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Biological Impacts of the Elwha River Dams and Potential Salmonid Responses to Dam Removal

Abstract

The Elwha River dams have disconnected the upper and lower Elwha watershed for over 94 years. This has disrupted salmon migration and reduced salmon habitat by 90%. Several historical salmonid populations have been extirpated, and remaining populations are dramatically smaller than estimated historical population size. Dam removal will reconnect upstream habitats which will increase salmonid carrying capacity, and allow the downstream movement of sediment and wood leading to long-term aquatic habitat improvements. We hypothesize that salmonids will respond to the dam removal by establishing persistent, self-sustaining populations above the dams within one to two generations. We collected data on the impacts of the Elwha River dams on salmonid populations and developed predictions of species-specific response dam removal. Coho (*Oncorhynchus kisutch*), Chinook (*O. tshawytscha*), and steelhead (*O. mykiss*) will exhibit the greatest spatial extent due to their initial population size, timing, ability to maneuver past natural barriers, and propensity to utilize the reopened alluvial valleys. Populations of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon will follow in extent and timing because of smaller extant populations below the dams. The initially high sediment loads will increase stray rates from the Elwha and cause deleterious effects in the egg to outmigrant fry stage for all species. Dam removal impacts will likely cause a lag in recolonization and population rebuilding. These negative sediment effects will be locally buffered by the extent of functioning floodplain, and management attempts to minimize sediment impacts. Resident life forms of char (*Salvelinus confluentus*), rainbow trout (*O. mykiss*), and cutthroat (*O. clarki*) will positively interact with their anadromous counterparts resulting in a positive population level response.

Introduction

The effects of dams on riverine ecosystems have been well-documented throughout the world (Petts 1984, Ward and Stanford 1987). Dams alter hydrologic regimes and disrupt sediment and organic matter transport (Petts 1984, Ward and Stanford 1987**,** Dynesius and Nilsson 1994), leading to downstream changes in water quality, energy flow, and stream channel dynamics and morphology (Ligon et al. 1995). Dams also affect ecological functions and aquatic organisms by blocking migration into upstream habitats (Petts 1984, Ward and Stanford 1987, Kanehl et al. 1997). Perhaps the most obvious effect on fish populations, especially anadromous populations such as salmonids, is blocking fish migration (Ligon et al. 1995). Such blockages reduce population sizes, alter life history diversity, and shift the spatial structure of meta-populations (Ligon et al. 1995, Heinz Center 2002, Beechie et al. 2006).

Dams, fishing, habitat degradation, hatcheries, climate change, and introduction of non-native species are considered the main causes of salmon population declines in the United States (NRC 1996, Montgomery 2003). Many salmonids that occupy dammed rivers have precariously low population levels and have recently been listed as either threatened or endangered under the United States Endangered Species Act (NRC 1996, Montgomery 2003). Coincident with these listings, the removal of aging and uneconomical dams is now considered a viable river management and salmon restoration alternative in the United States (Stanley and Doyle 2003). Over 500 dams have been removed in the past two decades, with over 20% of these removed since 1999 (Stanley and Doyle 2003). Over 75,000 dams greater than 2 m in height have been constructed in the United States (Graf 1999), and approximately 85% of those dams will reach the end of their operational design life by the year 2020 (Stanley and Doyle 2003). The number of case studies examining effects of removing of small dams (<15 m high) is increasing (Stanley and Doyle 2003), but removals

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of large dams (>30 m in height) with historically large populations of salmonids are rare. The Elwha River in northwestern Washington is one such case where large dams have impacted aquatic habitat condition and salmonid populations, but are scheduled for removal for the purposes of salmonid restoration.

The Elwha River dams have blocked upstream migration of salmonids to over 90% of the watershed for over 90 years and have disrupted the downstream movement of habitat forming inputs such as sediment and wood. Together this has resulted in a loss of spawning and rearing habitat upstream of the dams, as well as reduced spawning and rearing habitat below the dams due to habitat degradation. The result of this and other impacts has led to a 90% reduction of salmonid population size, a loss of specific upstream stocks, and a shift in species composition.

Simultaneous removal of the two large dams on the Elwha River will begin pending the completion of infrastructure (Duda et al. 2008). How will ecosystem processes such as primary and secondary production (Morley et al. 2008), stream channel and floodplain dynamics (Kloehn et al. 2008), and aquatic habitat conditions change with the removal of the Elwha River dams? How will changes to these processes and conditions affect resident and anadromous fish communities? The Elwha poses a unique situation because the action will allow existing salmon populations to access and recolonize nearly pristine habitats above the dams. Dam removal will also cause large-scale sediment disturbance that will impact salmon populations and their ability to recolonize. The salmonid populations will thus have expanded habitat and broad-scale impacts occurring simultaneously. Additionally, extant resident salmonid populations above the dams will be exposed to anadromous colonizers. These resident salmonids will also be able to freely migrate downstream.

We provide data on the impacts of the Elwha River dams to aquatic habitat and salmonid populations, develop a list of factors that affect salmonid recolonization, and develop species-specific predictions of salmonid response to the planned dam removals. Providing an ecological context of the impacts of the dams is necessary because our recolonization hypotheses are based both upon the long-term impacts of the dams as well as the effects their removal. Our predictions of salmonid response to the removal of the dams are based on recolonization hypotheses which focus on salmonid response to increased habitat availability above the dams due to dam removal, reduced habitat quality below the dams due to increased sediment supply from dam removal, and the role of resident populations in reducing or accelerating anadromous salmonid population response.

Study Area

The Elwha River flows for 72 km from its source in the Olympic Mountains to the Strait of Juan de Fuca on Washington State's Olympic Peninsula (Figure 1) (Duda et al. 2008). It drains 833 km^2, with 83% of the watershed protected within the boundaries of Olympic National Park. Historically the Elwha River had 10 anadromous fish stocks (Table 1). Construction of two dams without fish passage facilities on the Elwha River at rkm 7.9 in 1912 and 21.6 in 1925 directly reduced accessible habitat for anadromous salmonids by 90% (DOI 1996). This resulted in the immediate decline of several "upriver" life history types including spring Chinook salmon, pink salmon, summer steelhead, sea-run cutthroat, and anadromous char. It is also a major contributor to the current population status of all 10 anadromous salmonids, several of which are either critically low or extirpated (DOI 1996). The combination of blocking upstream migration and overall loss of anadromous salmonids has also led to a potentially significant decline in marine derived nutrients (MDN) levels throughout the Elwha River Basin, which can effect aquatic and terrestrial ecosystem productivity (Gende et al. 2002).

Methods

To assess existing impacts due to the Elwha River dams we used: 1) existing information (e.g., peer-reviewed publications, gray literature reports, historical survey information); 2) remote sensing techniques; and 3) field surveys to quantify the change in aquatic habitats and anadromous salmonid populations. We compared current salmonid habitat utilization of aquatic habitats below the dams to examine correlations among habitat type, quality, and salmonid use at several life stages.

Aquatic Habitat

Several types of aquatic habitat data (e.g., habitat types, stream temperature) were available

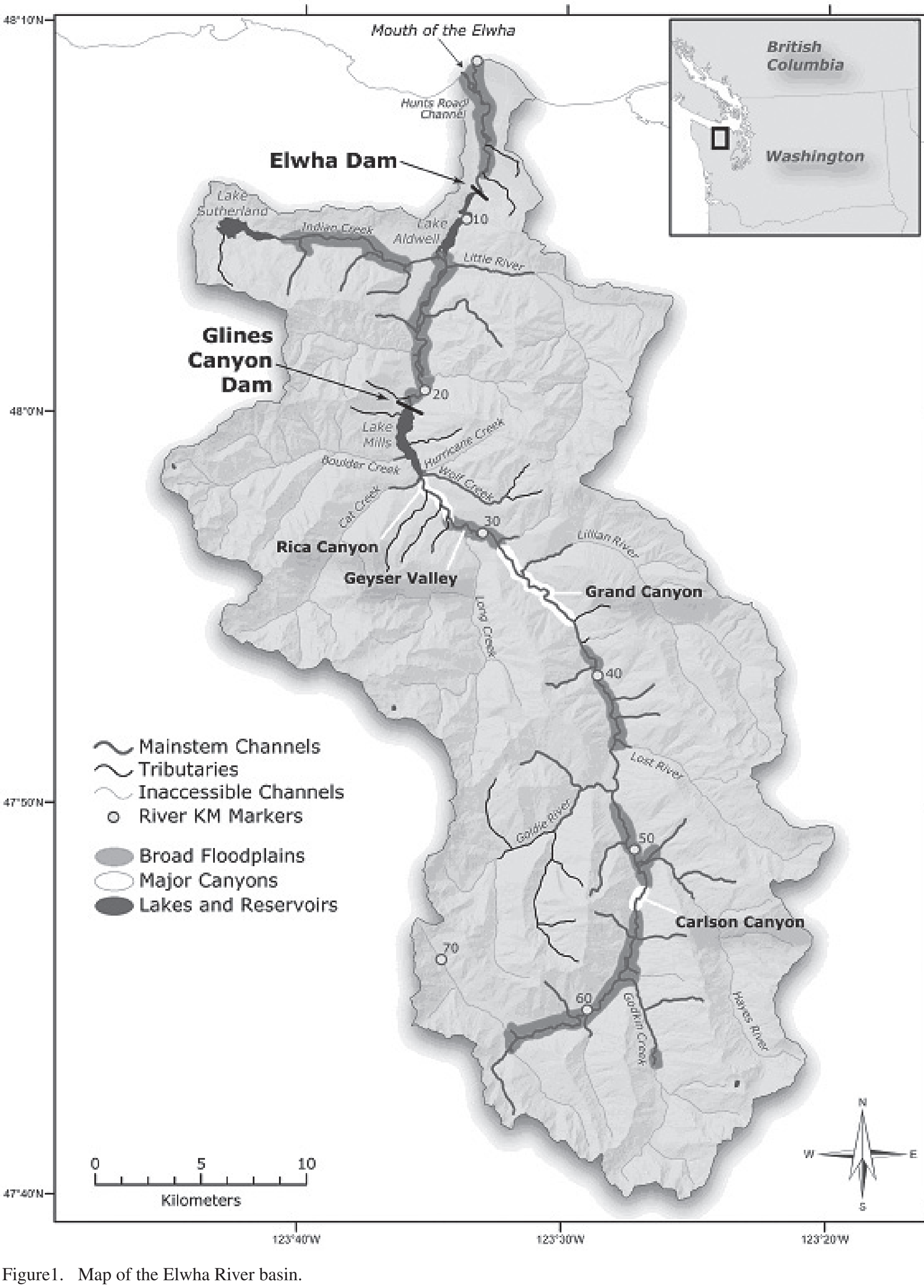

Figure1. Map of the Elwha River basin.

TABLE 1. Anadromous salmonid populations of the Elwha River. Estimated population sizes following dam removal (DOI 1994, see Winter and Crain 2008) and current population sizes (McHenry et al. 2000) based upon escapement estimates.

Species	Estimated Population Size	Estimated Current Escapement	Hatchery Contribution (%)
Spring Chinook	9120[1]	unknown	50 (WDFW 1993)
Summer/Fall Chinook	21280[1]	3000	unknown
Coho	30400	2900	76
Chum	3420	1000	0
Pink	266000	150	0
Sockeye	7600	50	0
Winter Steelhead	7980	1800	83
Summer Steelhead	3420	100	0
Sea-run Cutthroat	unknown	unknown	0
Char[2]	unknown	unknown	0

[1]Estimate of spring and summer/fall distribution based upon estimated proportional difference in life histories (McHenry et al. 2000).

[2]Bull trout and brook trout

for reaches of the Elwha River upstream of the dams (Hosey and Associates 1990, Munn et al. 1999), but equivalent data were generally lacking between and below the dams. To supplement existing data sets, we used aerial photographs and field surveys to further quantify habitat conditions. We classified habitat units at the reach scale (i.e., 100's of meters) using attributes such as mainstem channels, floodplain channels, and tributaries as well as at the habitat-scale (i.e., 10s of meters) using attributes such as pools, riffles, and glides (Beechie et al. 2005). For each habitat unit, we measured surface area, estimated in-channel bank cover, and identified the dominant and sub-dominant channel substrate type. In pool habitats we measured residual pool depth (maximum depth minus minimum outlet depth) and the dominant pool forming factor. Floodplain channels were classified by the type of water connectivity to the mainstem. Surface water floodplain channels had a direct mainstem connection during summer low flow. Over-flow channels had a direct mainstem connection only during bankfull or higher flow events. Groundwater channels did not have a mainstem channel connection at their upstream end, but had an identified source of sub-surface flow. Combination channels had each of the preceding characteristics.

We inventoried in-channel wood below Elwha Dam in 2001 and 2002. Our goal was to assess the relationship between wood and habitat (riverine and floodplain) forming processes and then to monitor expected changes in wood loading following dam removal. During low flow periods, individual logs (e.g., snags) (>30 cm diameter, >10 m length) and logjams (accumulations of >50 pieces of wood) were located and measured within the mainstem and floodplain channels of the Elwha River. Individual snags were tagged with a numbered aluminum disc at both ends of the log. A global positioning system (GPS) was used to map each snag and the following parameters were recorded: taxon, decay factor (1 to 5), orientation, diameter at breast height, diameter at top, overall length, and root wad area. Logjams were also located using GPS and the following features measured: average height, width, and length; the number of key pieces within and their orientation; and an estimate of the number of logs stacked on each other within the jam (Abbe et al. 2002).

We used sequential aerial photographs and conducted interviews with both short-time observers and one long-time observer of fish populations in the Elwha River to document changes in spawning area used by large concentrations (20 or more pairs) of adult salmonid spawners over time. Aerial photographs (National Park Service and Washington State Department of Natural Resources) for the years 1939, 1955, 1974, 1990, and 2002 were used to document spatial changes in spawning area. For each photo year, we asked observers to locate areas that supported consistent spawning activity of pink and Chinook salmon. The recent observers were typically fisheries biologists or technicians who have worked on the Elwha River since the late 1980's. Long-term observers were typically fisherman who had spent > 50 years on the Elwha River. We selected these taxa as indicators of overall spawning activity because water clarity and flow conditions during their late summer/early fall spawning period maximize detectability. Once identified as a significant spawning site on the aerial photograph, a polygon was drawn to approximate the spawning area for each year analyzed. We used a geographic information system (GIS) to conduct spatial analysis and graphically display changes in spawning area over time.

Salmonid Habitat Utilization

We assessed the spatial distribution of adult spawning Chinook salmon in the lower Elwha River from 2000-2003. Spawning ground surveys were conducted by boat or on foot at 7-10 day intervals between August 1-October 15 in the mainstem and large floodplain channels of the lower Elwha River to enumerate spawning populations. During each survey, we located active salmon redds and recorded their location using GPS, and measured stream depth, stream velocity, substrate size, habitat type, distance to streambank, distance to pool, and distance to nearest accumulation of woody debris.

Snorkel surveys were used to quantify the seasonal distribution and abundance of all juvenile and adult salmonids below the Elwha dam. All juvenile and adult fish species were identified and their lengths visually estimated during the snorkel surveys. Fish censuses were conducted by dividing each habitat unit into three or four sections of similar size (snorkel lanes). An observer in each lane moved upstream to count and identify each fish. On several occasions multiple snorkel counts occurred within the same unit in order to estimate observer variation (Hankin and Reeves 1988). We calculated fish abundance as the number of species observed by size class of fish per habitat unit (m^2). We completed habitat surveys prior to any juvenile and adult enumeration efforts in order to: 1) identify the distribution of habitat types within each reach; and 2) select which habitat units to sample for juvenile salmonid distribution and abundance.

Daytime snorkel surveys were conducted when water temperatures were >10 °C because salmonids do not seek refuge in the substrate during daylight hours (Hillman et al. 1992). This allowed for an entire census of all main stem habitats and the largest floodplain channels below the Elwha dam. Night snorkels within selected habitat units were necessary during the winter and spring as juvenile salmonids generally seek refuge in the substrate during daylight when water temperatures are < 10 °C (Hillman et al. 1992, Roni and Fayram 2000).

Intrinsic Potential Maps

We combined topographic data, potential migration barriers, existing salmonid habitat utilization data from below the dams, and salmonid habitat preferences to develop intrinsic potential spawning maps for six salmonid species. Reach-level channel characteristics (slope and width) and valley form were derived from topographic data using hydrologic and terrain modeling, respectively (Davies et al. 2007, Jenness 2006). Salmonid barrier data from previous studies in the Elwha were used to identify limits to salmonid extent for each species (Hosey and Associates 1990, Brenkman et al. 2008). Current juvenile and adult habitat utilization data below the dams were used to identify the relative importance of general habitat types such as differences in mainstem and floodplain channel use. Lastly we used species-specific information on spawning habitat preferences based on stream channel slope and bankfull width (Groot and Margolis 1991, Montgomery et al. 1999).

Results

Impacts of the Dams

The primary impact of the Elwha dams on the Elwha River ecosystem is the longitudinal disconnection of the upper and lower portions of the watershed (Figure 1). This has resulted in two main effects. The first is that salmon are blocked from migrating upstream above rkm 7.9 and subsequently utilizing most of the watershed. Second, disruption in the downstream movement of sediment and wood has caused habitat degradation and reduced habitat complexity between and below the dams (Kloehn et al. 2008). Habitat loss and degradation have affected the distribution and abundance of juvenile and adult salmonids, and have played a major role in the decline in salmonid populations in the Elwha since dam construction (Table 1).

Blockage to upstream migration

Approximately 90% of the potential salmonid spawning and rearing habitat in the Elwha River basin has been inaccessible for over 90 years. As much as 146 km of mainstem and tributary habitat are blocked to anadromous salmonids above the dams (Hosey and Associates 1990, Munn et al. 1999). However, those estimates did not consider floodplain channel habitats in seven low-gradient, alluvial valley bottoms, which constitutes an additional 41 km (28%) of the total area of available habitat in the Elwha River.

Loss of access to these reaches has reduced habitat capacity for salmonid populations, and also led to decreased life-history diversity (Beechie et al. 2006). For example, historically the majority of spring Chinook, pink salmon, and summer steelhead migrated upstream above Elwha dam in the late spring and early summer to access river habitats that have more suitable temperatures for holding and spawning (Figure 2). Over the last 90 years such habitat has not been accessible and spring Chinook could only utilize the lower Elwha, where peak summer temperatures typically reach 18-21 °C.

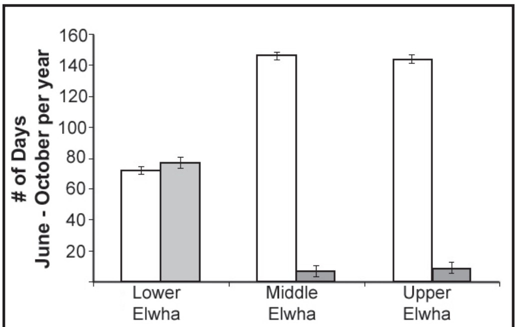

Figure 2. Days per year (SE) of preferred (open) and detrimental (grey) temperatures for incubation of Chinook salmon embryos in the Elwha River during 1992 to 1996.

Loss of salmonid spawning habitat

The construction of the Elwha dams truncated the alluvial transport of sediment which has resulted in the coarsening of river bed in the middle and lower Elwha (Pohl 2004), leading to the loss of salmonid spawning habitat below the dams (Figure 3). From 1939 to 2002, the lower Elwha River lost over 75% of the available spawning habitat for salmonids. The decline in spawning area was initially slow following dam construction. The number and average size of spawning sites was similar between the 1939 (22) and 1956 (23) photo years, and the total area of habitat declined by less than 25% (Figure 3). The number of sites decreased from 23 in 1956 to 13 in 1971 and available spawning area decreased by 60% from 1956 estimates. By 1990 only 12 significant spawning sites remained in the lower Elwha and the total spawning area had decreased another 60% from 1971 estimates. Between 1991 and 2002 the decline in spawning area was reversed, as the river shifted course into the Hunt's Road channel (HRC), exposing a relatively large area of newly created spawning habitat. The fifteen additional spawning sites include a total area of 19,000 m^2, an increase of 56% from 1991.

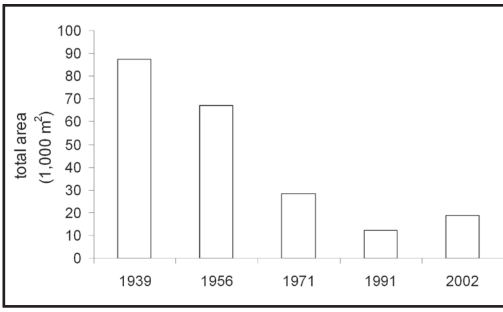

Figure 3. Total salmon spawning area in the lower Elwha River between 1939 and 2002.

A loss of in-channel wood

Wood loading, in the form of snags and logjams, below Elwha dam was four times higher in floodplain channels than in the mainstem (Figure 4). In the lower river, the majority of wood was mostly found in two locations – the HRC (rkm 2.5 to 1.5) and in the mainstem immediately above tidewater (rkm 0.5 to 0.3). Over half of the snags below the Elwha dam were associated with the HRC (Figure 4). Three large logjams that fully spanned the HRC accounted for most of the wood volume in the entire lower Elwha. Tracking individual piece locations in the lower Elwha between years showed that the majority of key, immobile pieces in the floodplain channels were derived from local sources of wood such as patches of mature floodplain forest immediately upstream, rather then the fluvial transport of wood from locations further upstream.

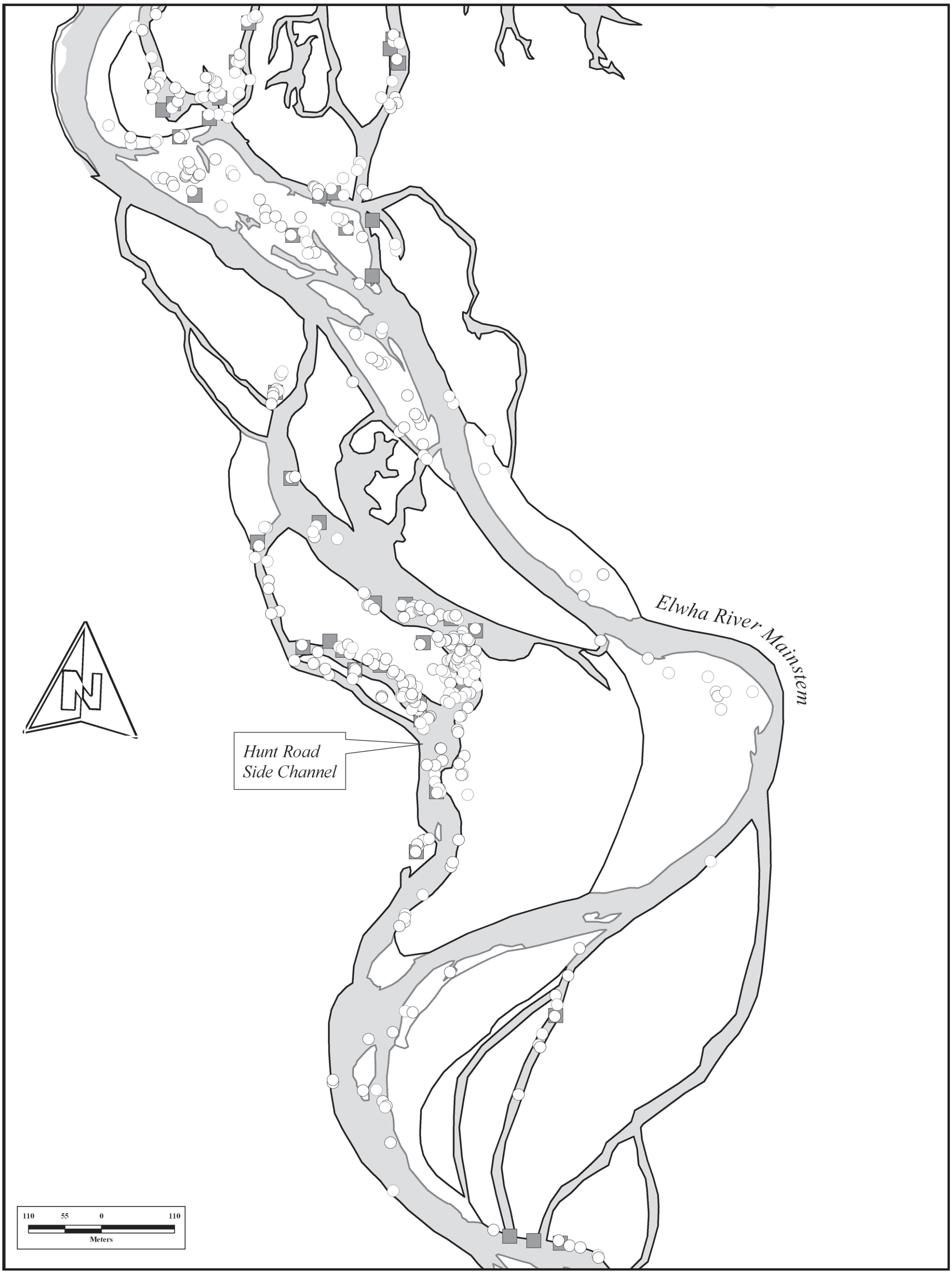

Figure 4. Overhead view of large wood snags (open circles) and logjams (grey squares) in the Hunt's Road channel and mainstem lower Elwha River (rkm 1.5 to rkm 2.5).

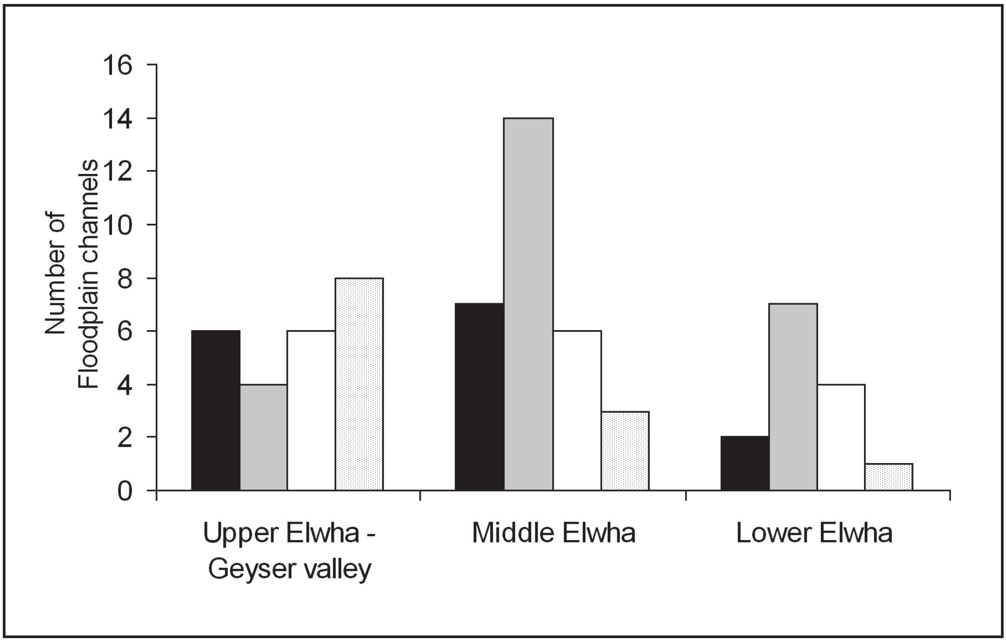

Figure 5. Number of overflow (black), surface water (grey), ground water (open), and combination (dotted),channel types in floodplains in Geyser Valley (above the dams; rkm 32.0 to 28.1), middle Elwha, and lower Elwha.

The continued importance of floodplain channels

An inventory of floodplain channels in the Geyser Valley (the first main valley in the upper Elwha), middle Elwha, and lower Elwha River revealed that approximately 80% of the floodplain channels had flowing water connected to the mainstem, however the type of low-flow connectivity to the mainstem varied by valley location (Figure 5). Geyser Valley had a relatively even distribution of water connection types with the majority being a combination of surface and groundwater connected channels (33%). The middle and lower Elwha were dominated by surface water connections (47% and 50%, respectively), whereas the number of combination channels were less than all other channel types (10% and 7%, respectively).

Salmonid distribution and abundance

We found between 25% and 40% of coho, Chinook, and rainbow/steelhead juveniles in the HRC (Figure 6a). The density of juvenile rainbow/steelhead in the mainstem was greatest immediately below the Elwha dam. This canyon reach also had the highest stream channel gradient (>1%), the least amount of accessible floodplain area, and highest density of boulders and bedrock outcrops in the lower Elwha. Juvenile coho salmon densities were highest in the mainstem between rkm 3.0 and 4.0. These relatively high densities were associated with logjams, as the mean density of 0.05 fish/m^2 in logjams was an order of magnitude higher than the mean density in non-logjam locations (0.005 fish/m^2) (Pess et al. 2003a). The highest densities of juvenile Chinook salmon were found near the mouth to rkm 1.0 (Figure 6a).

Juvenile salmonid density was typically higher in floodplain habitats than in mainstem habitats and varied with water source (Figure 7). Water connection type was associated with salmonid species distribution in the lower Elwha. We found that over 85% of the salmonids in groundwater dominated channels were coho salmon, while 70% of the salmonids in surface-water channels were trout of varying size classes.

Species overlap was much greater for adults than for juveniles (Figure 6b), with the highest densities of adults between rkm 1.5–2.5 and rkm 5.0–6.0. As with juvenile salmonids, high densities of adult salmonids between rkm 1.5 and 2.5 were associated with the HRC (mean density of 0.02 fish/m^2 in the HRC versus 0.004 fish/m^2 in the

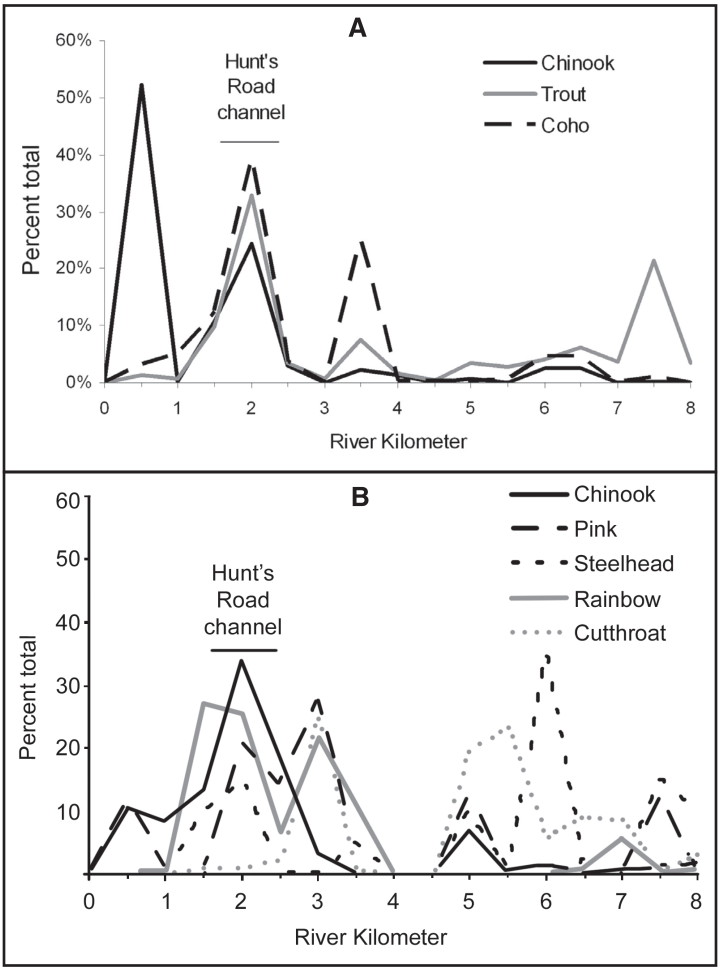

Figure 6. Distribution by river km of (a) juvenile Chinook, trout, and coho in the lower Elwha during the summer of 2002 and (b) adult Chinook, steelhead, rainbow trout, and cutthroat in the summer of 2003. Based upon snorkel surveys.

main channel). The majority of adult salmonids observed between rkm 5.0- 6.0 were associated with several large pools and glides.

Reduction of salmonid populations

Historic estimates of the total anadromous salmonid population is estimated between 380,000 to 500,000 annual returns (DOI et al. 1994, DOI 1996, Munn et al. 1999). The historic relative abundance of species, in descending order, is estimated as: pink, chum, coho, Chinook, steelhead, and sockeye salmon (DOI et al. 1994; DOI 1996; Munn et al. 1999; Gregory et al. 2002). Between 1990 and 2000 the average number of salmonids migrating to the Elwha was 5,500 (<5000 – 19,800)—a large-scale reduction from historic estimates (McHenry et al. 2000). Seven of ten native salmonid stocks are at critically low levels including spring Chinook salmon, pink salmon, chum salmon (*O. keta*), sockeye salmon (*O. nerka*), summer steelhead, cutthroat trout, and bull trout (Wunderlich et al. 1994, McHenry et al. 2000). Summer Chinook salmon, coho salmon and winter steelhead are currently supported by hatchery production. Estimates of relative abundance have also shifted with the majority of salmonids in the Elwha today being coho salmon, Chinook salmon, steelhead, chum salmon, pink salmon and sockeye salmon, although it is not known if sockeye are strays or a remnant spawning population. The three most numerous species all have a significant hatchery influence (Table 1) (McHenry et al. 2000). Snorkel surveys of all mainstem and major floodplain channel habitats below the dams during the summer months of 2002 and 2003 indicated that the majority of adults were Chinook (GRP, personal observation). Coho tended to be the dominant adult species during the fall, and steel-

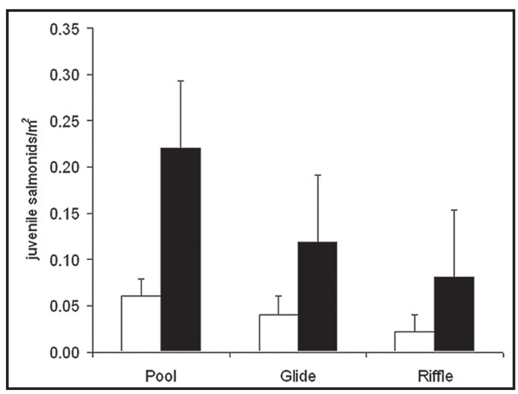

Figure 7. Juvenile salmonid density (#·m^{-2} with SE) by habitat type in mainstem (open) and floodplain (black) channels of the lower Elwha river.

head was the most prevalent during the winter (MLM, personal observation).

Discussion

The Elwha River dams have disconnected the upper from the lower portion of the Elwha watershed for over 90 years. This has blocked anadromous salmonid migration from access to the majority of salmonid spawning and rearing habitat in the watershed. In addition the dams have altered the life forms of specific salmonids such as char, rainbow trout, and cutthroat trout by isolating resident populations above the dams, and creating habitats for potamodromous life histories. The dams have also disrupted the downstream movement of both sediment and wood, which has reduced the quantity and quality of salmon habitat, as well as salmonid abundance and distribution. Remnant populations persist below the dams and are associated at the juvenile and adult life stage with floodplain habitats. Summarizing and understanding these impacts is important because the factors influencing recolonization of anadromous salmonids to the areas above the dams will be a function of the long-term impacts as well as the effects of dam removal.

Factors Affecting Salmonid Recolonization

We began identifying variables affecting salmonid recolonization with two questions in mind. What are the key factors that determine salmon recolonization success? How do differences in salmonid species, population dynamics, and habitat conditions affect salmon recolonization success? To answer these questions it is important to understand two alternative behaviors that affect salmon recolonization — homing and straying (Hendry et al. 2004). Homing is the return of mature salmon to the general location of their natal site (e.g., where their parents bred) to spawn, whereas straying is the return of mature salmon to a non-natal site to spawn (Hendry et al. 2004). The majority of salmon home to their natal sites, though straying is the behavior that has allowed salmonid populations over the course of thousands of years to colonize new habitats (Quinn 1984, Hendry et al. 2004).

Salmonids can quickly colonize new habitats and establish self-sustaining populations (Hendry et al. 2004). For example, in deglaciated streams of southeast Alaska, multiple 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, natural colonization has led to self-sustaining populations within 1 to 5 years (Bryant et al. 1999, Glen 2002, Pess et al. 2003b). Recolonization and establishment of pink salmon in the Fraser River above Hell's Gate landslide required approximately 20 to 30 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 conditions may favor increased growth and survival at key life stages, resulting in higher population growth rates that lead to self-sustaining populations (Withler 1982). Colonization can also lead to divergence of life history traits over decadal time frames (Kinnison et al. 2001). 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 small number of successful colonization efforts, both natural and artificial, among hundreds of attempts. 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.

The persistence of self-sustaining populations in newly opened 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, 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 2). 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 will allow for

TABLE 2. Factors affecting salmonid recolonization.

Factor	↑ Dispersal and Recolonization	↓ Dispersal and Recolonization
Barriers to movement	Few, small	Many, large
Distance from source population	Near	Far
Population Size	Large	Small
Population Stray Rate	High	Low
Habitat Area	Large	Small
Adaptation to local habitat	High	Low
Habitat type[1]	Similar	Different
Habitat condition	Good	Poor
Interaction with existing fish population	Positive	Negative

[1]Similarity of habitats between source and recolonized areas

the exchange of individuals within and between populations. The ability to maneuver past natural barriers varies considerably with species and migration timing. For example, steelhead, coho, and Chinook salmon combine swimming ability and appropriate flow levels to successfully maneuver past substantial barriers (Groot and Margolis 1991, Quinn 2005). Chum salmon are not known for their ability to pass natural barriers (Groot and Margolis 1991, Quinn 2005). Pink and sockeye have been known to be affected by modest barriers, but can also maneuver past barriers and rapidly colonize habitats when flows are amenable (Roos 1996). The degree to which char, cutthroat, and brook trout can move past natural barriers are less understood.

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 recolonization.

Population size and stray rate are another set of factors that will influence the dispersal and ability of salmonids to recolonize. Large population size or high stray rates result in relatively more individuals seeking new habitats, creating self-sustaining spawning populations in other reaches of the same watershed or in entirely different watersheds (Pess et al. 2007). Conversely, low population size or low stray rates result in fewer individuals seeking non-natal habitats and reduces the probability of dispersal and recolonization. Stray rate will vary by species (Hendry et al. 2004). For instance pink salmon stray rates average 6% and range between 4 and 34%, while steelhead typically have stray rates that average 7% and range between 5% and 26% (Hendry et al. 2004, Keefer et al. 2005). Within a given species, run-timing and different life history strategies may also result in different stray rates. Keefer et al. (2005) 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. > 20 ºC) for longer time periods than late migrants, increasing the likelihood to temporarily stray into cooler lower Columbia River tributaries. Population stray rates can thus either buffer or enhance the effect of population size.

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. Changing environmental conditions, such as turbidity levels, can play a critical role in the magnitude and timing of salmon colonization and recolonization. The eruption of Mt. St. Helens drastically changed habitat conditions that provoked an immediate straying response in returning adult salmonids. Adult 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, it was uncertain if these strays were productive enough to produce future spawning populations (Leider 1989). Milner and Bailey (1989) compared the density of salmonid colonization in two recently deglaciated, geomorphically similar, and adjacent streams in southeast Alaska. They found that turbidity was a dominant factor influencing spawning density with 2.4 times the spawning density in the stream with lower turbidity. Streams with lower turbidity levels were associated with a higher proportion of preferred spawning temperature range (12 to 15°C), a more attenuated hydrology, and greater intact riparian vegetation structure. In each case colonization and re-colonization occurred and the abundance of eventual 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).

Interactions with existing fish populations will also affect salmonid recolonization potential. Interactions between resident and anadromous salmonids could have a positive or negative effect on the extent and rate of anadromous salmonid recolonization. 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. 2007). 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). Brenkman et al. (2008) provide a more detailed description of resident/anadromous interactions in the Elwha River.

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 population sizes, relatively higher stray 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, relatively lower stray rates, greater variation in their life history, and greater freshwater residence time and complexity, making them 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.

Predicting Salmonid Response to Dam Removal in the Elwha River

The Elwha River dam removal project provides an interesting ecological juxtaposition of habitat expansion and degradation. Factors influencing recolonization are a function of both the impacts of the dams and the effects of dam removal (Table 3). The dams have dramatically reduced habitat availability, altered habitat quality, isolated resident and

TABLE 3. Key factors that can influence salmonid recolonization in the Elwha River.

Factor	Impacts of Dams	Effect of Dam Removals	Effect on Recolonization
Anthropogenic barriers	Loss of habitat availability	Access to spawning and rearing habitat	Attraction to specific specific habitat types
			Natural barriers
			Distance from source population
Sediment	Reduced spawning and rearing habitat below dams	Large-scale increase in sediment supply	Increased straying and "barrier" to migration due to turbidity
			Decreased straying due to sediment management and buffering of sediment effects due to floodplains
			Decrease in spawning habitat quality (short-term)
			Increase in spawnable area (long-term).
Resident populations	Isolation of resident and anadromous populations	Interaction between anadromous and resident fish	Competition and predation between anadromous and resident fish

anadromous populations, and altered the proportion of natural and hatchery fish in the watershed. Dam removal will open large stretches of river above the dams for the first time in nearly a century, allowing anadromous salmonids to recolonize nearly pristine freshwater habitat. Between the dams there will be the simultaneous re-opening of existing salmonid habitat and a large scale pulse of sediment that will change stream channel morphology and salmonid habitat. Changes to channel morphology and salmonid habitat will be even more pronounced in the reservoir sections and immediately below the dams. Much of the change to salmonid habitat will result in unstable channel features such as stream bed aggradation and movement due to an increase in sediment supply for the first five years, which can result in detrimental effects on salmon habitat capacity and survival (Beechie et al. 1996). Anadromous and resident populations in the Elwha will have newly opened habitats to colonize and will have the opportunity to survive from deleterious sediment impacts in existing habitats. We hypothesize that in general salmonids will respond to dam removal by establishing persistent, self-sustaining salmonid populations in the middle and upper Elwha within in one to five generations (two to twenty years) following dam removal.

Chinook salmon are likely candidates to colonize the majority of mainstem and floodplain habitats in the Elwha River (Figure 8a). Their arrival time to the Elwha as returning adults in the late spring and summer potentially allows them to migrate upstream during relatively high flows that typify snowmelt dominated systems in Puget Sound (Beechie et al. 2006, Duda et al. 2008). In addition, their spawn timing in late summer and early fall occurs during the lowest average monthly flows when sediment transport is minimal (USDOI 1994), thus the large increase in suspended sediment due to the dam removals will have relatively less impact on their ability to migrate and find spawning areas. Distance to a source population will be short, as with most salmonid species in the Elwha, and their population size is larger than all other species with the exception of coho salmon. The type of habitat that will become available to Chinook salmon also fits well with their life history strategy of utilizing both mainstem and floodplain habitats for the juvenile and adult life stage (Figures 6a, 6b, and 7), as well as their diverse life history strategies that includes both ocean and stream-type rearing (Beechie et al. 2006). The expression of a stream-type life history strategy may be particularly important due to lower year-round stream temperatures (Figure 2) that may limit juvenile growth rates in the upper Elwha basin.

Spawning behavior above the dams should mimic what currently occurs below the dams, so we expect that mainstem and floodplain channel habitats will initially be colonized by Chinook salmon, as well as steelhead and coho salmon. We hypothesize Chinook salmon will likely utilize the mainstem, and to lesser extent large floodplain channels similar to the HRC in the lower Elwha. The spatial distribution of spawning Chinook salmon in the lower Elwha is currently clumped in four primary locations. These include large floodplain channels and mainstem mid-channel islands. All four sites contain significant deposits of gravels, have flow characteristics typical of Chinook salmon spawning areas, and contain multiple channels. Mid-channel islands and larger floodplain channels will thus have greater densities of salmonids for the spawning life stage (Coulombe-Pontbriand and Lapointe 2004).

The interactions between existing resident populations and juvenile Chinook salmon is an unknown, however there is a potential for resident salmonids to focus their feeding efforts on Chinook (Tabor et al. 2004, Kiffney et al. 2007). Trout were found to consume over 25% of the natural Chinook salmon production in nearby watersheds in the Puget Sound region (Tabor et al. 2004). Juvenile Chinook salmon may increase their exposure to predation in order to obtain additional food resources relative to other salmonid species (Abraham and Healey 1993). In addition, spawning anadromous salmonids are known to attract large trout because of the opportunity to feed on energy-rich eggs or emerging fry (Willson and Halupka 1995).

Coho salmon and steelhead are also likely to colonize the majority of mainstem, floodplain, and tributary habitat made available to them with dam removal due to their initial population size and run timing, ability to maneuver past natural barriers in the canyon reaches, and their propensity to utilize alluvial valley bottoms and tributary habitats (Figure 8a). Distance to a source population for both coho salmon and steelhead is short because both already occur in relatively larger

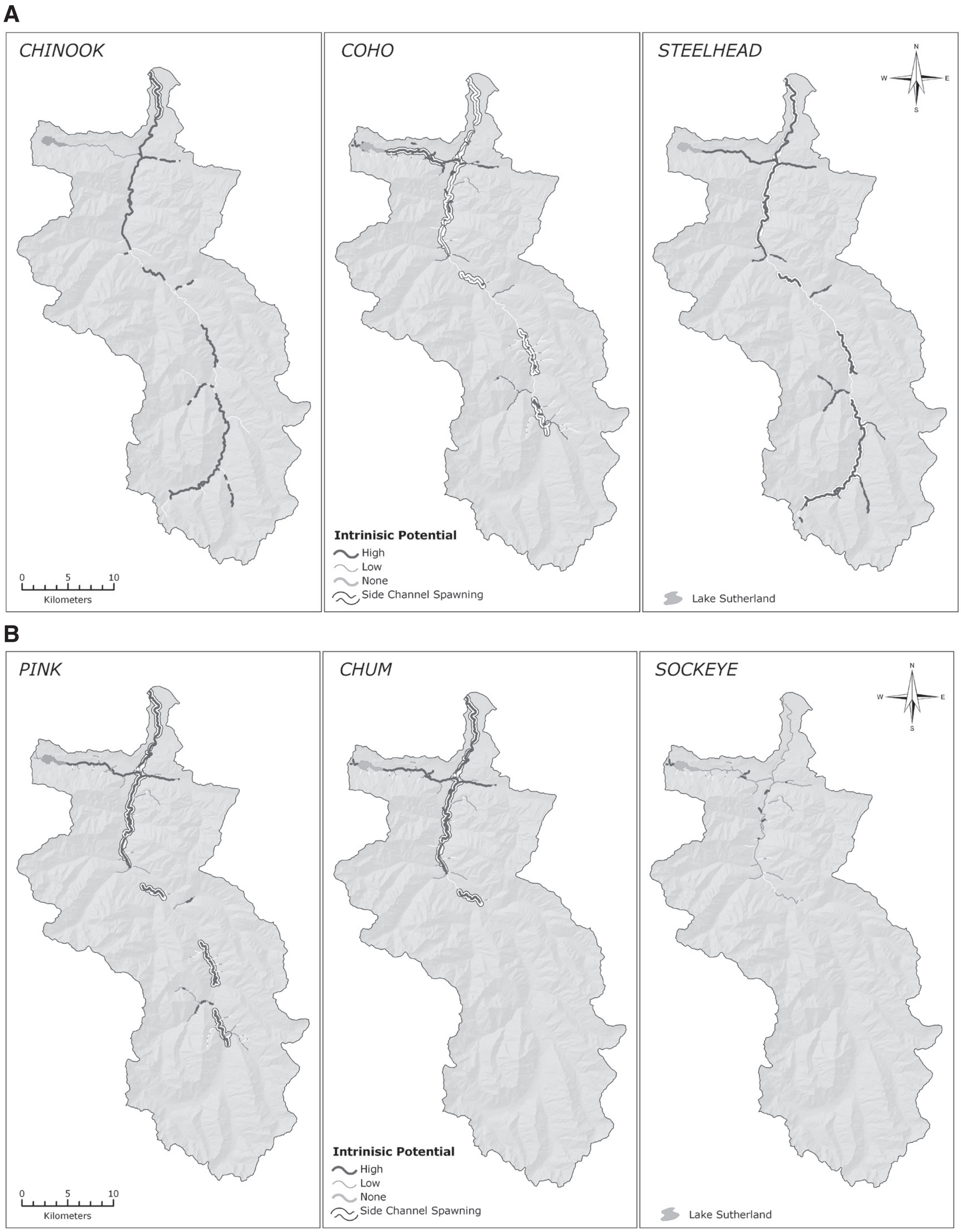

Figure 8. Intrinsic potential maps of (a) Chinook salmon, coho salmon, and steelhead and (b) pink salmon, chum salmon, and sockeye salmon in the Elwha River.

numbers below the dams (Table1). In addition, there is a self-sustaining population of resident *O. mykiss* above the dams (Brenkman et al. 2008) which could be an important contributor to the recolonization of anadromous *O. mykiss* due to interbreeding (Seamons et al. 2004, McMillan et al. 2007).

We hypothesize that migrating and spawning coho salmon and steelhead will face higher sediment loads as their run timing occurs during naturally higher winter and spring flows. Higher turbidity levels during that time period, whether natural or related to dam removal, will thus affect migration into the middle and upper Elwha. However it is uncertain whether this will result in a higher proportion of colonizers due to less desirable conditions in the lower Elwha or more coho salmon and steelhead entirely avoiding the Elwha River.

Both coho salmon and steelhead are more freshwater-dependent than other salmonid species thus their ability to utilize the newly opened mainstem, floodplain, and tributary habitat should be strong. Both species also utilize mainstem margins and floodplain channels below the dams which suggest that the same may occur above the dams. Even though many Elwha tributaries will have limited spawning use due to their steepness (Munn et al. 1999), there are at least stretches of larger, low gradient tributaries in the uppermost portion of the upper Elwha such as Hayes, Lillian, Lost, and Goldie that could be utilized by both coho salmon and steelhead. The middle Elwha could also have rapid tributary colonization by coho salmon and steelhead due to the greater proportion of low gradient tributary habitat relative to mainstem and floodplain habitat. Indian Creek is likely to attract coho salmon because it has a large amount of rearing habitat associated with Lake Sutherland and adjoining wetlands, an important factor in the relative abundance of coho salmon throughout Puget Sound (Pess et al. 2002). Even if adult coho salmon do not colonize tributary and floodplain habitats first, it is possible for juvenile coho to recolonize tributary and floodplain habitats (Anderson et al. in press). The Little River, a major middle Elwha river tributary, may see steelhead play a dominant role in recolonization because the existing rainbow trout populations are most similar to wild Washington coastal steelhead (Phelps et al. 1994).

The current juvenile fish distribution below the dams provides a natural analog to what may occur above the dams. *O. mykiss* typically utilize areas with a relatively higher proportion of higher velocity water and larger substrate habitat types, while coho salmon dominate in habitats where stream velocity is lower, habitat complexity is high due to a greater amount of wood loading, variation in flow is less, and food abundance is high (Milner and York 2001, Pess et al. 2003a). Floodplain channels are typically critical areas for juvenile salmonid utilization (Pess et al. 2005) and such areas occur in the alluvial valley bottoms of the Elwha. Floodplain channel habitat complexity and water source are also likely to affect species distribution and abundance. Similar to the lower Elwha, we hypothesize that groundwater influenced channels will be dominated by one or two species such as coho, while more complex surface water dominated channels will have a greater diversity of species.

Pink, chum, and sockeye salmon are unlikely to colonize the majority of habitats throughout the Elwha for mutual and specific reasons (Figure 8b). Historically, the longitudinal extent of pink and chum salmon was up to ~rkm 25, and sockeye were assumed to extend to Lake Sutherland (Winter and Crain, 2008). Today all three species have low population sizes. Thus even though the distance to the nearest source population is similar to Chinook, coho, and steelhead, the total number of potential strays into middle and upper Elwha will likely be small even if the stray rate is high.

Migration timing for pink salmon coincides with periods of low sediment transport in the summer and fall. Summer and fall migration should provide the greatest difficulty in passing likely natural barriers in the canyon reaches due to low flows (Figures 1 and 8b). However, evidence from the Fraser River suggests that pink salmon can effectively migrate past barriers during the summer and fall low flow time periods due to their physiological ability to swim and efficiently migrate to newly opened habitats (MacNutt et al. 2006). Minimal diversity in life history characteristics, a brief time in freshwater, and habitats conducive to spawning such as floodplain channels could positively affect pink salmon recolonization in the Elwha River. Interactions with existing resident fish populations may initially be negative as the small founding populations may produce limited numbers of offspring vulnerable to predation.

Existing population size of Elwha River chum salmon is intermediate to other salmonid populations in the Elwha River (Table 1). Again distance to a source population is short, however the migration and spawn timing of chum salmon in the Elwha (fall and winter) will be limited beyond Rica and the Grand Canyon (Figure 8b). In addition there may be temporary barriers due to elevated sediment loads during that time period. Habitat area and life history adaptation to local habitat characteristics should be favorable to chum salmon due to the large proportion of mainstem and floodplain habitats, while interactions with existing resident fish populations are similar to pink salmon and assumed to be minimal.

Whether or not sockeye salmon will re-establish a self-sustaining population is perhaps one of the biggest unknowns of all salmonid species in the Elwha River basin. Small numbers of sockeye are seen every year in the lower Elwha (Table 1), and there is an established kokanee salmon population in Lake Sutherland. However sockeye recolonization potential is unknown for several reasons. First, distance to source population is unknown because sockeye in the lower Elwha could be strays from another population or a small, persistent Elwha River population. Second, resident kokanee populations typically do not contribute significantly to the overall anadromous population (Foerster 1947, Kaeriyama et al. 1992) and may produce offspring that are maladapted to anadromous migrations (Taylor and Foote 1991). Finally, there has been alteration to the Lake Sutherland lakeshore due to development; potentially, habitat conditions are not as conducive to sockeye salmon spawning as historically was the case.

Summary and Conclusions

We identified several key aspects of salmon ecology that will affect recolonization following dam removal. Barriers to migration, distance from a source population, source population size, stray rates, the amount, quality, and type of habitat in relation to specific life stage needs, and interactions with existing fish populations will determine salmonid recolonization on a species-specific basis. Barriers to movement will affect some species such as chum salmon, sockeye salmon, and pink salmon more so than others such as Chinook salmon, coho salmon, and steelhead. Although distance from a source population is minimal for all species, it is uncertain whether pink salmon, chum salmon, and sockeye salmon are currently self-sustaining. Stray rates, which naturally vary among taxa, will further vary as a function of migration timing and associated turbidity levels during and following dam removal. Habitat area, type, and condition are the most certain variables in the upper Elwha, while conditions in the middle and lower Elwha will also depend upon the amount, timing, and composition of sediment. Interactions with existing fish populations will likely be positive for life forms that have both a resident and anadromous component, but may vary for the newly reintroduced species such as Chinook salmon, pink salmon, chum salmon, and coho salmon.

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