.698 (0.358)	0.204 (0.243)	-0.839 (0.241)	2.339e-06 (5.619e-07)		0.1.45 (0.078)				
BY, Length^3	-2.397 (0.295)	0.2108 (0.2428)	-0.8723 (0.240)	1.751e-06 (3.999e-07)						
BY, Length^3, Residual habitat depth	-2.180 (0.335)	0.171 (0.245)	-0.851 (0.241)	1.835e-06 (4.058e-07)			-0.578 (0.422)			
BY, Length^3, Trout biomass density	-2.472 (0.309)	0.228 (0.244)	-0.861 (0.241)	1.738e-06 (4.002e-07)				0.0217 (0.026)		
BY, Days in Rock Creek, Length^3	-2.190 (0.456)	0.227 (0.244)	-0.859 (0.241)	1.653e-06 (4.332e-07)					-8.098e-04 (1.363e-03)	
BY, Length^3, Coho biomass density in pool	-2.370 (0.300)	0.205 (0.243)	-0.852 (0.244)	1.767e-06 (4.015e-07)						-0.0219 (0.048)
BY, Days in Rock Creek, Non salmonid biomass density	-0.993 (0.308)	0.215 (0.245)	-0.939 (0.242)		0.164 (0.078)				-0.003 (0.001)	

9. Predicted vs. observed average apparent survival by brood year, stream reach, and tagging event in Rock Creek, Cedar River, Washington state.

Sample	Brood Year	Average observed apparent survival (%)			Average predicted apparent survival (%)		
		Rkm 0.0-0.5	Rkm 1.6-1.9	Rkm 2.2-2.5	Rkm 0.0-0.5	Rkm 1.6-1.9	Rkm 2.2-2.5
1	2004	0.23	0.11	0.00	0.16	0.18	0.16
2	2004	0.16	0.25		0.18	0.23	
3	2004	0.18	0.33		0.20	0.25	
4	2004	0.07	0.25	0.11	0.15	0.20	0.21
5	2005	0.24	0.33	0.29	0.20	0.27	0.32
6	2005	0.29			0.24		
7	2005	0.09	0.00	0.12	0.06	0.08	0.08
8	2005	0.06	0.10	0.10	0.08	0.09	0.09
8	2006	0.12		0.00	0.09		0.12
9	2006	0.23	0.11	0.00	0.16	0.18	0.16

Figure Captions

Figure 1. Map of Cedar River main stem and tributaries above Landsburg Diversion Dam and below Cedar Falls including reach breaks and natural upstream barriers to anadromous fish. Solid lines represent habitat available to anadromous fish and dashed lines inaccessible habitat above natural barriers. Figure from Anderson et al. 2008 and Kiffney et al. 2009.

Figure 2. A schematic map of the Cedar River/Lake Washington watershed. Solid black lines and circle denote freshwater, hashed black line denotes Puget Sound, thick hashed grey line denotes the Landsburg diversion dam, and the solid black circles denote MUX units in the watershed were outmigrating juvenile coho salmon were interrogated leaving Rock Creek and the Ballard Locks.

Figure 3. Proportion of all coho captured by residual habitat depth in Rock Creek 2007. Clear circles are coho salmon. The solid line is the regression: proportion of all fish captured that are coho = 0.38*(residual habitat depth) + 0.042.

Figure 4. Juvenile coho biomass density (g/m^2) as a function of distance from the mouth of Rock Creek. Each point is a sampled pool between the Summer 2005 and Spring 2008.

Figure 5. Mean percent total (±S.D.) of juvenile coho salmon detected leaving Rock Creek by BY 2004 to BY 2006. No detections occurred in July and August.

Figure 6. a. Date adjusted juvenile coho salmon length (mm) v. the date leaving Rock Creek BY2005. Size was adjusted to October 31, 2006 in order to negate differences in tagging date. b. Date adjusted juvenile coho salmon length (mm) v. distance from mouth of Rock Creek (rkm) where individual fish were originally tagged. c. Date leaving through the Ballard Locks v. distance from mouth of Rock Creek (rkm) where individual fish were originally tagged.

Figure 7. a. Apparent survival of coho salmon from tagging to the smolt stage by BY from Rock Creek, Cedar River, Washington (mean +/- S.E.) b. A comparison of apparent survival in Rock Creek and the main stem Cedar River/Lake Washington for BY 2004 to BY 2006 (mean +/- S.E.). Clear bars are mean apparent survival, while solid lines with perpendicular solid lines at end are standard deviation bars.

Figure 8. Trajectories of movement and survival of Rock Creek coho salmon, combining data from BY 2004 through 2006, expanded by incorporating detection efficiency (Table 5). Numbers below each season are the number of fish detected at Rock Creek Pit tag array. Numbers in boxes below June are the numbers of tagged coho detected for each seasonal outmigration period at the Ballard Locks. All juvenile coho salmon left the Cedar River in the months of May and June.

Figure 9. Differences in coho length by date captured between apparent survivors and non-survivors from Rock Creek (BY 2005). Detected juvenile coho salmon are the solid

plus signs, while undetected juvenile coho salmon are the clear diamonds. Detected juvenile coho salmon are offset 10 days so they can be seen relative to the undetected juvenile coho salmon data even thought all fish were collected at the same time. Regression for detected juvenile coho salmon is fork length (mm) = 0.0811(date captured) - 3081.4. $R^2 = 0.22$. Regression for undetected juvenile coho salmon is fork length (mm) = 0.065(date captured) – 2457.3. $R^2 = 0.16$ Solid line is detected regression, hashed line is undetected regression. b. Differences in coho weight by date captured between detected and undetected from Rock Creek (BY 2005). Regression for detected juvenile coho salmon is weight (grams) = 0.0125(date captured) – 480.95. $R^2 = 0.13$. Regression for undetected juvenile coho salmon is weight (grams) = 0.0094date captured) – 360.2. $R^2 = 0.09$.

Figure 1.

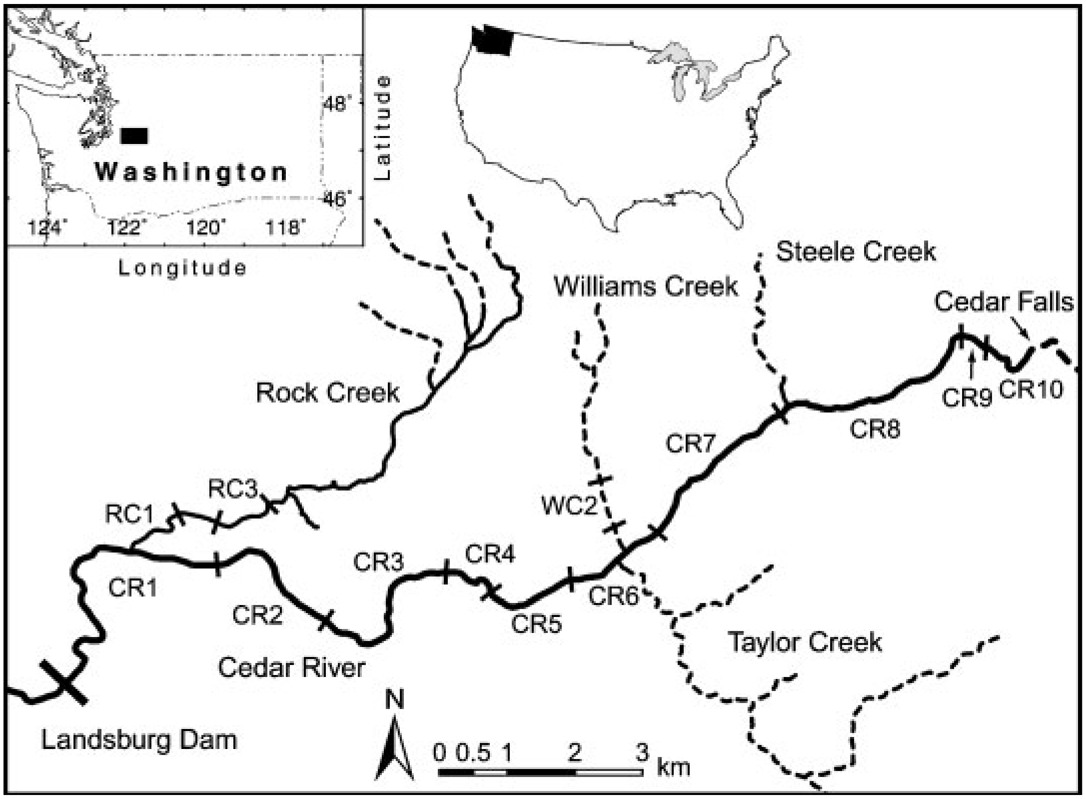

Washington
48°
46°
124°
122°
120°
118°
Latitude
Longitude
Steele Creek
Williams Creek
Cedar Falls
Rock Creek
CR9
CR10
CR8
CR7
RC3
RC1
WC2
CR1
CR3
CR4
CR2
CR5
CR6
Taylor Creek
Cedar River
Landsburg Dam
N
0 0.5 1 2 3 km

Figure 2.

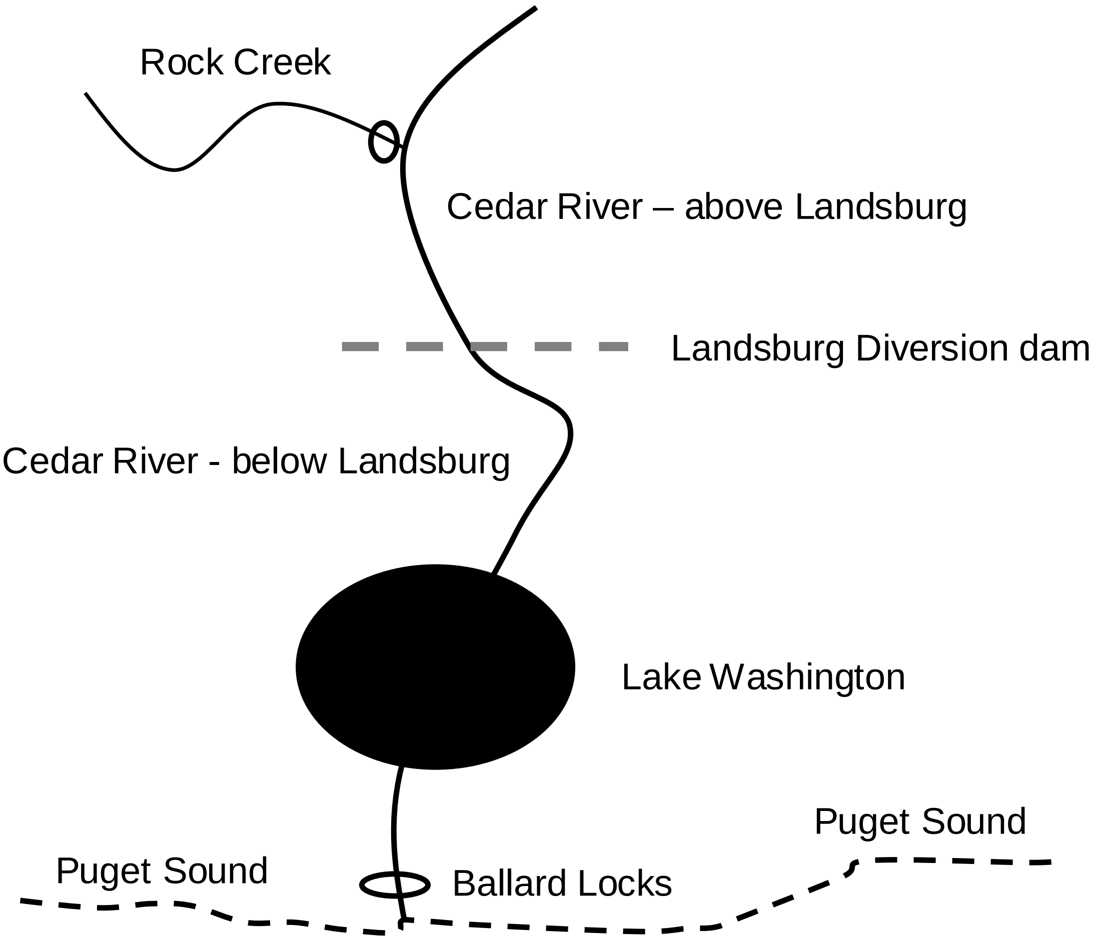

Rock Creek
Cedar River – above Landsburg
Landsburg Diversion dam
Cedar River - below Landsburg
Lake Washington
Puget Sound
Puget Sound
Ballard Locks

Figure 3.

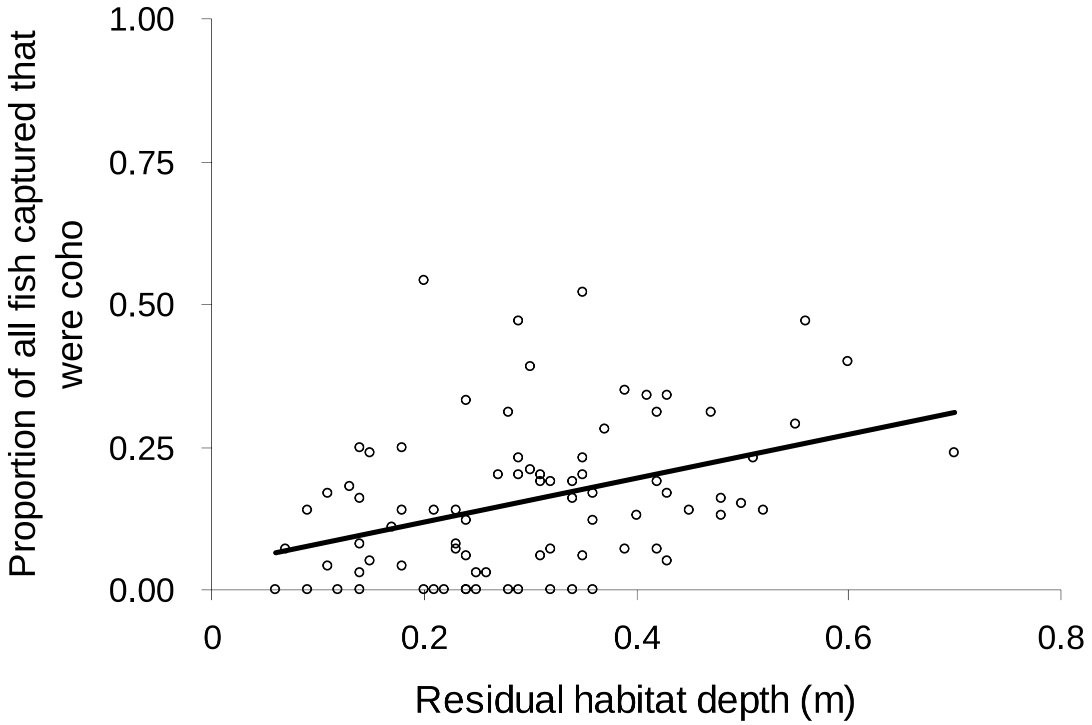

1.00
0.75
0.50
0.25
0.00
0
0.2
0.4
0.6
0.8
Proportion of all fish captured that were coho
Residual habitat depth (m)

Figure 4.

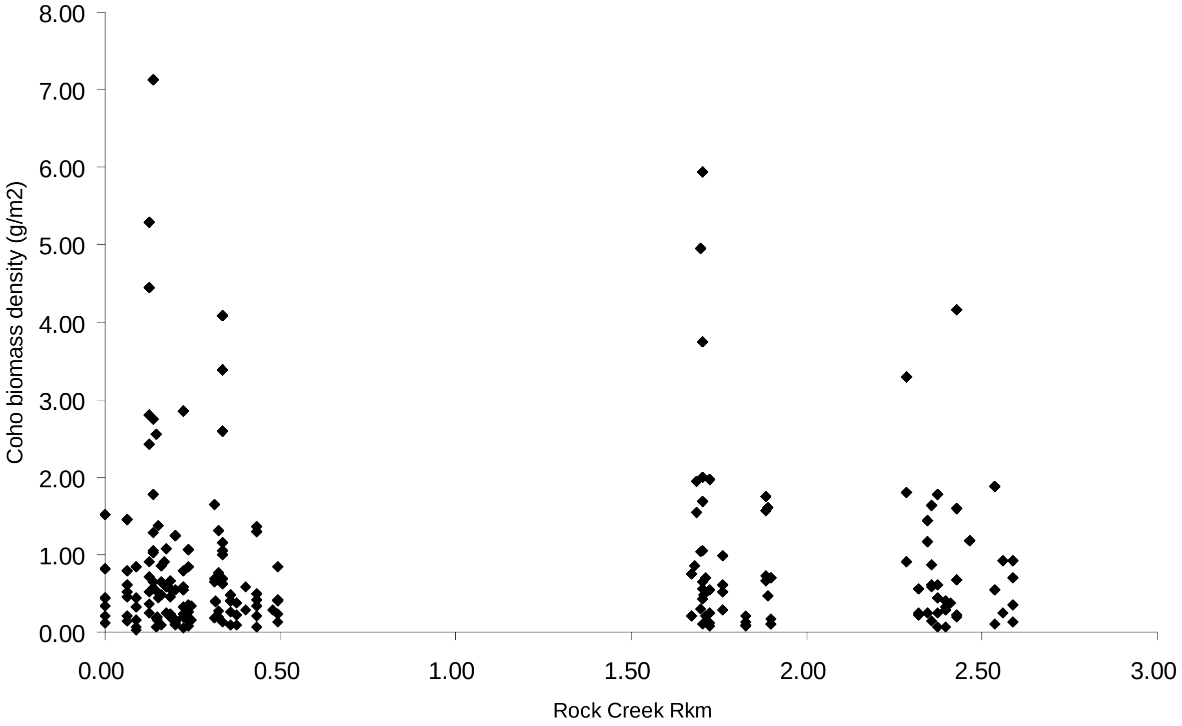
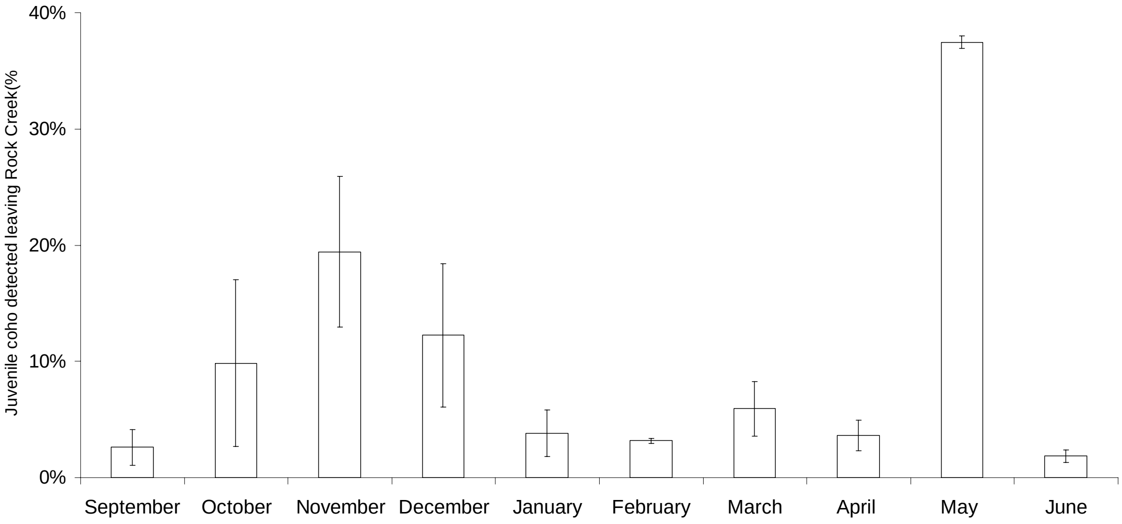

8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
Coho biomass density (g/m2)
0.00
0.50
1.00
1.50
2.00
2.50
3.00
Rock Creek Rkm

Figure 5.



Juvenile coho detected leaving Rock Creek(%
40%
30%
20%
10%
0%
September
October
November
December
January
February
March
April
May
June

Figure 6.

a.

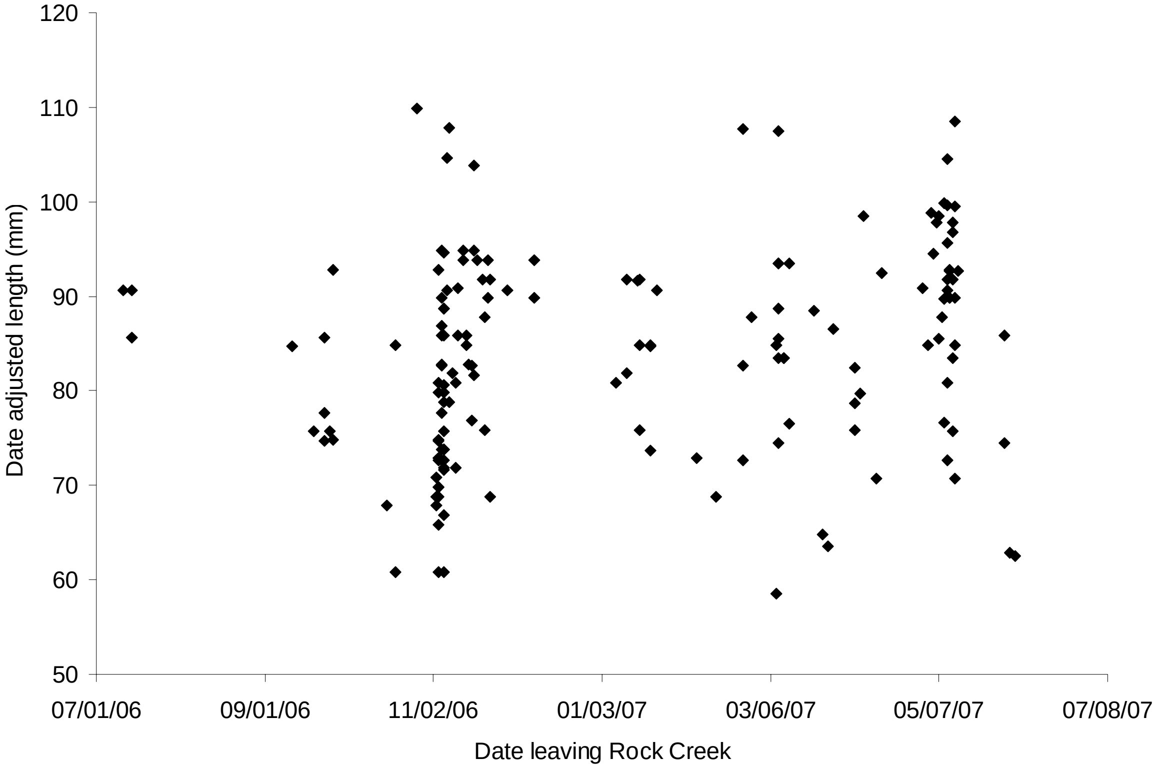

120
110
100
90
80
70
60
50
Date adjusted length (mm)
07/01/06
09/01/06
11/02/06
01/03/07
03/06/07
05/07/07
07/08/07
Date leaving Rock Creek

Figure 6.

b.

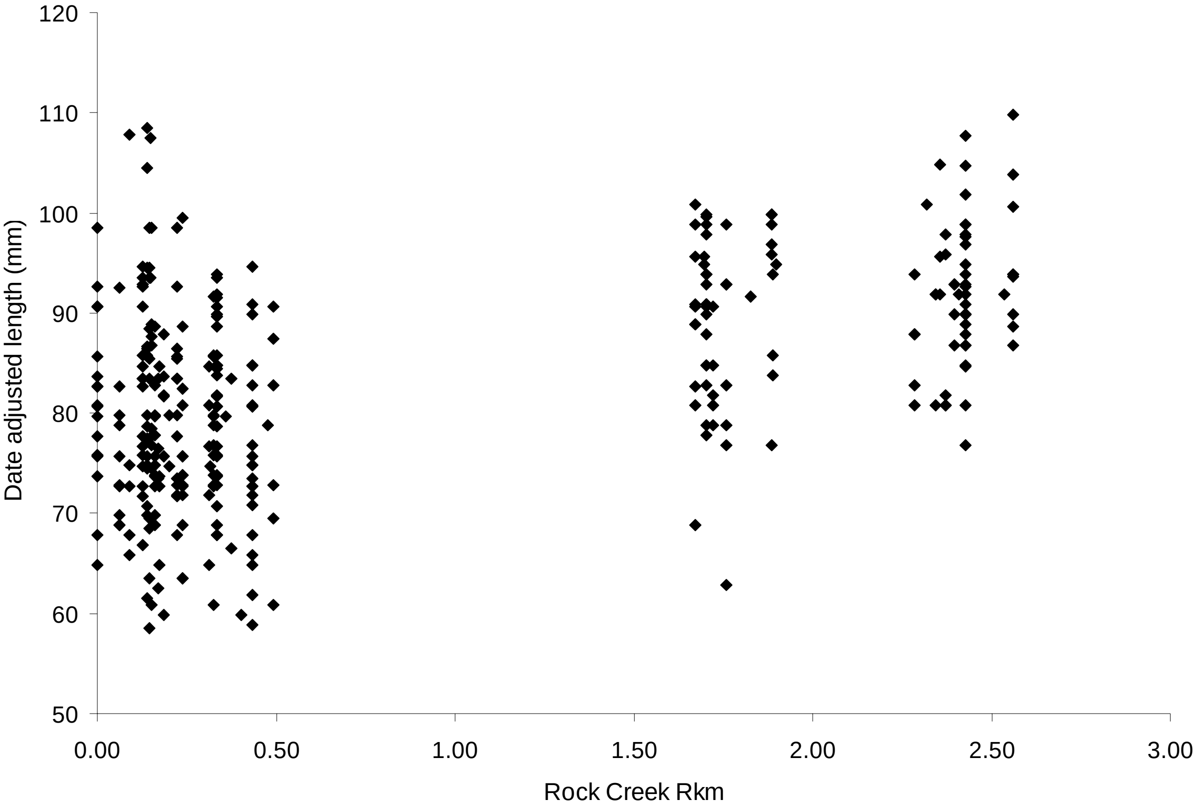

120
110
100
90
80
70
60
50
Date adjusted length (mm)
0.00
0.50
1.00
1.50
2.00
2.50
3.00
Rock Creek Rkm

Figure 6.

c.

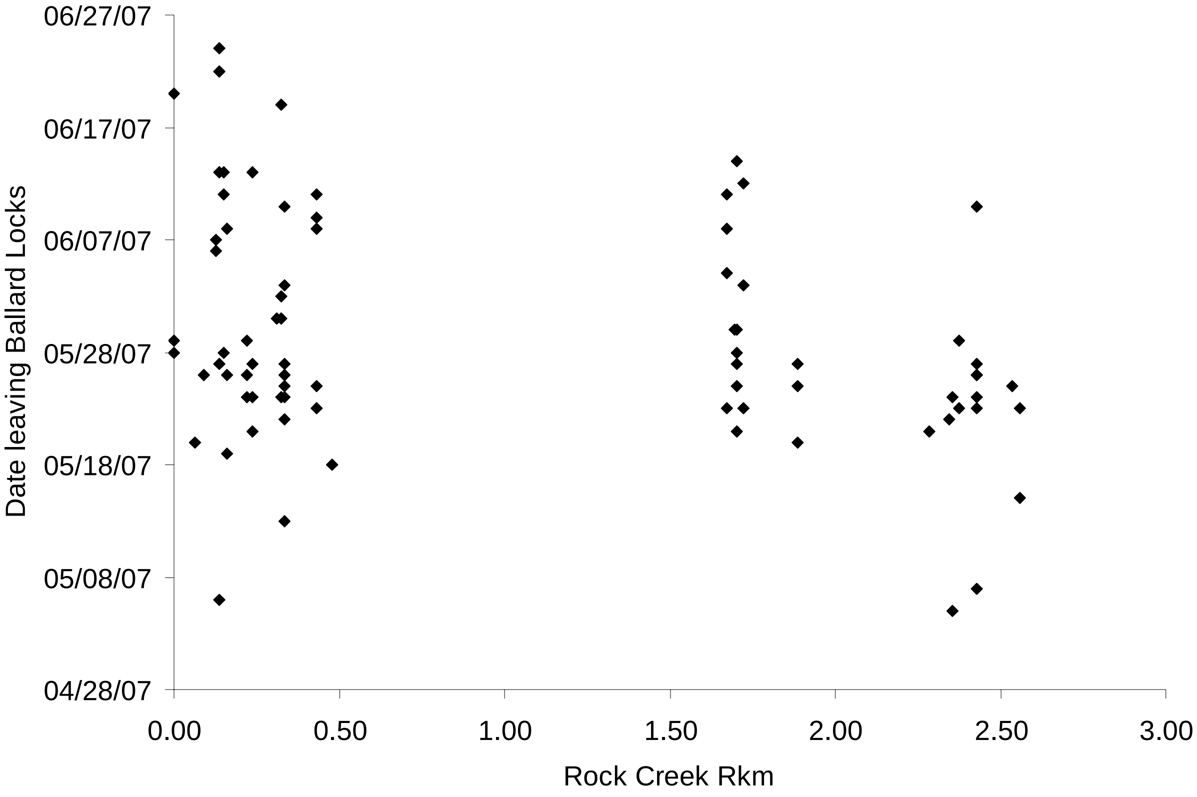
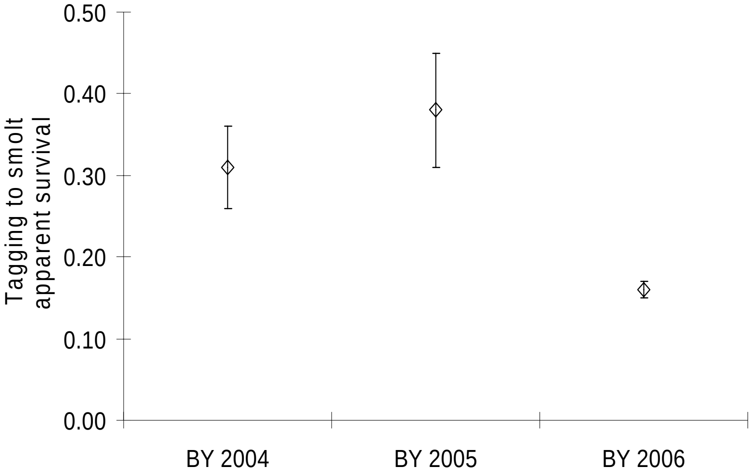

06/27/07
06/17/07
06/07/07
05/28/07
05/18/07
05/08/07
04/28/07
Date leaving Ballard Locks
0.00
0.50
1.00
1.50
2.00
2.50
3.00
Rock Creek Rkm

Figure 7.

a.


0.50
0.40
0.30
0.20
0.10
0.00
Tagging to smolt apparent survival
BY 2004
BY 2005
BY 2006

b.

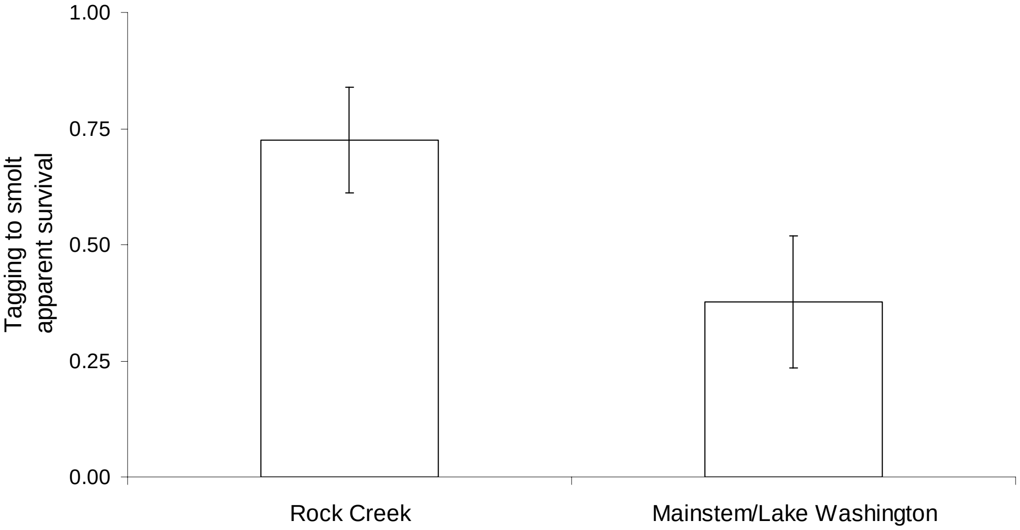

1.00
0.75
0.50
0.25
0.00
Tagging to smolt apparent survival
Rock Creek
Mainstem/Lake Washington

Figure 8.

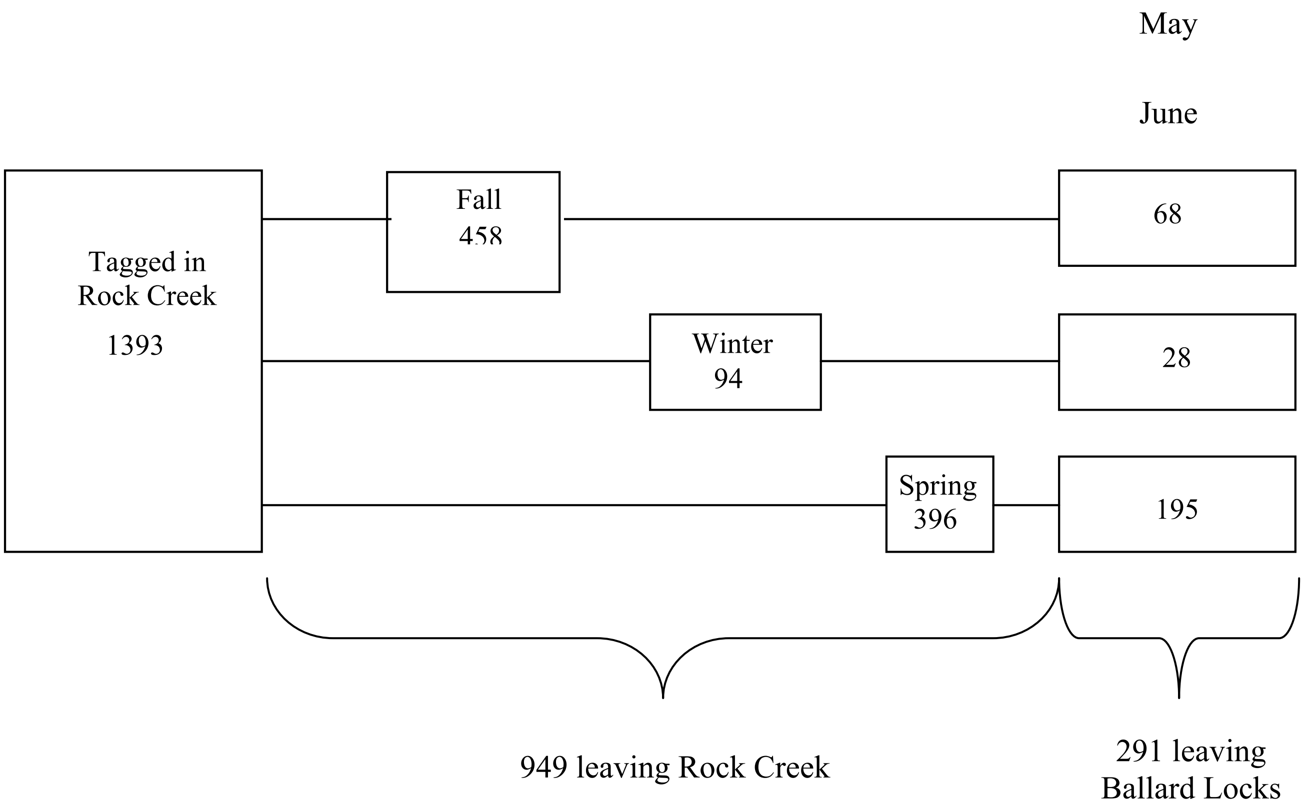

May
June
Tagged in Rock Creek
1393
Fall
458
Winter
94
Spring
396
68
28
195
949 leaving Rock Creek
291 leaving Ballard Locks

Figure 9.a.

a.

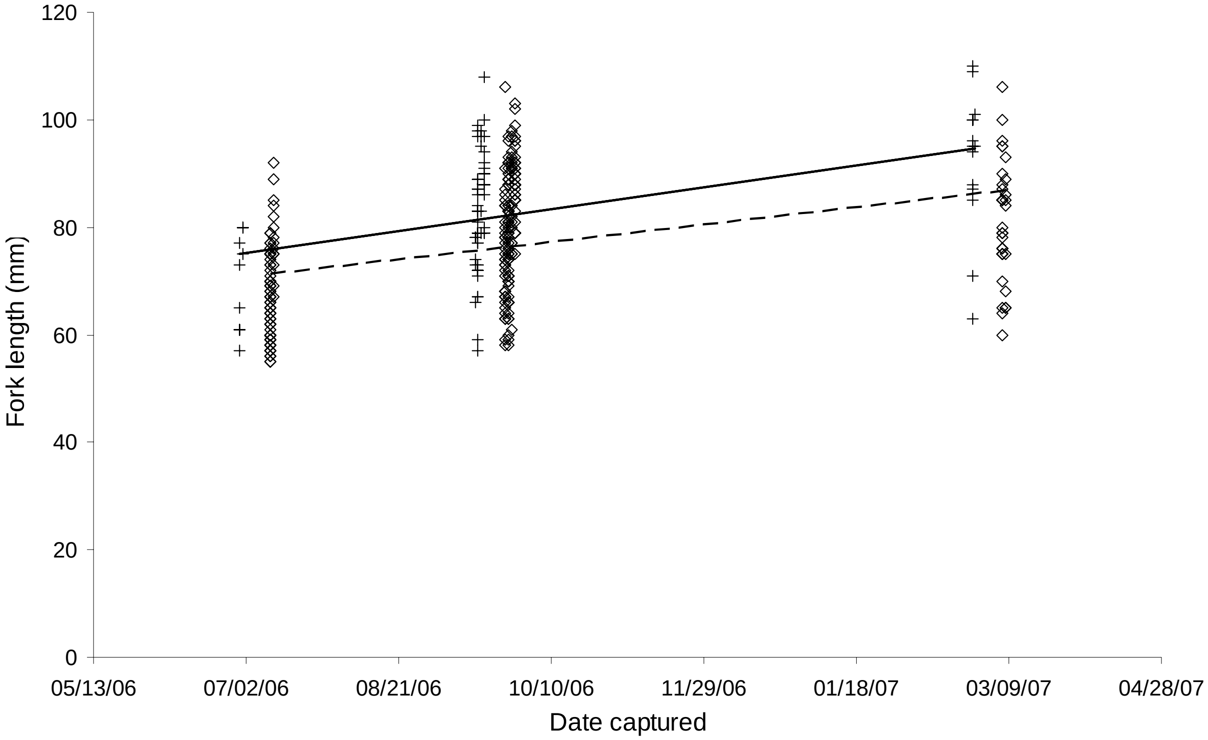
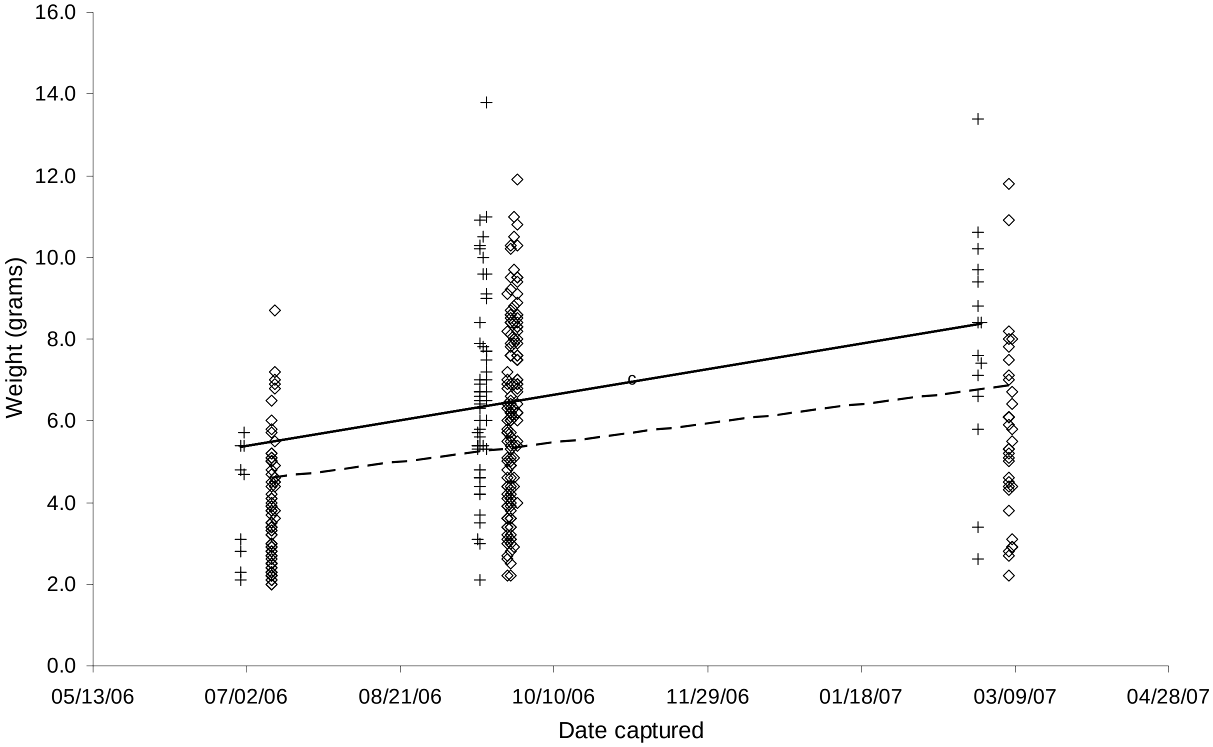

120
100
80
60
40
20
0
Fork length (mm)
05/13/06
07/02/06
08/21/06
10/10/06
11/29/06
01/18/07
03/09/07
04/28/07
Date captured

Figure 9.

b.


16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Weight (grams)
05/13/06
07/02/06
08/21/06
10/10/06
11/29/06
01/18/07
03/09/07
04/28/07
Date captured
c