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Predicting Recolonization Patterns and Interactions Between Potamodromous and Anadromous Salmonids in Response to Dam Removal in the Elwha River, Washington State, USA

Abstract

The restoration of salmonids in the Elwha River following dam removal will cause interactions between anadromous and potamodromous forms as recolonization occurs in upstream and downstream directions. Anadromous salmonids are expected to recolonize historic habitats, and rainbow trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) isolated above the dams for 90 years are expected to reestablish anadromy. We summarized the distribution and abundance of potamodromous salmonids, determined locations of spawning areas, and mapped natural barriers to fish migration at the watershed scale based on data collected from 1993 to 2006. Rainbow trout were far more abundant than bull trout throughout the watershed and both species were distributed up to river km 71. Spawning locations for bull trout and rainbow trout occurred in areas where we anticipate returning anadromous fish to spawn. Nonnative brook trout were confined to areas between and below the dams, and seasonal velocity barriers are expected to prevent their upstream movements. We hypothesize that the extent of interaction between potamodromous and anadromous salmonids will vary spatially due to natural barriers that will limit upstream-directed recolonization for some species of salmonids. Consequently, most competitive interactions will occur in the main stem and floodplain downstream of river km 25 and in larger tributaries. Understanding future responses of Pacific salmonids after dam removal in the Elwha River depends upon an understanding of existing conditions of the salmonid community upstream of the dams prior to dam removal.

Introduction

The Elwha River was historically a highly productive river for anadromous salmonids on the Olympic Peninsula, Washington, and is one of the few rivers that supported all anadromous salmonids native to the Pacific Northwest (Wunderlich et al. 1994). Dam construction from 1910 to 1913 prevented anadromous fish from accessing over 130 km of habitat, most of which occurs in Olympic National Park (ONP). Within the next few years, the National Park Service (NPS) is scheduled to remove the Elwha and Glines Canyon dams in one of the largest river restoration projects in the United States.

The removal of the Elwha dams poses a unique situation that will allow existing anadromous salmon populations to regain access to nearly pristine habitats upstream of the dams in ONP. Large-scale disturbance is expected downstream of the dams as accumulated sediments (~18 million m^3) erode from the reservoirs following dam removal. Increased levels of sediments are expected to have a major impact on the ability of anadromous salmonids to recolonize the upper river. Consequently, the returning salmonids will simultaneously face expanded habitats in the river upstream from the dams and habitat related impacts from newly released sediments in those areas downstream of the dams.

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Populations of rainbow trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) isolated above the dams for nearly a century will be exposed to competitive interactions with anadromous colonizers after dam removal. These potamodromous forms will likely migrate downstream and resume anadromous life history forms after dam removal making for an upstream and downstream recolonization of the watershed. We use the term potamodromous to differentiate between rainbow trout and bull trout above the dams from their anadromous counter parts that occur downstream of Elwha Dam. Potamodromous fishes migrate entirely within freshwater (Myers 1949). We believe that "potamodromous" most precisely defines the populations above the dams, and eliminates the use of other common substitutes such as "non-anadromous" that only defines what a fish is not (Gresswell 1997).

A major question related to dam removal pertains to how potamodromous salmonids will interact with their anadromous counterparts after dam removal. Interactions between the two life history forms could negatively affect the extent and rate of anadromous salmonid recolonization. Interspecific competition is affected by both habitat quality and fish density (Harvey and Nakamoto 1996, Volpe et al. 2001). Low levels of habitat complexity can lead to greater competition and result in growth and survivorship 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).

Interactions between potamodromous and anadromous salmonids may positively affect colonization of a watershed. For example, potamodromous rainbow trout and bull trout that migrate downstream may increase the extent and rate of colonization by spawning with their anadromous counterparts. The interaction between the two life history forms may increase the overall number of spawners immediately following dam removal. A recent study on the Olympic Peninsula suggests that resident rainbow trout and anadromous steelhead trout spawn together throughout an entire watershed (McMillan et al. 2007). Purely resident life forms of *O. mykiss* can also colonize downstream areas, spawn, and contribute to the anadromous population by producing a small percentage of the emigrating smolts (Ruzycki et al. 2003). Similarly, coastal bull trout co-occur as anadromous and non-anadromous forms on the Olympic Peninsula, and females of both forms produce progeny that are anadromous (Brenkman et al. 2007).

The opportunity to begin a long-term study of Pacific salmonids and species interactions in the context of dam removal and river restoration in the Elwha River requires an understanding of existing conditions of the fish community prior to dam removal. Our goal is to formulate hypotheses about the interactions between salmonids with potamodromous life forms and their anadromous counterparts after dam removal. Here, we summarize existing data on natural migration barriers and the current spatial extent, relative abundance, and distribution of potamodromous life forms at the watershed scale. This information will allow us to predict: 1) where in the watershed these interactions will occur, and 2) at which life stages these interactions will occur. We focus on these questions with respect to bull trout, rainbow trout, brook trout, and to a lesser extent, cutthroat trout.

Study Area

The Elwha River flows 72 km from glaciers and icefields, drains 833 km^2, and descends in elevation from 1,372 m at the headwaters to its confluence with the Strait of Juan de Fuca. Over 80% of the watershed is protected within the boundaries of ONP, with 83% of the river kilometers within the park boundary (Figure 1). Two hydroelectric dams were constructed without fish passage facilities at river kilometer (rkm) 7.9 in 1912 and rkm 21.6 in 1925. Anadromous salmonids currently have access to 7.9 km immediately downstream of the Elwha Dam (Figure 1). The impoundments created by the dams, Lake Aldwell and Lake Mills (Figure 1), are 4 km long and 108 hectares and 4.5 km long and 168 hectares, respectively.

A total of 8 anadromous salmonid species inhabit the Elwha River downstream from Elwha Dam including Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), steelhead trout, cutthroat trout (*O. clarkii*), and bull trout. Hatchery programs currently supplement populations of coho salmon, Chinook salmon, and winter steelhead trout in the lower river. Non-salmonid species below Elwha Dam include sculpin (*Cottus spp.*),

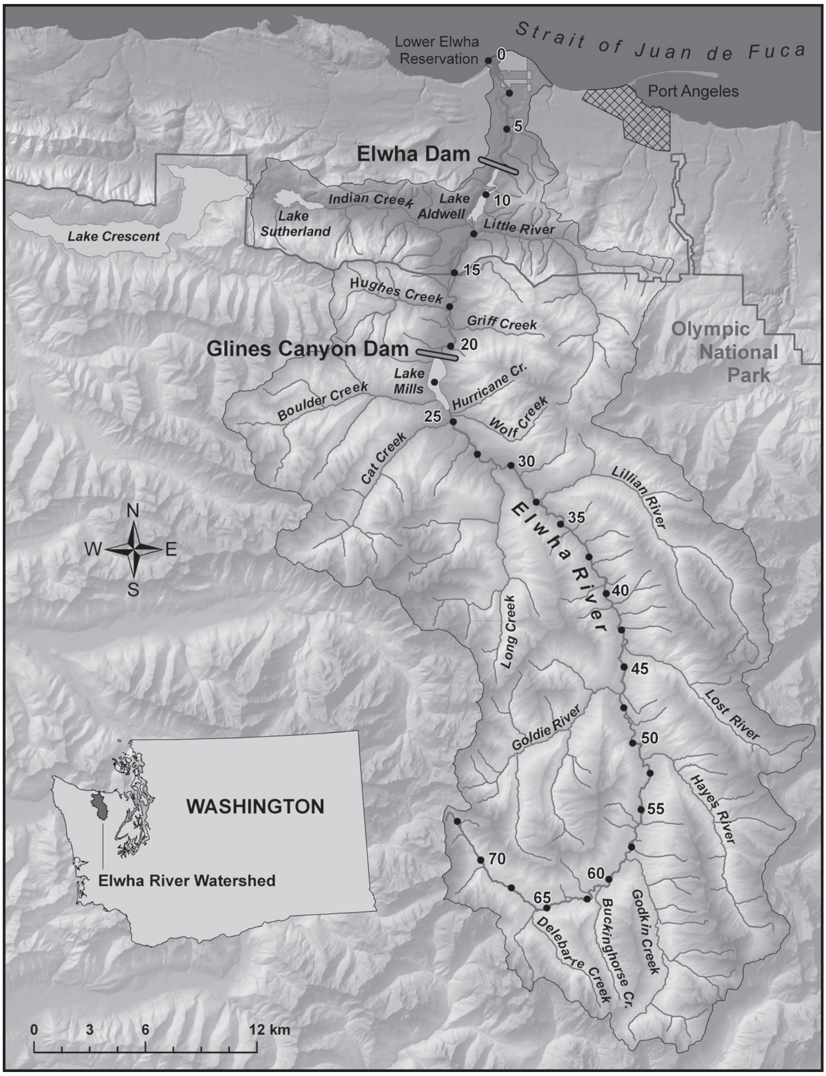

Figure 1. Study area and location of hydroelectric dams in Elwha River Basin. Distance upstream from the river mouth is indicated in kilometers.

threespine stickleback (*Gasterosteus aculeatus*), Pacific lamprey (*Lampetra tridentata*), eulachon (*Thaleichthys pacificus)*, and surf smelt (*Hypomesus pretiosus)*. Sockeye salmon are considered extirpated, but kokanee salmon (*O*. *nerka*) exist in Lake Sutherland. Populations of bull trout, rainbow trout, non-native brook trout, and sculpins exist between the two dams. Redside shiner (*Richardsonius balteatus*) occur in Indian Creek (Jack Ganzhorn, Peninsula College, unpublished data). In areas upstream of the dams, populations of bull trout, rainbow trout, and cutthroat trout occur, with cutthroat trout being limited to Long Creek. Non-native brook trout were planted in tributaries and lakes in the upper basin until 1976.

Methods

Recent studies afford a unique opportunity to examine spatial extent, relative abundance, and distribution of life history forms of potamodromous salmonids in the Elwha River basin. We compiled and reviewed published and unpublished records of data collected from 1993 to 2006 (e.g., ONP, fisheries data archives). Our analysis revealed that these studies collectively offered important baseline information on potamodromous fish species in the basin. The collection methods and protocols for these studies were similar but not identical, and sampling effort was not standardized among all years. Consequently, we limited our analyses to the identification of broad-scale patterns of distribution and relative abundance of bull trout, rainbow trout, and brook trout. We assumed that no Dolly Varden (*Salvelinus malma*) were present in the Elwha River.

Our analysis was based upon the Elwha River having three main sections, delineated by the presence of the dams. The lower river occurred below the Elwha Dam, the middle river occurred between the dams and included Lake Aldwell, and the upper river occurred upstream of the Glines Canyon Dam, including Lake Mills.

Habitat Data

We used field surveys of anadromous salmonid habitat conducted by James River (1988 a, b) to map perennial and seasonal velocity barriers in the main stem and tributaries of the Elwha River. We approximated the locations of barriers by comparing tributary junction-to-barrier distances measured by James River (1988 a, b) in the field to distances measured on digital hydrographic maps derived from 1:24,000-scale U.S. Geological Survey (USGS) topographic quadrangles. Map manipulations and distance calculations were performed using a geographic information system (GIS). Although some discrepancy existed between the respective scales of distances measured in the field and those derived from digital hydrographic maps, the spatial accuracy of barrier locations was sufficient for assessing broad-scale patterns of accessible tributary habitat to anadromous salmonids. River channel gradient (%) was calculated as the change in elevation in meters divided by river section length measured on USGS 30-m digital elevation models (DEM) and 1:24,000-scale topographic maps.

Biological Data

We delineated the distribution of life history stages for each species longitudinally from the Elwha Dam (rkm 7.9) to the headwaters of the Elwha River (rkm 71). The spatial extent and distribution of life history stages was based upon a compilation of data collected by single-pass backpack electrofishing, snorkeling, trapping, gill-netting, or angling throughout the Elwha River basin. First, data were pooled from several sources (e.g., Hiss and Wunderlich 1994, ONP, unpublished data, Morrill and McHenry 1995) into 19 gradient-based reaches that were defined by James River (1988 a, b) and Adams et al. (1995). For sampling purposes, those reaches were sequentially numbered in the upstream direction to the headwaters of the Elwha River. We then pooled the biological data for fish into young-of-the-year (<50 mm), juvenile (>50 to 200 mm), and adult (>200 mm) length classes.

We determined the relative abundance of rainbow trout and bull trout in the upper basin by analysis of snorkel surveys that were conducted from Lake Mills to rkm 71 and in the tributaries upstream of Lake Mills by Adams et al. (1995) (Figure 1). These daytime snorkel surveys were conducted throughout three randomly selected sections within a designated river reach. Within each >400 m section of river, a minimum of three riffles, runs, or pools were surveyed (Adams et al. 1995). Divers proceeded in a downstream direction and counted fish by species. Observed fish were classified into length classes of <100mm, 100 to 200 mm, 201 to 300 mm, and >301 mm. Snorkel surveys did not provide information on young-of-the-year fishes.

We also determined the relative abundances of rainbow trout and bull trout based upon extensive snorkel surveys conducted by the NPS, NOAA Fisheries, Lower Elwha Klallam Tribe, and U.S. Fish and Wildlife Service in the river downstream of the Elwha Dam (rkm 7.9 to 0.0) and between the dams (rkm 12.5 to 21.3) in August or September of 1995, 1996, 2000, 2002, 2003, and 2004. In September and October, 2006, snorkel surveys were conducted upstream of Lake Mills from rkm 27.5 to the Lake Mills inlet at rkm 24.6 during the presumed upstream spawning migration of bull trout.

To determine spawning locations of rainbow trout in the middle river and the area immediately upstream of Lake Mills, we conducted spawner surveys in 12 tributaries and in the main stem from rkm 17.7 to rkm 28.9 from April to June, 2006. We conducted spawner surveys for bull trout from rkm 27.5 to 24.6 in September and October, 2006. The estimates of spawn timing for Elwha

River resident rainbow trout, winter steelhead, and bull trout were based on run timing reconstructions for rainbow/steelhead trout in the Quileute River (McMillan et al. 2007) and for bull trout in North Fork Skokomish River from 1994 to 2006 (Brenkman et al. 2001). Both rivers occur on the Olympic Peninsula. We used the proportion of spawners and cumulative distribution of spawning throughout each month to evaluate possible temporal interactions among potamodromous and anadromous species in the Elwha River.

Results

The Role of Physical Barriers

The 7.9 km of main stem habitat currently available to anadromous salmonids in the Elwha River will increase to 71 km following dam removal. Possible seasonal velocity barriers exist in three main stem Elwha River canyons during periods of high river flows (Figure 2)—Rica (rkm 26.1 to rkm 27.3), Grand (rkm 31.1 to rkm 35.3), and Carlson Canyons (rkm 53.0 to rkm 54.5). Rica Canyon consists of bedrock, large boulders, and high-velocity water with several cascades and falls up to 1.8 m in height. The upstream portion of Grand Canyon contains several cascades and low waterfalls, and the lower 2.4 km of Grand Canyon contains approximately 15 cascades and falls. Carlson Canyon has a single waterfall that is 2 m in height (Washington Department of Fisheries 1971).

Seasonal velocity barriers in the Elwha River occur where the river channel is constrained by steep canyon walls and boulder- and bedrock-dominated substratum. Canyon reaches have channel gradients that are up to two times steeper (2% in Rica, Grand, and Carlson Canyons) than the average gradient for the entire 69 km of the main stem river (1%). High-flow events resulting from early winter storms and spring runoff create high-velocity cataracts that may constitute seasonal migration barriers to salmonids moving upstream. In contrast to these steep canyons, other sections of the Elwha River are much more gradual, with gradients of 0.3% from the mouth to Elwha Dam, 0.8% from Elwha Dam to Glines Canyon Dam, and 1.4% from Glines Canyon Dam to the headwaters of the main stem.

There are 49 named tributaries in the Elwha Basin and 125 km of tributary streams (Phinney and Bucknell 1975). None of these named tributary streams are currently accessible to anadromous salmonids. After dam removal, accessible tributary habitat will increase by 16 km between the dams and 28 km upstream from Glines Canyon dam. Twelve streams each contain at least one kilometer of available salmonid habitat (Figure 2), although quality of spawning and rearing habitat is unknown. Because of the steep topography throughout the basin, the total area of accessible tributary habitat to anadromous salmonids is limited in the Elwha River basin, occurring primarily above rkm 45 in the Goldie River, Hayes River, and Godkin Creek (Figure 3).

Historic Spatial Extent of Anadromous Fish

Scientific study of pre-dam distribution and abundance of Pacific salmonids is unavailable and information on historic distributions is limited to recollections of residents, incomplete written records, and testimony of Indian elders (DOI et al. 1994). Presumed historic distributions of Pacific salmonids suggest that summer steelhead trout and spring/summer Chinook salmon extended up to rkm 71 (Figure 3). Winter steelhead trout and coho salmon also were distributed in the uppermost portions of the river and were believed to occur up to rkm 55 (Figure 3). The presumed spatial extent of chum salmon and pink salmon was limited to below rkm 25 near the current location of Lake Mills. Sockeye presumably extended upstream from the river mouth to Lake Sutherland (Figure 1) (DOI 1995).

Existing Spatial Extent of Potamodromous Fish by Life Stage

We were able to compile records that collectively sampled 44.7 km out of a total 71 km available habitat based on data collected from 1993 to 2006. Potamodromous fish were sympatric with the presumed historic distribution of anadromous salmonids in the Elwha River. Rainbow trout and bull trout were distributed up to rkm 71 in the Elwha River (Figure 4). Juvenile and adult life history stages for bull trout and rainbow trout were observed throughout the main stem river, although observations of young-of-the-year (<50 mm) were limited to rainbow trout downstream from rkm 30 (Figure 4). Brook trout were confined to the middle and lower Elwha River, and none were observed upstream from Glines Canyon

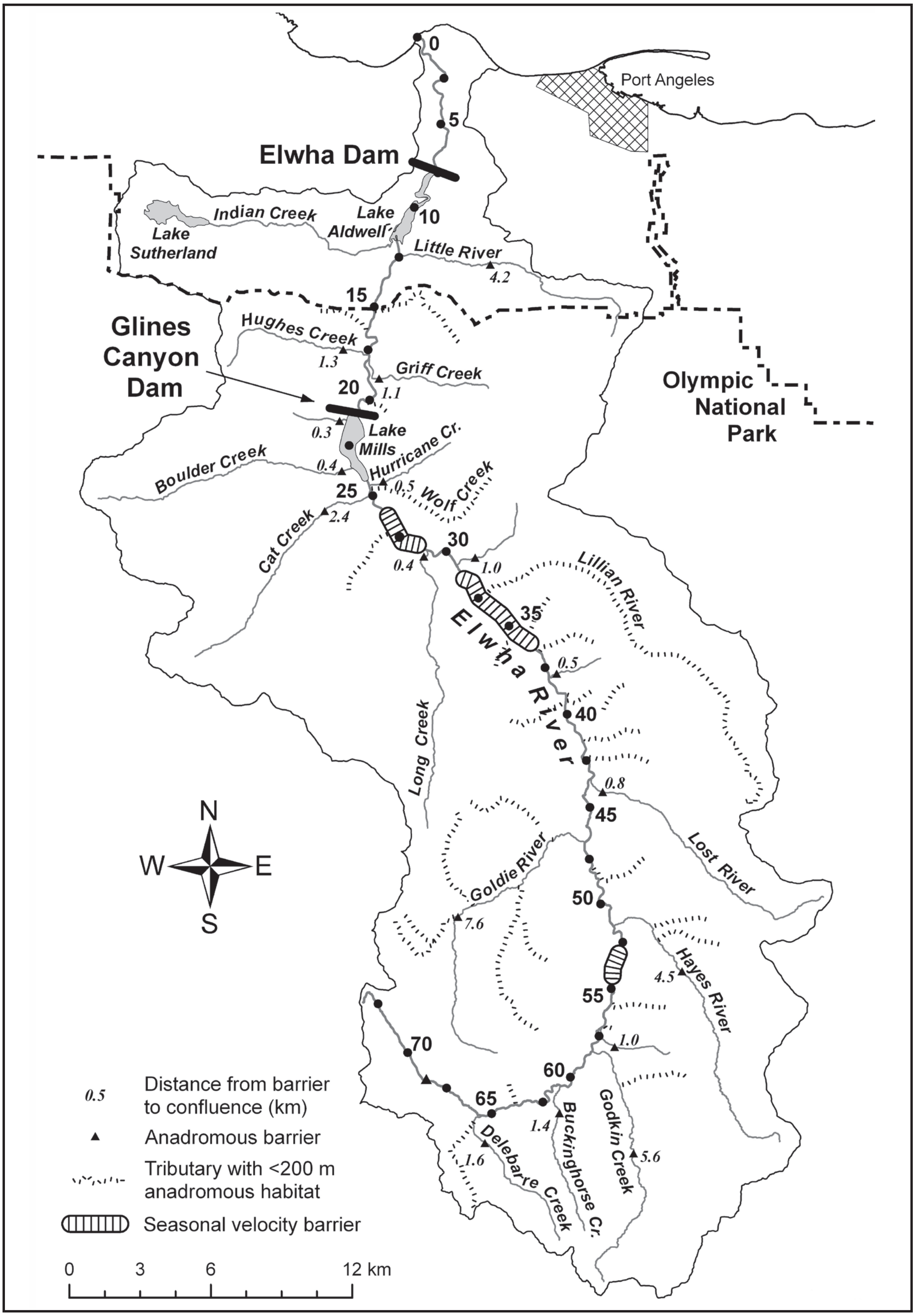

Figure 2. Distribution of seasonal velocity and physical barriers that may impede upstream migrations of Pacific salmonids after dam removal in the Elwha River basin. Numbers in italics near tributaries denote the distance (km) to an anadromous barrier.

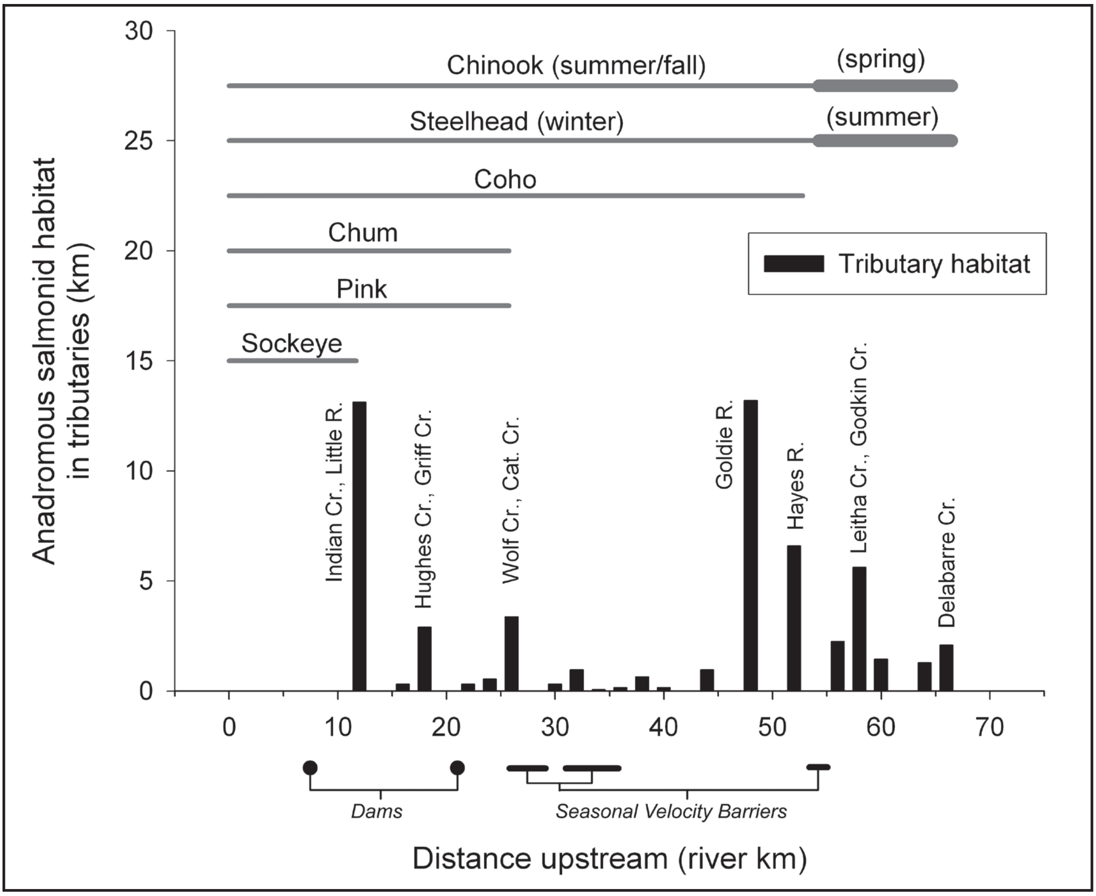

Figure 3. Presumed historic distributions of anadromous salmonids in the Elwha River and the extent of available habitat in tributaries (darkened bars) along a longitudinal gradient. Locations of dams (solid circles) and seasonal velocity barriers (darkened horizontal bars) are indicated in relation to their distance upstream and linear extent, respectively. The amount of available habitat in tributaries is summarized longitudinally in 2-km bins along the main stem Elwha River. Tributaries containing relatively large amounts of available habitat are labeled near their respective bin locations along the main stem.

Dam despite extensive surveys in the upper basin (Figure 4). The observation of brook trout in the lower river was based on one individual captured in a screw trap (Mike McHenry, Lower Elwha Klallam Tribe, personal communication).

Rainbow trout were distributed throughout tributaries to middle and upper Elwha River and occurred in 19 (of 20) streams (Table 1). Rainbow trout were also found in Lake Aldwell and Lake Mills. Bull trout occurred in 12 (of 20) tributaries although they were not detected in Indian Creek and Madison Creek in the middle river. Bull trout also occurred in Lake Aldwell and Lake Mills. Generally, bull trout and rainbow trout were sympatric in tributaries in the basin.

Brook trout were observed in the main stem Elwha River, Lake Aldwell, and in five tributaries to the middle river. No brook trout were reported in tributaries in the upper river (Table 1). Brook trout and bull trout did co-occur in Little River, South Branch Little River, Hughes Creek, and Griff Creek (Table 1). All life stages of rainbow trout, bull trout, and brook trout were detected in a low number of tributaries, and young-of-the-year were the least detected life history stage for all species in tributaries (Table 1). The lack of detection of young-of-the-year fish could be attributed to methods that undersample that life history stage.

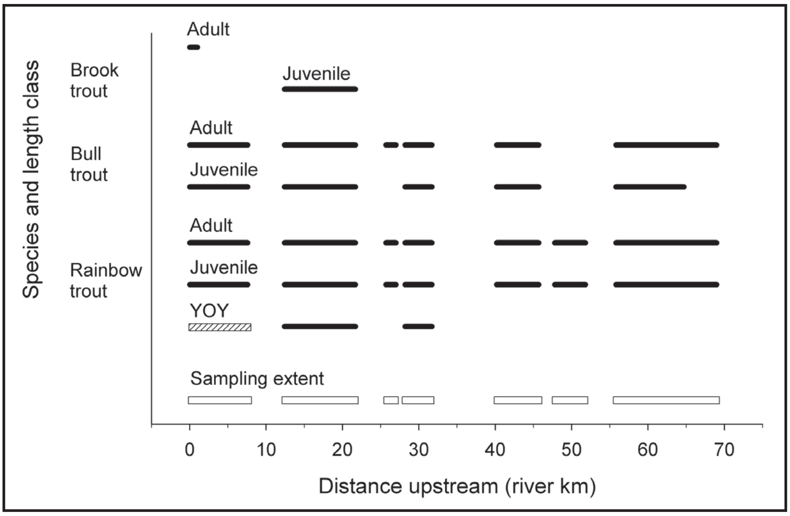

Figure 4. Current spatial distributions of adult (>200 mm), juvenile (50 to 200 mm), and young-of-the-year (<50 mm) potamodromous salmonids in the Elwha River. Dashed lines for young-of-the-year reflect presence of steelhead trout in the lower river.

TABLE 1. Current spatial distributions of adult (**A**, >200mm), juvenile (**J**, 50-200mm) and young-of-the-year (**Y**, <50mm) potamodromous salmonids in tributaries of the Elwha River. Data derived from published and non-published reports (see text). Other entries include non-detections (ND) and cases where species are listed as present (Pr) but no length data were available.

Tributary	Confluence with Elwha (rkm)	Rainbow Trout	Bull Trout	Brook Trout
In-Between Dams				
Lake Aldwell		**A**	**A**	**A**
Indian Creek	12.1	**J**, **A**	ND	**J**
Little River	12.6	**J**, **A**	Pr	Pr
S. Branch Little River	12.6	**J**, **A**	Pr	Pr
Madison Creek	15.6	Pr	ND	ND
Hughes Creek	18.2	**Y**, **J**, **A**	**Y**, **J**, **A**	**J**
Griff Creek	18.4	**Y**, **J**, **A**	**J**	**J**, **A**
Above Dams				
Lake Mills		**J**, **A**	**J**, **A**	ND
Stukey Creek	22.1	**Y**, **J**	ND	ND
Boulder Creek	24.3	**Y**, **J**, **A**	**Y**, **J**, **A**	ND
Wolf Creek	25.4	**Y**	ND	ND
Cat Creek	25.6	**J**, **A**	**J**, **A**	ND
Long Creek	29.8	**J**	**J**	ND
Lillian River	33.6	Pr	ND	ND
Stony Creek	43.5	**J**, **A**	**J**	ND
Lost River	44.6	Pr	ND	ND
Goldie River	47.3	ND	ND	ND
Hayes River	51.3	**J**, **A**	**A**	ND
Leitha Creek	56.7	**J**, **A**	ND	ND
Godkin Creek	58.1	**J**, **A**	**J**,**A**	ND
Buckinghorse Creek	60.4	**J**, **A**	**J**	ND
Delabarre Creek	65.0	**Y**, **J**, **A**	Pr	ND

Relative Abundance of Potamodromous Salmonids

Rainbow trout were far more abundant than bull trout throughout the Elwha River (Figures 5 and 6). The highest abundances for these species occurred upstream of rkm 50 (Figure 5). In the middle Elwha River, rainbow trout were over 100 times more abundant than bull trout, based on snorkel surveys conducted in August, 2000. Adams et al. (1995) estimated abundances of 559 (+/- 316) bull trout and 8,506 (+/-2,140) rainbow trout upstream of Lake Mills based on snorkel surveys by river reach, and extrapolation to estimate the entire population from the reservoir upstream to the upper limit of fish distribution. Additionally, 483 (+/- 416) bull trout were estimated to occur in tributaries upstream of Lake Mills and in those portions of tributaries downstream from natural barriers.

In the lower river, there was <1 adult bull trout per 100 m from 1995 to 2004 (Table 2). During those years, snorkel counts averaged 9 adult bull trout per 7.9 km. Rainbow trout were not counted in the lower river due to difficulty in distinguishing between anadromous and resident forms. Adult bull trout were also more abundant in the river immediately upstream from Lake Mills (~rkm 24) in September and October, 2006 during the presumed spawning migration. Rainbow trout were more abundant than bull trout in most tributaries (Figure 6). Cat Creek and Godkin Creek supported the highest numbers of bull trout whereas rainbow trout were most abundant in Indian Creek and Little River.

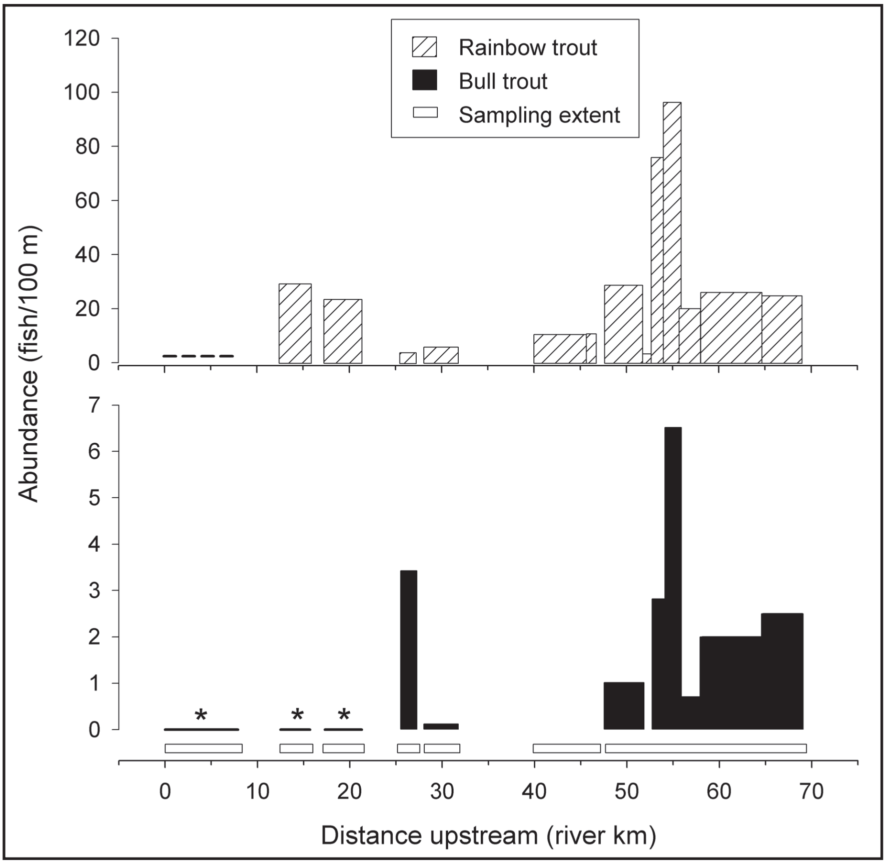

Figure 5. Relative numbers of rainbow trout and bull trout (fish/100 m) in the Elwha River based on snorkel surveys from July to September, 1995 [adopted from Adams et al. (1995)]. Dashed lines in upper graph represent *O. mykiss* (rainbow and/or steelhead trout below the dams). Asterisk indicates <1 bull trout/100 m.

TABLE 2. Relative abundances of adult bull trout and rainbow trout in the upper, middle, and lower Elwha River based upon snorkel surveys in 1995, 1996, 2000, 2002, 2003, 2004, and 2006.

Date	# Adult Bull Trout	# Rainbow Trout	Location in Elwha River (rkm)
9/12/95 [a]	2	NA	Lower (7.9 - 0.0)
9/27/95 [a]	5	NA	Lower (7.9 - 0.0)
9/4/96 [a]	4	NA	Lower (7.9 - 0.0)
8/14/02 [c]	7	NA	Lower (7.9 - 0.0)
8/25/03 [c]	32	NA	Lower (7.9 - 0.0)
9/25/04 [c]	3	NA	Lower (7.9 - 0.0)
8/1600 [b]	9	907	Middle (15.7-12.5)
8/16/00 [b]	7	845	Middle (21.3-17.3)
9/20/06 [a]	39	27	Upper (27.5-24.6)
10/18/06 [a]	22	12	Upper (27.5-24.6)

[a]National Park Service, [b]*Salvelinus confluentus* Curiosity Society, [c]NOAA Fisheries and the Lower Elwha Klallam Tribe.

Spawning Location and Timing

We observed rainbow trout spawning in 10 of 15 sampling sites in the Elwha including in 8 of 12 tributaries that were surveyed from April to June (Figure 7). Additionally, bull trout spawned in the river immediately upstream from the Lake Mills inlet based on observations of staging adults and visible redds detected during snorkel surveys in September and October, 2006. The observed peak spawn time for *O. mykiss* occurred between April and May, whereas bull trout peak spawn time occurred during October and November. In both cases, the observed spawning of rainbow trout and bull trout in the Elwha River were similar to other Olympic Peninsula watersheds (Figure 8).

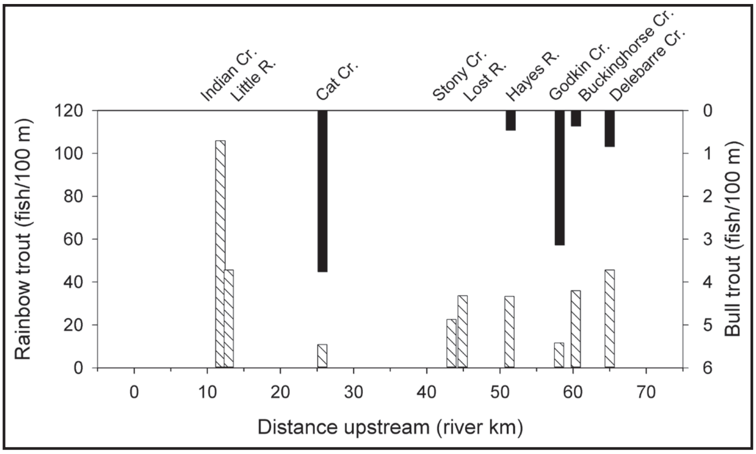

Figure 6. Relative numbers (fish/100 m) of rainbow trout (dashed) and bull trout (black) in tributaries to the Elwha River based on snorkel surveys from July to September, 1995 (adapted from Adams et al. [1995]).

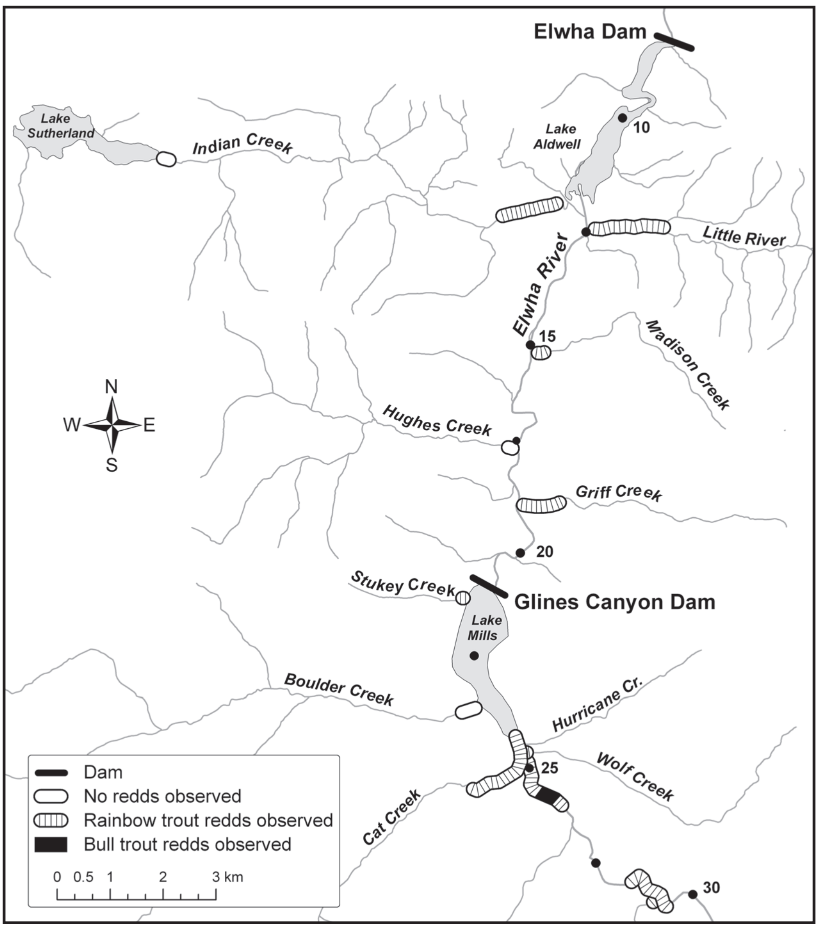

Figure 7. Location of rainbow trout and bull trout spawning areas in the Elwha basin. Spawning surveys did not occur in the uppermost portion of the Elwha basin.

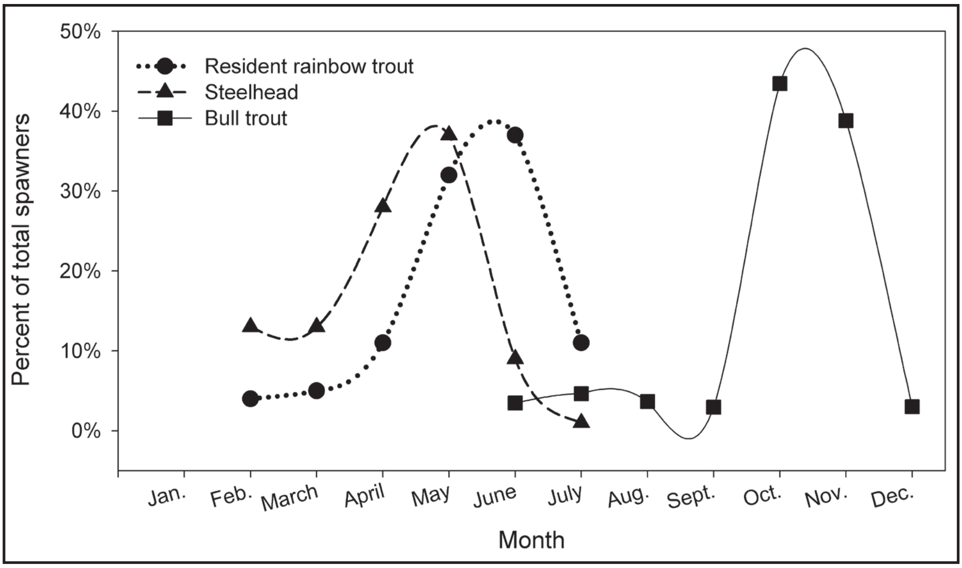

Figure 8. Presumed spawn timing for resident rainbow, winter steelhead, and bull trout in the Elwha River. Values were derived from reconstruction of spawn timings of Quileute River *Oncorhynchus mykiss* and North Fork Skokomish River bull trout.

Discussion

We compiled existing records of fish populations throughout the Elwha River basin to assess the distribution and relative abundance patterns of anadromous and potamodromous salmonids. These records, analyzed in the context of landscape features that will serve as natural barriers to movement and dispersal, allowed us to make predictions about the possible species interactions following dam removal. Although the total number of anadromous salmonids that may return to their historic range in the Elwha River is unknown, past annual returns were estimated between 380,000 and 500,000 fish (Pess et al. 2008). The level of interactions between salmon and potamodromous populations will differ throughout the basin, because the returning populations will not be evenly distributed throughout the basin (Pess et al. 2008). We predict that biotic interactions will increase from rkm 25.0 downstream to the mouth of the river; however the importance of these biotic interactions to individual survivorship or population abundance is unknown. Rainbow trout and bull trout were observed throughout the Elwha basin, although bull trout abundances were low below the Elwha Dam. Migratory and spawning times of each species will also influence the extent of interactions.

The Role of Physical Barriers as Related to Recolonization in the Elwha River

The majority of habitat accessible to colonizing anadromous salmonids after dam removal will be in the main stem river and its floodplain. We believe that presumed seasonal velocity barriers in Rica, Grand, and Carlson Canyons may limit recolonization in the upper river, particularly for species such as coho salmon and winter steelhead that migrate upstream during periods of high water in autumn and winter. Consequently, we expect most interactions between potamodromous and anadromous salmonids will occur in the main stem river below rkm 25.

The extent of tributary habitat is exceptionally limited throughout the Elwha River basin. Steep topography and the presence of physical barriers will limit the extent of recolonization in tributary streams. However, we do expect interactions between anadromous and potamodromous salmonids in Indian Creek and Little River in the middle river. Additionally, there is accessible tributary habitat upstream of rkm 45 in the Goldie River, Hayes River, and Godkin Creek (Figure 3), assuming upstream passage of fish through the three canyons.

Anadromous species including Chinook salmon, pink salmon, chum salmon, coho salmon, and sockeye salmon should reoccupy historic riverine habitat (Pess et al. 2008). Other reintroduced life history forms such as winter and summer steelhead and anadromous bull trout should also be able to recolonize historically available habitats up to rkm 71. Wampler (1984) transplanted radio tagged summer steelhead above the dams, and those fish migrated upstream through Grand Canyon (rkm 31.1 to rkm 35.3), a section of river with numerous cascades and falls. However, these fish did not migrate through Carlson Canyon. We expect that seasonal velocity barriers in the main stem river will prevent chum salmon, sockeye salmon, and to a lesser extent pink salmon from recolonizing the upper portions of the basin.

We anticipate that the removal of dams will allow for upstream and downstream recolonization by existing populations of rainbow trout and bull trout that inhabit sections of the river below, between, and above the dams. We do not expect resident brook trout to colonize the upper watershed after dam removal because seasonal velocity barriers (e.g., Rica Canyon) will limit upstream-directed movements. Brook trout are only known to inhabit tributaries and the main stem river in areas between and below the dams. However, brook trout are known to be well suited in disturbed environments with dams in place and are able to colonize after disturbance events (Roghair and Dolloff 2005).

We hypothesize that recolonization of cutthroat trout will occur after dam removal and will be influenced by existing populations that inhabit the Elwha River below Elwha Dam. The life history organization of cutthroat trout in the lower Elwha River remains unknown, but anadromous coastal cutthroat trout are expected to recolonize from the lower river upstream to Rica Canyon. We do not expect anadromous coastal cutthroat to ascend Rica Canyon because of steep gradients and high river velocities. Cutthroat trout populations that occur in Indian Creek, Lake Sutherland, and Little River (Morrill & McHenry 1994) may contribute to recolonization in the middle and lower river since those areas are among the only systems where cutthroat exist today. However, there is limited potential for recolonization of cutthroat trout from the upper watershed (i.e., upstream and downstream) as they only inhabit one tributary in the upper river, Long Creek. It is expected that anadromous cutthroat will spawn in tributaries from late winter through spring, and juveniles may remain in streams for two or more years (Trotter 1989). Most anadromous cutthroat trout on the Olympic Peninsula emigrate to the ocean at three or four years of age (Trotter 1989, Leider 1997).

Interactions Between Potamodromous and Anadromous Life History Forms

Bull trout and rainbow trout occur throughout the Elwha watershed and will generally be subjected to competitive interactions with anadromous salmonids throughout the basin. Most life stages for these species will spatially overlap with anadromous forms in each section of the Elwha River. Perhaps the highest level of competitive interactions between life history forms will occur from rkm 25 to the mouth where all species of anadromous and potamodromous forms are likely to co-occur (Figure 3). These biotic interactions may include increased competition for available habitat and food among juveniles of each species and competition for spawning and rearing habitat among adults of each species.

We expect the reestablishment of anadromous life history forms of rainbow trout, bull trout, and cutthroat trout in the Elwha River from existing populations upstream of the dams. Previous studies in the Elwha River revealed that rainbow trout exhibited smolt-like characteristics below the Glines Canyon Dam (Hiss and Wunderlich 1994), and that these fish may serve as a source of anadromy. Bull trout also are known to be anadromous along coastal Washington (Brenkman and Corbett 2005, Brenkman et al. 2007). The resumption of anadromy and reestablishment of diverse migratory patterns is expected after dam removal. Considerable life history variation is common in rainbow trout and cutthroat trout populations (Gresswell et al. 1994, Meka et al. 2003). We are unaware of anadromy in non-native brook trout populations throughout the western United States, and therefore do not expect resident forms in the upper river to resume anadromy.

Potamodromous life history forms will likely benefit from anadromous spawning during the fall and spring months due to the influx of eggs, carcasses, and juvenile fish. The consumption of eggs by resident salmonids during the spawning season is well documented throughout rivers in Pacific Northwest (Eastman 1996, Bilby et al. 1998). Resident salmonids, particularly the highly piscivorous bull trout, will benefit from the consumption of emigrating smolts during the winter, spring, and early summer months (McPhail and Baxter 1996). Additionally, the return of salmon-derived nutrients to the middle and upper Elwha River could increase primary and secondary production, which can also benefit salmonids through increased prey availability (Munn et al. 1999).

Interactions between potamodromous and anadromous species and life history forms will occur in most tributaries of the Elwha River. All stages of rainbow trout, bull trout, and brook trout currently reside in some tributaries; however the degree and type of interaction will vary according to life history stage, relative abundance of each species, and the potential for anadromous species to use each tributary habitat made available with dam removal. Interactions will likely be greatest between rkm 10 and 25. We also anticipate competitive interactions among coho salmon, bull trout, and brook trout where juvenile coho salmon presumably will compete with young-of-the-year and yearling char in areas of sympatry. At the young-of-the-year life history stage, coho salmon may emerge earlier (two to three weeks) and at longer lengths (6 to 21 mm) than brook trout, and larger individuals usually have a competitive advantage for resources when compared to smaller individuals (Fausch and White 1986).

The relative effects of brook trout on native potamodromous species in the Elwha River are expected to be minimal. Non-native brook trout impact federally threatened bull trout in the western United States through competitive displacement and hybridization (Markle 1992, Gunkel et al. 2002, Kanda et al. 2002, Rieman et al. 2006). Our analysis revealed that there was limited overlap among brook trout and other species in the main stem river, and brook trout were not reported in the upper watershed. Most interactions would be expected to occur in tributaries where brook trout and bull trout co-occur. Brook trout generally did not occur in streams where rainbow trout were present. Rainbow trout generally are adapted to greater range of channel gradients than brook trout, which are best adapted to low gradient sections of streams (Platts 1976).

Relative Abundance of Non-Anadromous Salmonids

Rainbow trout are the most abundant non-anadromous salmonid throughout the Elwha River basin. The relative abundances of both rainbow trout and bull trout were consistently higher in the watershed upstream of Lake Mills. In the main stem river, the highest abundances of rainbow trout and bull trout occurred upstream of rkm 50, and the varying levels of abundance were consistent for both species along the entire longitudinal gradient of the river. Bull trout were in low abundances in the lower river downstream of Elwha Dam during each of six different snorkel surveys from 1995 to 2004. The peak count of bull trout occurred in 2003 although only 32 fish were observed. In tributary streams, rainbow trout were most abundant in Indian Creek in the middle river.

Spawning Location and Timing

Spawning locations for bull trout and rainbow trout in the middle and upper Elwha River overlap those areas where we anticipate anadromous species to spawn after dam removal. The spawning time for Elwha River rainbow trout (April to June) coincides with that of winter steelhead in nearby Olympic Peninsula rivers (McMillan et al. 2007). We also observed limited bull trout spawning in September and October, which was generally earlier than bull trout populations that spawn from October to December in the North Fork Skokomish and Hoh Rivers (Brenkman et al. 2001, Brenkman et al. 2007). We expect increased competition for spawning habitats among bull trout and anadromous recolonizers, particularly coho salmon, because spawning times overlap. The spawn timing of Elwha River brook trout remains unknown, but brook trout typically spawn from September through November (Blanchfield and Ridway 1997). Hybridization can occur between bull trout and brook trout (Markle 1992), but such hybridization in the Elwha River seems unlikely due to the limited overlap in habitats between the two species. Also, natural barriers will limit the extent that brook trout move upstream after dam removal.

Predicting Spatial and Temporal Interactions Between Potamodromous and Anadromous Salmonids

We hypothesize that the interactions between potamodromous and anadromous salmonids will be limited by migration barriers and the existing distribution and abundance of rainbow trout and bull trout. Our findings suggest that the potential for interactions among potamodromous and anadromous species will be highest in the main stem Elwha River downstream of Rica canyon because: 1) the greatest overlap of salmonid species will occur here, 2) the relative abundance of potamodromous salmonids will be greater than the lower Elwha River, 3) there is a high proportion of tributary habitat (compared to the lower river) likely to be used as spatial refugia from high in-channel sediment levels once the dams are removed, and 4) there are no known main stem velocity barriers in that river section. Both anadromous and potamodromous salmonids are likely to seek out these limited habitats as initial refugia during dam removal and periods of high sediment loads. Major tributaries where interactions may occur include Indian Creek and Little River. We also hypothesize that there will be less interaction in the upper watershed above Lake Mills because barriers to the upper watershed (i.e., Rica, Grand, and Carlson canyons) will reduce species overlap. However, there will be key areas for interactions between potamodromous and anadromous salmonids in tributaries such as Goldie River, Hayes River, and Godkin Creek.

Anadromous and potamodromous salmonids have evolved to rapidly take advantage of the multitude of habitats created by natural disturbance in a changing landscape (Northcote 1992). This diversity in life-history forms effectively allows for a more efficient use of habitat available both seasonally and spatially. The removal of Elwha River dams will functionally allow this phenotypic plasticity in salmonid life-history forms to be reexpressed and may lead to potamodromous populations giving rise to anadromous juveniles. However, the degree of reproductive isolation may vary according to distance and natural barriers. On the other hand, evidence also exists for increased reproductive isolation between sympatric resident and anadromous forms of rainbow trout (Zimmerman and Reeves 2000). Potential interactions between anadromous and potamodromous salmonids as a result of dam removal thus may be mitigated by the tendencies of sympatric life-history forms to spatially segregate both in spawning and in rearing. Such segregation may result in preferential use of tributary and upper main stem habitats by potamodromous forms, with anadromous forms using floodplain habitats in larger river sections downstream.

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