A riverscape perspective of Pacific salmonids and aquatic habitats prior to large-scale dam removal in the Elwha River, Washington, USA

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Abstract Dam removal has been increasingly proposed as a river restoration technique. In 2011, two large hydroelectric dams will be removed from Washington State's Elwha River. Ten anadromous fish populations are expected to recolonise historical habitats after dam removal. A key to understanding watershed recolonisation is the collection of spatially continuous information on fish and aquatic habitats. A riverscape approach with an emphasis on biological data has rarely been applied in mid-sized, wilderness rivers, particularly in consecutive years prior to dam removal. Concurrent snorkel and habitat surveys were conducted from the headwaters to the mouth (rkm 65–0) of the Elwha River in 2007 and 2008. This riverscape approach characterised the spatial extent, assemblage structure and patterns of relative density of Pacific salmonids. The presence of dams influenced the longitudinal patterns of fish assemblages, and species richness was the highest downstream of the dams, where anadromous salmonids still have access. The percent composition of salmonids was similar in both years for rainbow trout, *Oncorhynchus mykiss* (Walbaum), coastal cutthroat trout, *Oncorhynchus clarkii clarkii* (Richardson) (89%; 88%), Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) (8%; 9%), and bull trout, *Salvelinus confluentus* (Suckley) (3% in both years). Spatial patterns of abundance for rainbow and cutthroat trout

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(r = 0.76) and bull trout (r = 0.70) were also consistent between years. Multivariate and univariate methods detected differences in habitat structure along the river profile caused by natural and anthropogenic factors. The riverscape view highlighted species-specific biological hotspots and revealed that 60–69% of federally threatened bull trout occurred near or below the dams. Spatially continuous surveys will be vital in evaluating the effectiveness of upcoming dam removal projects at restoring anadromous salmonids.

KEYWORDS: dam removal, recolonisation, riverscape, salmonid, snorkel survey.

Introduction

The placement of hydroelectric dams on rivers causes physical and biological effects that operate at multiple spatial scales (Rosenberg *et al.* 1997; Petts & Gurnell 2005). Attenuated annual and seasonal discharge cycles, disrupted sediment and wood transport, altered nutrient dynamics and increased water temperatures have been widely documented in regulated rivers (Baxter 1977; Petts 1984; Hart *et al.* 2002). In the Northwestern United States and elsewhere, large hydroelectric projects have multiple, interacting effects on fish populations, including the decline of anadromous salmonids (Raymond 1979; Kareiva *et al.* 2000; Williams *et al.* 2005), changed evolutionary trajectories of life-history strategies (Williams *et al.* 2005), fish migration patterns that are altered within individual rivers (Lignon *et al.* 1995) and disrupted hydrological connectivity (Fullerton *et al.* 2010).

Dam removal has been increasingly proposed for river restoration (Bednarek 2001; Hart *et al.* 2002; Heinz Center 2002, Stanley & Doyle 2003). Dam removal projects completed to date have typically involved low-head dams with structural heights of <6 m (Heinz Center 2002; Doyle *et al.* 2005). Larger dam removal projects have occurred, or are planned, at locations across the western United States, including Matilija Dam (Ventura Basin, CA), Marmot Dam (Sandy River, OR), Savage Rapids Dam (Rogue River, OR), Condit Dam (White Salmon River, WA), Klamath River Dams (OR and CA) and the Glines Canyon and Elwha Dams (Elwha River, WA). These dam removal projects provide opportunities to examine the responses of fish populations, particularly Pacific salmonids, to dam removal.

Olympic National Park (ONP), a World Heritage Site and Biosphere Reserve located on Washington State's Olympic Peninsula, contains one of the largest contiguous areas of relatively pristine habitat (373 525 ha) throughout the range of several western US coastal fish species. The park contains 12 major watersheds and some 5600 km of rivers and streams. However, two large hydroelectric dams (Elwha Dam and Glines Canyon Dam, 64 and 32 m in height, respectively) constructed in the early 1900s on the park's Elwha River eliminated access for anadromous salmonids to some 95% of the watershed.

Prior to dam construction, there were eight species of Pacific salmonids, including a large-bodied form of Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), with some individuals exceeding 45 kg (Wunderlich *et al.* 1994; Roni & Quinn 1995). Estimates of historical population sizes describe a river that produced large numbers of salmonids relative to other regional rivers (Wunderlich *et al.* 1994; Winter & Crain 2008). Pacific salmonids that inhabit the Elwha River are now at critically low numbers, and anadromous populations are limited to the lowest 7.5 river kilometres (rkm) below the lower dam, where there are no facilities providing upstream passage for anadromous fish.

Removal of the two Elwha River dams, scheduled to begin in 2011, will occur over a 2- to 3-year period. This project – the concurrent removal of two high dams (12 km apart) in a river that drains directly into marine waters – will be one of the largest dam removals in terms of structural height and sediment release in North America and is the second largest ecological restoration project in the National Park Service (the first being Everglades restoration). Although primarily intended to restore anadromous fish populations, the dam removal project is becoming a living laboratory for studying the ecological effects of dam removal and river restoration and could serve as an important benchmark for future dam removal projects (Duda *et al.* 2008).

A key to studying watershed recolonisation by Pacific salmonids after a large-scale dam removal is the collection of spatially continuous baseline information before dam removal. In the Elwha River, numerous baseline studies exist (see Winter & Crain 2008), and recent research has characterised characterised existing fish communities and predicted the responses of Pacific salmonids to dam removal (Brenkman *et al.* 2008a,b; Connolly & Brenkman 2008; Burke *et al.* 2008; Pess *et al.* 2008; Roni *et al.* 2008; Winans *et al.* 2008; Duda *et al.* in press). Although these studies provide useful baseline information, most were

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conducted at the site scale, within index reaches, or on a section of the river downstream of the dams, and were not spatially continuous. Because the dynamics of recolonisation will be expressed across multiple spatial and temporal scales, a riverscape perspective (Fausch *et al.* 2002; Torgersen *et al.* 2006) should prove useful in tracking vital rates, including the extent of recolonisation and species-specific interactions among recolonising anadromous fish with their resident counterparts. Many ecological frameworks (such as the River Continuum Hypothesis, intermediate disturbance hypothesis and ideal-free distribution) could be applied to explain future patterns of recolonisation following dam removal, warranting the collection of data at the riverscape scale.

Aquatic environments are inherently difficult to sample (Fausch *et al.* 2002), and large systems such as the Elwha River pose numerous challenges to collecting information about fish populations. The use of traditional fisheries methods is particularly challenging in the Elwha River because of prolonged periods of high flow, low water visibility from glacial melt, difficult access in rugged wilderness areas and restrictions on allowable sampling methods in National Park waters. Additionally, these challenges are compounded by the presence of migratory fishes, whose extensive movements in rivers add complexity to sampling.

A current limitation of riverscape surveys is the paucity of biological data (Carbonneau *et al.* 2011), particularly related to fish communities. Hankin and Reeves (1988) used spatially continuous surveys to map aquatic habitat throughout small streams, but their fish surveys were not spatially continuous. Other recent studies illustrated the use of single-pass electric fishing to map fish distributions in small streams (Bateman *et al.* 2005; Gresswell *et al.* 2006). A continuous view of fish and aquatic habitat has rarely been applied in mid-sized rivers (see Torgersen *et al.* 2006), particularly in wilderness rivers.

The paper describes concurrent fish and habitat surveys from the headwaters of the Elwha River to its mouth, provides baseline data prior to dam removal and facilitates inferences about salmon recolonisation following dam removal. This riverscape approach to collecting and analysing data provides a spatially continuous perspective of fishes and their associated habitats. The goal was to characterise fish assemblage structure, spatial distributions, relative abundances and densities of salmonids, and the major habitat features throughout the river during summer base flows in 2007 and 2008. Specific objectives were to: (1) determine the spatial extent of existing salmonids in the main stem Elwha River from rkm 65 to rkm 0; (2) assess the patterns of species composition, relative abundances and relative densities throughout a longitudinal gradient of consecutive channel units; and (3) assess patterns of habitat structure (e.g. habitat type, large woody debris (LWD) and substrate composition) in relation to observed fish patterns throughout the river.

Study area

The Elwha River originates in ONP on Washington's Olympic Peninsula (Fig. 1). The 6th-order (Strahler 1957) river drains 833 km^2 and constitutes 19% of ONP. The Elwha River flows 72 km from glaciers and ice fields and descends from 1372 m at the headwaters to its confluence (at sea level) with the Strait of Juan de Fuca in the Pacific Ocean. The uppermost portions of the Elwha River are remote, and only a walking trail parallels the upper 45 km. Eighty-two percent of the watershed occurs in ONP and is managed by the National Park Service as a wilderness area. The remaining portions of the river flow through State, private and tribal lands. There is road access from Glines Canyon Dam to the river mouth, a distance of 22 km.

Three river sections were defined as the upper river above Glines Canyon Dam (hereafter UE), the middle river in-between Glines Canyon and Elwha Dams (ME) and the lower river downstream of Elwha Dam (LE). The UE is free flowing, whereas ME and LE have flows attenuated by dam operations (largely run-of-the-river) for the generation of hydroelectric power. The dams have physically isolated fish populations for 98 years, eliminated access to spawning and rearing habitats for anadromous fish above rkm 7.5 and changed in-river migration patterns of steelhead trout, *Oncorhynchus mykiss* (Walbaum), coastal cutthroat trout, *Oncorhynchus clarkii clarkii* (Richardson), and bull trout, *Salvelinus confluentus* (Suckley).

The geomorphology of the Elwha River Basin is a series of alternating canyons and floodplains (Pess *et al.* 2008). The major canyons of the Elwha River from mouth to headwaters include Elwha Canyon (1.7 rkm in length), Glines Canyon (0.8 rkm), Rica Canyon (1.9 rkm), Grand Canyon (5.5 rkm), an unnamed canyon (1.2 rkm) and Carlson Canyon (2.3 rkm) (Duda *et al.* 2008). Rica Canyon consists of bedrock, large boulders and high-velocity water with several cascades and waterfalls up to 1.8 m in height. The upstream portion of Grand Canyon contains 15 cascades and falls, and Carlson Canyon has a bedrock cataract 100 m in length with a 2.0 m

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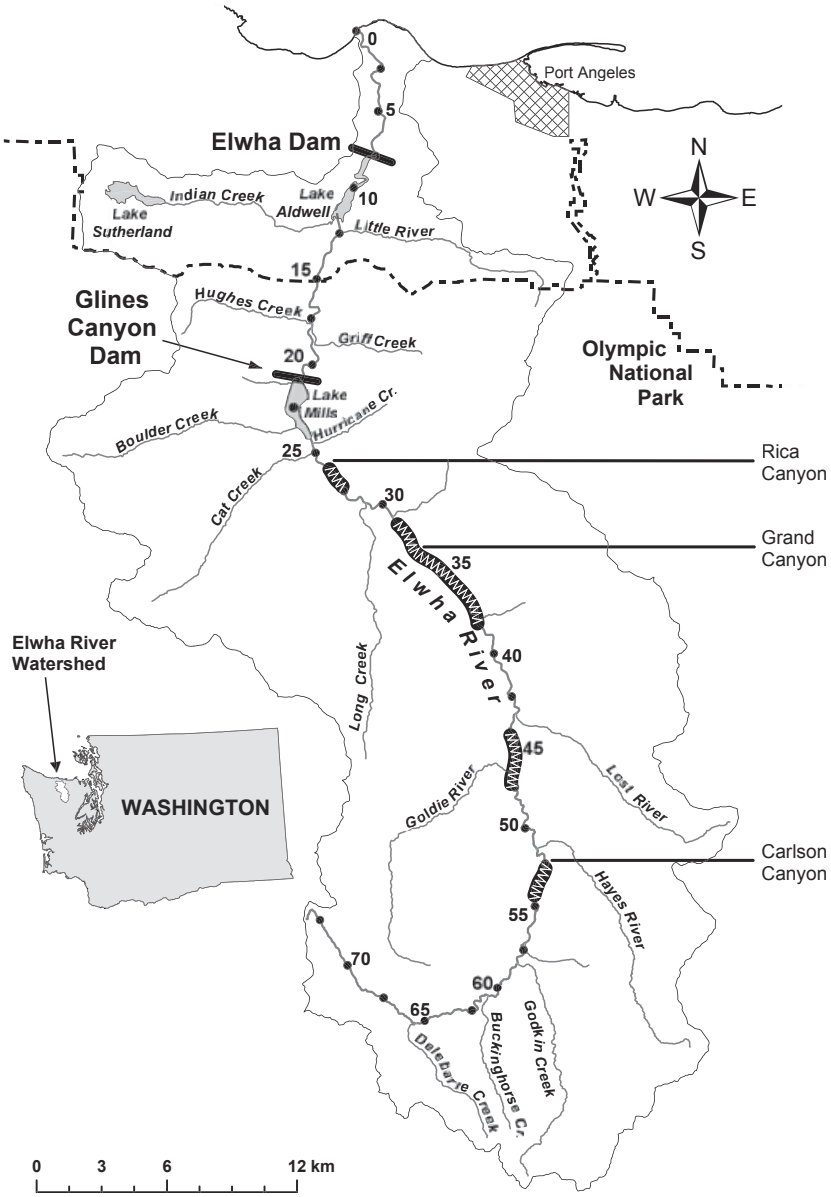

Figure 1. Map of the Elwha River watershed, Olympic Peninsula, Washington, where spatially continuous fish and habitat surveys were conducted from rkm 65 to the mouth in 2007 and 2008. Distance upstream from the river mouth is demarcated on the map by black dots annotated with river kilometres.

waterfall (Washington Department of Fisheries 1971, Brenkman *et al.* 2008a). Floodplain reaches occur between the alternating canyons. These depositional reaches are generally lower in gradient, contain wide gravel bars and are anastomosing channels with pool-riffle morphology. There are 34 named tributaries that flow into the Elwha River, and 33 occur upstream of the dams and are not accessible to anadromous salmonids.

The mean daily discharge of the Elwha River is 42 $m^3 s^{-1}$, and annual minimum flows range from 8.5 to 14 $m^3 s^{-1}$ during summer (Curran *et al.* 2009). Average annual rainfall ranges from 100 cm yr^{-1} near the mouth to over 550 cm yr^{-1} in the headwaters (Duda *et al.* 2008). The estimated sediment contained in both reservoirs is 19 million m^3 ($\pm$3.5 million m^3), with the majority occurring in Lake Mills, the upstream reservoir (Bountry *et al.* 2010). During and following dam removal, the river will naturally erode existing sediment deposits from the reservoirs.

The salmonid community in the Elwha River Basin comprises wild, natural-origin, hatchery and non-

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native fish. Salmonid species that inhabit the river downstream from Elwha Dam include Chinook salmon, coho salmon *Oncorhynchus kisutch* (Walbaum), pink salmon *Oncorhynchus gorbuscha* (Walbaum), chum salmon *Oncorhynchus keta* (Walbaum), sockeye salmon *Oncorhynchus nerka* (Walbaum), summer and winter steelhead trout, cutthroat trout and bull trout. Some of these salmonid populations have been supplemented by hatcheries since 1915 (Brenkman *et al*. 2008b). Non-salmonid taxa below Elwha Dam include sculpin spp. *Cottus* spp., threespine stickleback *Gasterosteus aculeatus* L., Pacific lamprey *Lampetra tridentata* (Richardson), redside shiner *Richardsonius balteatus* (Richardson), eulachon *Thaleichthys pacificus* (Richardson), starry flounder *Platichthys stellatus* (Pallas) and surf smelt *Hypomesus pretiosus* (Girard). Non-native brook trout *Salvelinus fontinalis* (Mitchill) occur below Glines Canyon Dam. Chinook salmon, steelhead, bull trout and eulachon are listed as federally threatened species under the US Endangered Species Act.

Fishery resources in the Elwha River are ecologically and culturally important and contribute to recreational, commercial and subsistence fisheries. Treaty fisheries occur for hatchery coho salmon and winter steelhead during autumn and winter. Catch-and-release recreational fishing opportunities exist from 1 June to 31 October in ONP.

Methods

Longitudinal surveys of fish species

*S*patially continuous snorkel surveys were conducted throughout 65 km of the Elwha River during summer low-flow in August 2007 and August and September 2008. Snorkel surveys can provide precise and reliable estimates of fish abundance (Northcote & Wilkie 1963; Schill & Griffith 1984; Thurow 1994) for use in quantifying the grain and extent of species distribution (Roper & Scarnecchia 1994; Torgersen *et al*. 2006). Additionally, the upper Elwha River could not be surveyed effectively with other methods (e.g. electric fishing) because of difficult access. The passive nature of the technique (e.g. no handling of fish) was necessary for sampling protected fish stocks that inhabit National Park waters. The impoundments created by the dams, Lake Aldwell (4 km long) and Lake Mills (4.5 km), and canyons with white water rapids were not surveyed.

Snorkel surveys were conducted with 20 surveyors in five teams of four from 21 to 24 August 2007 and from 26 to 29 August and 4 to 9 September 2008. As a result of high flows in August 2008, the latter 3 days of the survey were completed in September (i.e. for a span of 15 days instead of 5 days in 2007). Surveyors were professional biologists experienced in snorkelling techniques and fish identification. To access remote river sections, pack mules were used to carry and distribute field and camping equipment. Prior to the week-long surveys, aerial reconnaissance was conducted in a Cessna 172 to map log jams and other hazards along the river, while foot surveyors flagged upstream and downstream ends of each canyon.

In each team, two divers drifted downstream on each side of the river and counted individuals of each species. In wide sections of LE and ME, a third diver was used to sample the entire channel and to count fish in side channels. Divers recorded length classes of bull trout, cutthroat trout and rainbow trout in categories of 0–10, >10–20, >20–30 and >30 cm. Counts for cutthroat trout and *O. mykiss* (rainbow trout or juvenile steelhead) were combined because of the difficulty in distinguishing between these species and are hereafter referred to as trout. Young-of-the-year salmonids were noted but are not presented. When fish were observed in large aggregations or near wood jams, divers made two passes in their respective lanes and averaged counts when necessary. Divers recorded data at $\approx$ 100-m intervals to compare observations and avoid duplication of counts.

Although the extent of the snorkelling surveys was the same in 2007 and 2008, the grain differed between years. In 2007, fish counts were recorded in 21 reaches that were 1–8 km in length and only limited habitat data were collected. Reach boundaries were based on easily identifiable geographic features (i.e. bridges or tributary confluences) on topographic maps and aerial photographs. In 2008, fish counts and aquatic habitat descriptions were recorded for every channel unit.

Longitudinal surveys of aquatic habitat

In 2008, a spatially continuous habitat survey was conducted concurrent with the fish survey. In coordination with the divers counting fish, two habitat surveyors walked downstream and measured physical habitat variables including channel type (main, secondary or side channel), habitat type (riffle, glide-like riffle, glide-like pool and pool, in order of decreasing velocity), channel-unit length and wetted width. Wetted width was averaged from three measurements taken at 25, 50 and 75% of the distance from the upstream end of the unit. All distances were measured using a laser range finder. Hand-held global positioning system (GPS) units were used to map the longitudinal boundaries of each channel unit.

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Riffles longer than 200 m were subdivided and georeferenced at 200-m intervals. Field observations of tributary junctions and other landmarks were used as geographic reference points when satellite reception was limited. The GPS track-log function enabled temporally and spatially continuous collection of position and odometer data.

Cover and substrate were recorded for each channel unit including extent of overhanging vegetation, boulders, and number and area of log jams in each channel unit. The percent of river bank habitat with vegetation overhanging the wetted channel within 30 cm of the water surface was visually estimated. The percent of the channel-unit surface area covered by boulders (> 256 mm) was also visually estimated. Wood pieces > 10 cm in diameter breast height and aggregations (i.e. log jams) were counted, and their surface area was measured. The percentage of dominant and subdominant substrate types was visually estimated by the two divers according to categories in Cummins (1962): bedrock (including hardpan clay), boulder (> 256 mm, including riprap), cobble (64–256 mm), gravel (2–64 mm), sand (< 2 mm), silt (< 0.6 mm) and organic debris. The snorkelers estimated mean and maximum depth (cm) of each channel unit.

Geographical Information System (GIS) methods and data analysis

Linear referencing methods were used in ArcGIS (ESRI 2006) to map fish counts and channel units along the 65 km of the Elwha River. The National Hydrography Dataset (NHD 2009) was used for mapping the main stem Elwha River in the GIS, but recent aerial photographs (2006 and 2008) indicated that updates to this map layer were required because of channel migration (see Draut *et al*. 2010 for rates) that had occurred since the 1950s when the US Geological Survey hydrography layer (1:24 000-scale topographic quadrangles) was created. Modifications of the NHD hydrography were made using a combination of aerial photographs, GPS track-logs and field notes from the 2008 field survey. In the GIS, channel units and reaches were georeferenced based on cumulative distance upstream from the river mouth. This process involved digital rectification (i.e. dynamic segmentation) of channel-unit lengths, relative distances from landmarks (e.g. tributary junctions and bridges) and GPS waypoints (*sensu* Radko 1997).

Longitudinal patterns in fish abundance and aquatic habitat throughout the Elwha River were analysed by plotting the data vs distance upstream. Reaches (n = 21) were used to compare patterns of fish abundance between years because the 2007 survey was conducted at a coarser scale than in 2008. To evaluate spatial patterns of fish distribution, within each reach, the relative abundance (i.e. the number of a given species divided by the total number of all fish observed) was calculated and plotted against distance upstream for 3-D visualisation in GIS. The relative density, D_r, was also calculated for each species and size class to compare patterns of abundance among reaches. D_r is defined as $D_r = [(f_i/l_i)/(f_t/l_t)] - 1$, where f_i is the number of fish in reach i, f_t is the total number of fish in all reaches, l_i is the length of reach i and l_t is the total length of river surveyed. Normalised relative density was used to compare longitudinal patterns of D_r between years and was calculated by dividing D_r in each reach by the maximum D_r for all reaches. Positive and negative values of normalised relative density indicate densities that are, respectively, above and below the average density for the entire river.

Aquatic habitat data from summer 2008 were recorded for each channel unit, but to facilitate analysis throughout the entire 65 km of the Elwha River, data were summarised in 1-km bins as: (1) percentages based on channel-unit length (pool and riffle habitat, and gravel and boulder substrate); (2) means weighted by proportionate channel-unit length (wetted width and area of LWD jams); or (3) total count (LWD jams). For all longitudinal analyses, side-channel attributes were included in the calculations of fish abundance and aquatic habitat characteristics for the reaches and 1-km bins to which they were adjacent. Custom scripts developed in the R statistical package (R Development Core Team 2009) were used to plot longitudinal profiles of aquatic habitat variables.

Spatially continuous fish and habitat relationships

Several steps were used to relate fish species abundance to physical habitat variables collected in 2008. Principal components analysis (PCA) with joint points in PC-ORD (MjM Software, Gleneden Beach, OR) was used to reduce a subset of habitat variables to two orthogonal variables (linear combinations of the original variables) describing the river channel units. This allowed graphic analysis of the relatedness of 44, 1-km bins in different floodplain sections above, between and below the dams, as well as to quantify variables responsible for differences. For continuity with the 2008 survey results, channel-unit scores were averaged within each of the 2008 bins (n = 44) for 11 continuous habitat variables, which ensured a minimum ratio of variables to observations recommended for ordination. Skewed variables were

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square-root-transformed (i.e. number of jams and jam area), and then the data matrix was normalised to eliminate differences in measurement scale.

Next, species density (fish km^{-1}) was used as the response variable, and the 11 stream habitat characteristics were used as independent variables in a linear modelling approach. Akaike's Information Criterion, adjusted for small sample sizes (AICc), was used to determine which linear regression model best fits the data (Burnham & Anderson 2002). The difference between the AICc of a candidate model and the one with the lowest AICc provided the ranking metric (ΔAICc). Generally speaking, ΔAICc between 0 and 4 indicates substantial support for a model being as good as the best approximating model, ΔAICc between 4 and 7 represents less support and ΔAICc of >7 indicates very little support for a candidate model relative to the best model (Burnham & Anderson 2002).

Akaike weights (w_i) were calculated, representing the strength of evidence in favour of model i being the best model. The ratio of Akaike weights (w_i/w_j) represents the plausibility of the best-fitting model compared with other models (Burnham & Anderson 2002). Models with an evidence ratio of 10 or less were considered plausible. If models were not the best model based on the preceding criteria, then models within three AICc were considered competing models and results were averaged to determine the maximum likelihood estimate for the intercept and each of the independent variables that were part of the models (Burnham & Anderson 2002; Haring & Fausch 2002).

Results

The distributions, assemblage structure, abundances, normalised relative densities and length classes of Pacific salmonids in the Elwha River in 2007 and 2008 were summarised and analysed by continuously mapped habitat variables in 2008. River discharge (USGS stream-flow gauging station 12045500) during snorkel and habitat surveys ranged from 14.8 to 16.2 $m^3 s^{-1}$ and from 12.1 to 24.3 $m^3 s^{-1}$ in 2007 and 2008, respectively. In August 2008, a large rain event caused episodic increases in river discharge that reduced water visibility. A total of 6 cm of precipitation (90% of the monthly total) occurred immediately prior to, and during, the survey in the upper Elwha River.

Fish distribution and assemblage structure

Trout and bull trout were distributed from the upstream extent of the survey (rkm 65.2) to the mouth (rkm 0), while Chinook salmon and pink salmon were confined to LE because of the Elwha Dam (Fig. 2). In 2007, 7312 trout, 687 adult Chinook salmon, 215 bull trout and 26 pink salmon were counted throughout the Elwha River (8240 total fish). In 2008, 3218 trout, 316 adult Chinook salmon and 118 bull trout (3652 total fish) were observed. Non-native brook trout (LE and ME only), sculpin (spp.; LE and ME only), threespine stickleback (LE) and starry flounder (LE) were observed in low numbers each year.

The longitudinal fish assemblage patterns revealed that species richness was the lowest in UE (above Glines Canyon Dam) and highest in LE (Fig. 2). Trout were the dominant fish throughout the river and comprised 89% and 88% of the total fish assemblage in 2007 and 2008, respectively. The fish species assemblage also comprised Chinook salmon (8% in 2007; 9% in 2008), bull trout (3% in both years) and pink salmon (<1% in 2007 only). The highest total and relative abundances of bull trout were immediately upstream of Lake Mills and near the headwaters in both years (Fig. 2). Of the total numbers of bull trout observed, 60% and 69% were observed from Rica Canyon downstream to the river mouth in 2007 and 2008, respectively. The patterns of abundances for trout and bull trout were correlated between years despite the differences in river flows in 2007 and 2008 (Pearson's correlation, $r = 0.70$ for bull trout and $r = 0.76$ for trout, $P < 0.001$, Fig. 3).

Relative densities and length classes

Patterns of normalised relative densities of trout and bull trout varied among LE, ME and UE and between years in 2007 and 2008 (Fig. 4a, b). Analysis of fish among LE, ME and UE revealed a total of 295, 227 and 102 trout km^{-1} and 4, 6 and 4 bull trout km^{-1}, respectively, in 2007. Densities of 143, 159 and 25 trout km^{-1}, and 1, 3 and 3 bull trout km^{-1} were observed among river sections in 2008 (Table 1).

The highest normalised D_r of trout, for all length classes combined, occurred downstream of the two reservoirs (rkm 22–0) and was the lowest immediately upstream of Lake Mills (Fig. 4a). Normalised D_r of small trout (10–20 cm) generally varied between the 2 years throughout the river (Fig. 4a). Normalised D_r of larger trout (20–30 cm; >30 cm) was the highest immediately downstream of each dam (Fig. 4a).

Normalised D_r varied along the longitudinal gradient of the Elwha River in 2007 and 2008 (Figs 4a, b). The highest normalised D_r of bull trout, for all length classes combined, occurred upstream of Lake Mills and immediately downstream of Glines Canyon Dam

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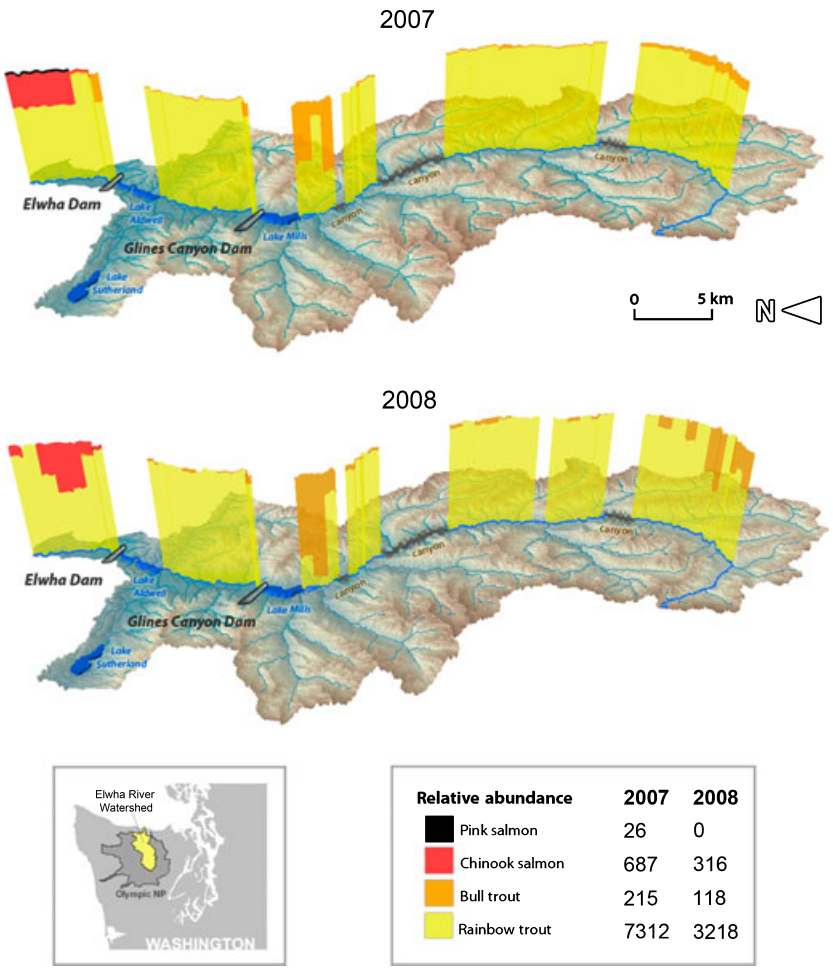

Figure 2. Distribution and relative abundance of salmonids in the Elwha River based on spatially continuous snorkel surveys conducted in the summers of 2007 and 2008 from rkm 65 to the river mouth. Stacked bars indicate the relative abundance (i.e. proportion of total abundance) for each species. The inset table provides total counts of fish by species in 2007 and 2008.

(Fig. 4b). The longitudinal patterns of high and low D_r of bull trout were consistent among the three size classes from the headwaters to the mouth. Normalised D_r patterns were also consistent between the 2 years (Fig. 4b). There was relatively low normalised D_r of large bull trout (>30 cm) throughout the UE (Fig. 4b).

Distribution of habitat variables along a longitudinal gradient

Differences were observed in the longitudinal distribution of major habitat features in the Elwha River from rkm 65.2 to rkm 0 in 2008. There were 316 individual channel units throughout the river, and there were distinct differences among UE, ME and LE (Table 1). The UE was the longest section surveyed (31 km surveyed) and had the highest gradient, the lowest mean wetted width and the highest number of named tributaries (n = 27) among river sections (Table 1). The UE also had the highest percentage of riffles by area and the lowest percentage of pools by area. Additionally, the UE had the highest LWD count and the highest LWD area per km (Table 1).

The section of the Elwha River between the two dams (ME) was the widest section (mean wetted width = 39 m) and had six tributaries. The number of channel units was the lowest in this section, but the channel units were the deepest for each of the habitat types (Table 1). This section of river had limited amounts of LWD and contained the lowest number and total area LWD.

The section downstream of Elwha Dam (LE) was the shortest section surveyed (7.2 km), had only one

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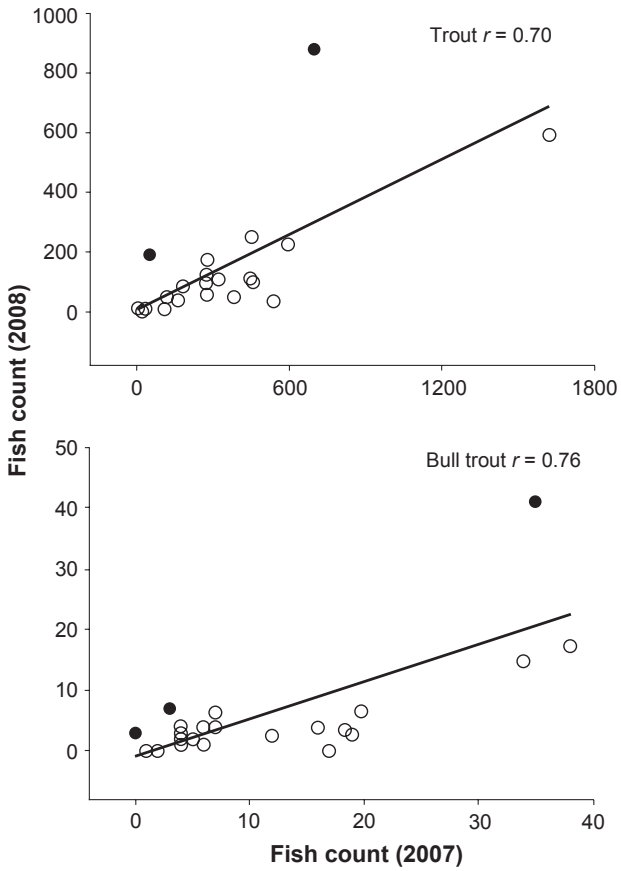

Figure 3. Pearson correlations of total trout (rainbow and cutthroat trout combined) and bull trout counts by reach (n = 21) in the Elwha River in 2007 and 2008. Solid black circles represent counts that were higher in 2008 than 2007.

tributary and had the lowest gradient. This section had the highest percent area of pools and glide-like pools and the lowest percent area of riffles and glide-like riffles. The mean depths of pools and riffles were lowest compared with the upper and middle river sections. The lower river had high amounts of LWD including the highest mean area of log jams and highest area of jams km^{-1} (Table 1; Fig. 5g).

The wetted channel width increased from the headwaters to the river mouth, as did percent pool habitat (Fig. 5b). Longitudinal patterns of riffles (total length, %) varied among UE and ME, and percentages were generally lowest in LE.

The UE and areas immediately upstream of Lake Mills were dominated by gravel substrates (Fig. 5d). The percentage of gravel substratum was low in large portions of the ME, LE and immediately upstream of rkm 25 (Fig. 5d). Boulders were the dominant substrate in the ME and LE below the dams. The total abundance of LWD was the highest in the headwaters although the peak abundance of wood occurred in LE (Fig. 5f).

The PCA extracted two significant axes ($P < 0.01$ based upon randomisation tests) that described 57% of the variance. Increases along the first principal component axis corresponded to higher number of log jams and percent gravel substrate, whereas decreases along this axis corresponded to higher percent boulder substrate, higher wetted width, greater channel-unit area and greater channel-unit depth. Correspondingly, sites in LE and ME were separated from sites in UE along this axis (Fig. 6). The second principal component axis differentiated units with higher percentages of cobble from those units with low percentages of sand and silt, but only explained 17% of the variation.

Spatially continuous fish and habitat relationships

There were consistent positive associations between trout and bull trout abundances and habitat unit area, substrate type, instream cover and river section variables. Almost all the trout models (total and each size class) with the best AICc scores included total habitat unit area (Table 2). The amount of boulder area or amount of instream boulder cover, large wood area or the number of log jams, and river section were in the majority of the best trout candidate models (Table 2). Total habitat unit area and gravel (%) were in all the bull trout candidate models with the best AICc scores (Table 3). River section and the total number of log jams were the only other independent variables that were in the bull trout candidate models with the best AICc scores.

The relationship between trout km^{-1} and total habitat area and boulders (%) was always positive, while there was always a negative correlation between trout km^{-1} and river section (Table 2). Large wood area and the number of log jams were, for the most part, positively associated with trout km^{-1}, while instream boulders (%) were for the most part negatively associated with trout km^{-1} (Table 2). Total habitat area, river section and gravel (%) were positively correlated with trout km^{-1}, while the number of log jams was negatively correlated with bull trout km^{-1} (Table 3).

Discussion

No previous studies have used a similar riverscape approach to describe spatially continuous fish and habitat relationships prior to dam removal, and

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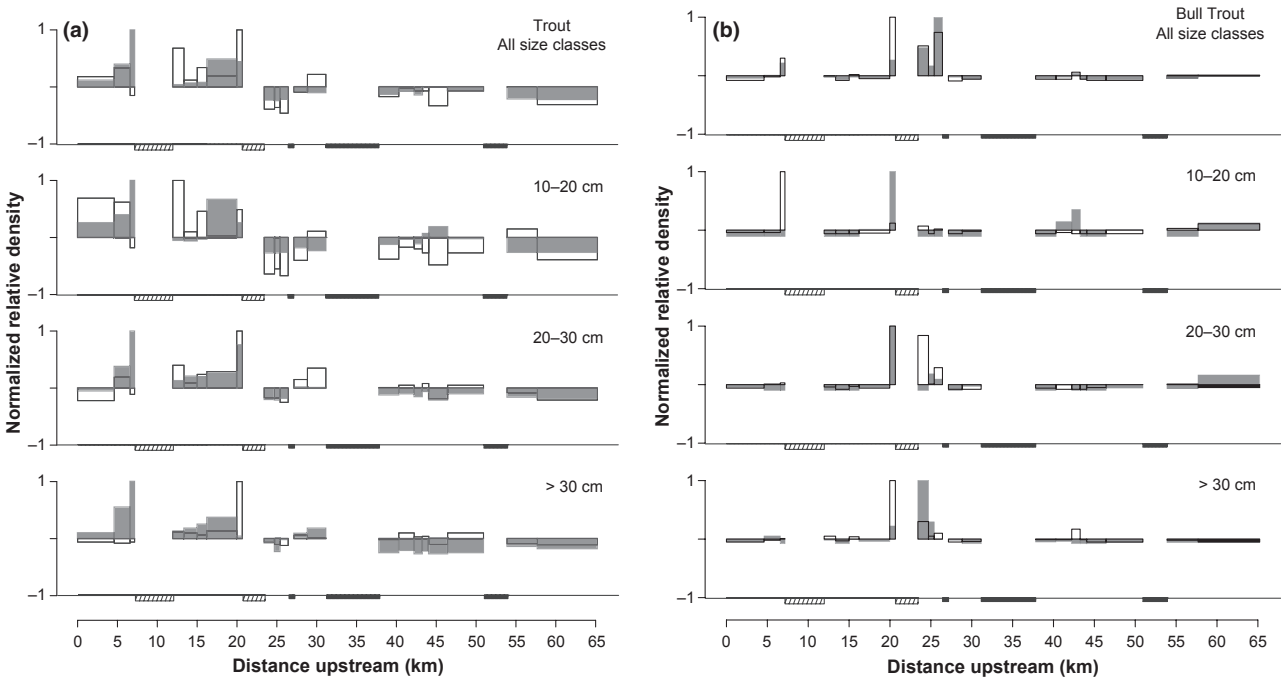

Figure 4. Normalised relative density of (a) trout and (b) bull trout length classes (10–20 cm; >20–30 cm; >30 cm) throughout the Elwha River based on snorkel surveys in the summers of 2007 (grey bars) and 2008 (white bars). Positive and negative values indicate densities that are above and below, respectively, the average density for the entire river. Reservoirs and other unsurveyed sections are indicated along the *x*-axis with hatching and thick black lines, respectively. Distance upstream corresponds to river kilometres in Fig. 1.

consecutive year studies of longitudinal patterns of riverine fish and aquatic habitats are rare (Labbe & Fausch 2000; Gresswell *et al.* 2006). The riverscape approach (Fausch *et al.* 2002; Torgersen *et al.* 2006) provided a spatially comprehensive view of the fish assemblage in the Elwha River and characterised physical habitat conditions from the headwaters to the mouth in two consecutive years. These spatially continuous surveys provided ecological insights based on data visualisations, which establish baselines of the Elwha fish community and important habitat variables prior to a historic dam removal project.

Using a riverscape approach, baseline information was collected on fish at the species, population and assemblage levels and observed patterns allowing analysis at the channel unit, river reach, valley segment or entire river scales (Frissell *et al.* 1986). This approach will be instrumental in understanding the recolonisation and rebuilding of salmon populations, a dynamic process that will be influenced across complex biological hierarchies and multiple spatial scales (Wiens 2002; Allan 2004).

The longitudinal analysis of fish patterns identified biological hotspots for different fish species. The spatial discontinuity of fish assemblages and abundance is not atypical of river networks (Benda *et al.* 2004; Kiffney *et al.* 2006; Rice *et al.* 2008; Torgersen *et al.* 2008). The network dynamic hypothesis and other more empirically based studies have suggested that areas such as tributary junctions and transitional areas between confined and unconfined portions of a drainage network can be areas of accumulation for biota, sediment, wood and nutrients (Baxter *et al.* 1999; Benda *et al.* 2004; Kiffney *et al.* 2006). Mapping patterns of relative abundance in GIS revealed that most (60–69%) of the federally threatened bull trout were observed near or below the reservoirs, areas that will be highly influenced by increased sediment levels during dam removal. The identification of these biological hotspots will be important in guiding future monitoring efforts, both during and following dam removal. In the face of much uncertainty about salmonid recolonisation, as well as limited monitoring budgets, it is important to know where to focus future monitoring efforts. Also, as a consequence of expected high turbidity levels during dam removal, the data on bull trout distribution and patterns of abundance will prove valuable for planning mitigation and protection strategies of this threatened fish species during dam removal.

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Table 1. Physical and biological characteristics of the lower (LE), middle (ME) and upper (UE) Elwha River based on snorkel and habitat surveys in summer 2008

	Elwha River section		
	LE	ME	UE
General characteristics			
Section boundaries	Downstream of Elwha Dam	Between Elwha and Glines Canyon dams	Upstream of Glines Canyon Dam
River km (rkm)	0–7.9	7.9–21.9	21.9–65.7
Number of named tributaries*	1	6	27
Elevation range (m)	0–62	62–184	184–1372
Natural wood recruitment	Altered by dams	Altered by dams	Yes
Natural sediment recruitment	Altered by dams	Altered by dams	Yes
Habitat survey results			
Kilometres surveyed†	7.4	8.6	31.9
Mean wetted width (m; SD)	29 (19)	39 (12)	19 (9)
Channel slope (%; SD)‡	0.4 (0.11)	0.8 (0.36)	1.3 (0.49)
Number of pool units	20	11	49
Number of glide-pool units	17	7	31
Number of glide-riffle units	11	9	42
Number of riffle units	19	17	83
% Pool units by length	30 (31)	25 (17)	24 (11)
% Glide-pool units by length	26 (39)	16 (14)	16 (15)
% Glide-riffle units by length	16 (8)	20 (29)	20 (21)
% Riffle units by length	28 (22)	39 (40)	40 (53)
Mean pool depth (m; SD)	1.24 (0.87)	2.05 (0.70)	1.43 (0.49)
Mean glide-pool depth (m; SD)	1.2 (0.45)	1.21 (0.36)	0.96 (0.41)
Mean glide-riffle depth (m; SD)	0.64 (0.15)	0.77 (0.22)	0.64 (0.31)
Mean riffle depth (m; SD)	0.50 (0.37)	0.90 (0.23)	0.60 (0.26)
LWD jams (count)§	38	8	197
LWD jam area (m^2)	11570	477	12597
LWD km^{-1}	5.1	0.9	6.8
Snorkel survey results			
ONMY km^{-1} (2007/2008)	295/143	227/159	102/25
SACO km^{-1} (2007/2008)	4/1	6/3	4/3

*From Williams *et al.* 1975.
†Excluding side channels, canyons (10.4 km) and reservoirs (7.6 km).
‡Excluding canyon sections.
§Large woody debris (LWD).

Spatially continuous fish and habitat relationships

Longitudinal patterns of fish assemblages were most strongly influenced by the presence of the two dams. The highest species richness occurred downstream of Elwha Dam where salmon still occur, whereas species richness was the lowest above Glines Canyon Dam where only isolated populations of trout and bull trout occur. Although the spatial distribution of local population size varied longitudinally, the patterns were largely consistent between years, despite the different hydrological conditions encountered during the two surveys. There were high correlations of trout and bull trout counts between 2007 and 2008, despite a greater than twofold difference in total fish observed in each year. The percent composition was similar for trout, Chinook salmon and bull trout throughout the 65 km of river.

Survey results revealed that trout were ubiquitous from the headwaters to the mouth and dominated the fish assemblage in both years. There was a difference between fish densities upstream and downstream of the dams. The high densities of trout downstream of Elwha Dam (LE) may be partially explained by the presence of wild and residual hatchery steelhead smolts in that section of the river. A total of 76 500 and 56 500 hatchery smolts were released in May 2007 and 2008, respectively.

The high numbers of *O. mykiss* throughout the Elwha River have important implications for steelhead

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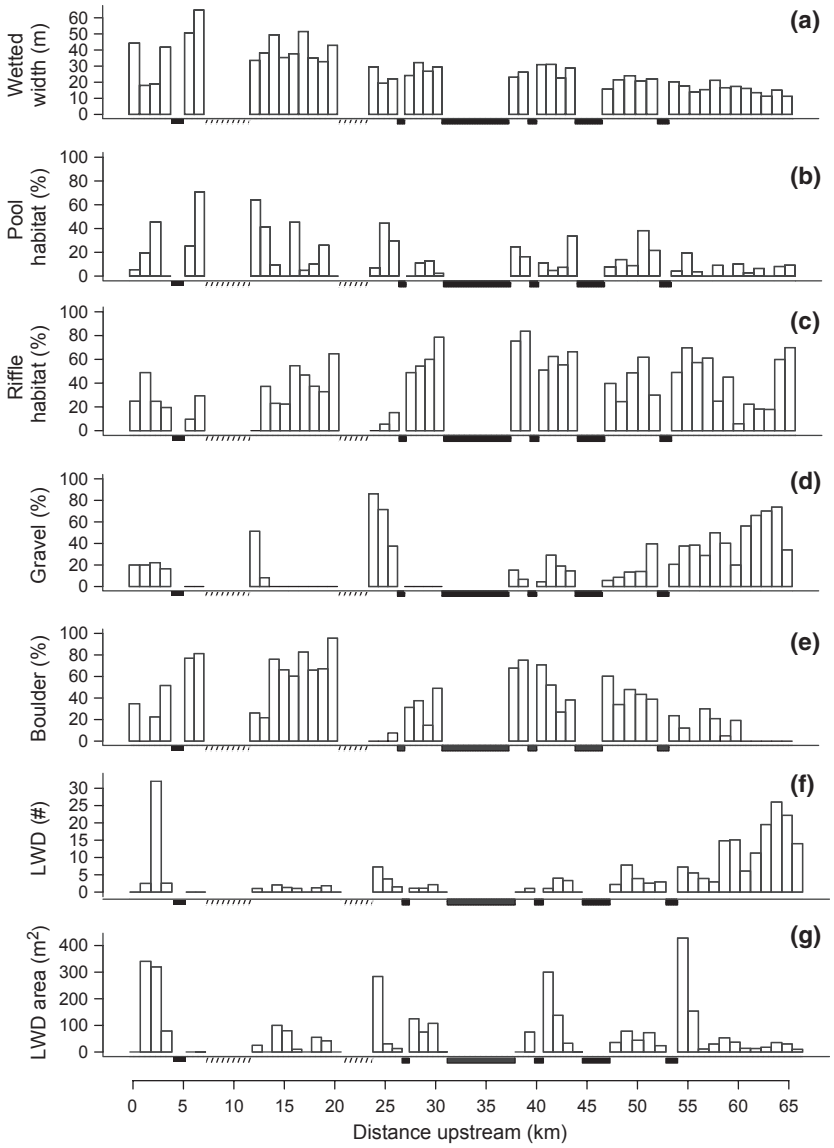

Figure 5. Longitudinal patterns of aquatic habitat in the Elwha River in summer 2008. Mean wetted width (a), percentages of pool (b) riffle (c) habitat and gravel (d) boulder (e) substrate, number (f), and mean area (g) of large woody debris (LWD) jams are summarised in 1-km bins. Reservoirs and other unsurveyed sections are indicated along the *x*-axis with hatching and thick black lines, respectively. Distance upstream corresponds to river kilometres in Fig. 1.

restoration and recolonisation, particularly because wild residents can contribute substantially to steelhead populations (Christie *et al.* 2011). It is anticipated that *O. mykiss* from the upper river will resume anadromy, contribute to recolonisation and interact with returning populations of summer and winter steelhead after dam removal (Brenkman *et al.* 2008a).

The patterns of physical habitat variables, from both univariate and multivariate perspectives, highlighted the effects of both natural (fluvial and geomorphic) and anthropogenic (dams and reservoirs) drivers. River width and depth increased steadily from the headwaters to the mouth because of increasing drainage basin size. This resulted in channel units having, on average, greater area, depth and width in the lower portions of the watershed, which has a role in structuring fish assemblage patterns (Gorman & Karr 1978). Substrate composition also varied naturally along the longitudinal profile of the river. Above the upper dam, gravel showed a nearly monotonic decrease from rkm 65 to 37, with an inverse increase in boulder cover. However, there were also impacts of

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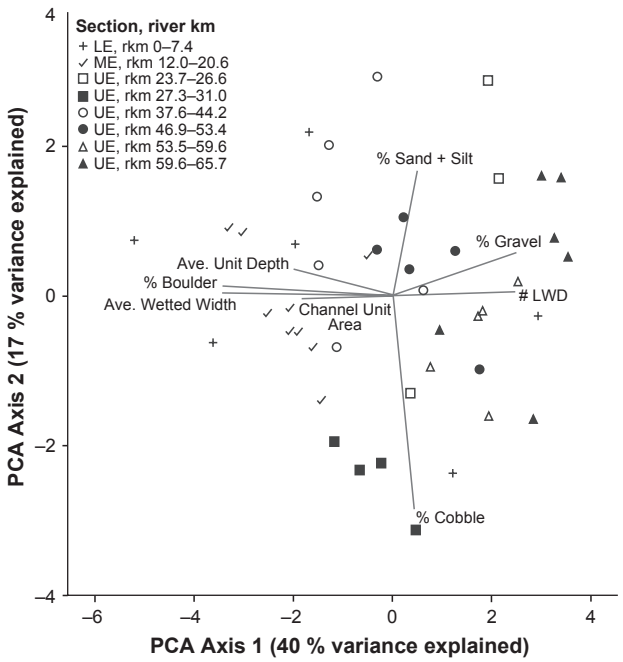

Figure 6. Principal components analysis of habitat variables in the Elwha River in summer 2008. Points in the ordination represent floodplain segments in habitat space. The coding for individual floodplain segments is provided in the legend, which indicates the section (LE, ME and UE; see Fig. 1) and the floodplain segment location in river kilometres. Vectors of the joint plot overlaid on the ordination indicate the orientation and magnitude of correlations of habitat variables with each axis.

the dams, especially in ME, as the dominance of boulders and paucity of gravel below the Glines Canyon Dam demonstrated. In LE below Elwha Dam, there was a less dramatic decrease in gravel, as this section of river still receives sand and gravel inputs from eroding bluffs and terraces, as well as interactions with the floodplain. Previous studies showed that the Elwha River below each dam is dominated by boulders and cobbles (Pohl 2004; Morley *et al.* 2008). Kloehn *et al.* (2008) and Draut *et al.* (2010) also showed reduced levels of channel migration in ME compared with LE, indicative of the increased channelisation and bed armouring in ME. The increase in boulder-dominated substrate has decreased spawning habitat available for anadromous salmonids and contributed to population declines (Pess *et al.* 2008).

The amount and area of LWD also showed different distribution patterns across the riverscape profile. There were more pieces of LWD at higher elevations in UE near the headwaters compared with the rest of the river. However, these were often single pieces rather than large accumulations of LWD, with some exceptions near the transitional reaches between floodplain channels and canyons. This could, in part, be explained in the UE by relatively larger average wood piece size and a relatively smaller wetted channel width. There were smaller LWD jam area and lower density in the ME because of wood entrainment in Lake Mills reservoir and reduced wood recruitment from this river section. Additionally, the ME has a large number of smaller, unsurveyed floodplain channels that contain wood accumulations. The distribution of wood in the LE has been much influenced by human activity through historical removal and recent installation of engineered log jams, as well as natural wood recruitment (Pess *et al.* 2008). The size of LWD accumulations is important as the larger accumulations have a greater and longer-lasting impact on fish habitat, retain higher amounts of organic debris and sediment and exert greater hydrological control by creating larger, longer-lasting scour pools (Abbe & Montgomery 1996). Smaller pieces, on the other hand, lead to finer scale and temporally transient effects during low flows and are transported downstream during larger flows (Hyatt & Naiman 2001).

Habitat area, percent overhanging vegetation and boulder cover, and streambed substrate size were significantly correlated with the abundance of trout and bull trout in the Elwha River. Bull trout persistence has previously been positively correlated with an increase in habitat area (Watson & Hillman 1997; Dunham & Rieman 1999). For other adult salmonid species, such as pink, chum and Chinook salmon, occurrence and abundance patterns have also been correlated to increasing habitat area in Alaska (Pess 2009) and throughout the Pacific Rim (Liermann *et al.* 2010). An increase in habitat area alone, without a change in habitat type or increased resilience to disturbance, can increase the occurrence and abundance of animals (Connor *et al.* 2000). The amount of in-channel cover, regardless of type (e.g. boulder, wood, depth), has consistently been shown to be positively correlated with salmonid fish densities (Shirvell 1990; Fausch 1993; Beechie *et al.* 2005). *Oncorhynchus mykiss* prefer boulder, overhead cover (Shirvell 1990; Fausch 1993) and wood cover (Beechie *et al.* 2005). The correlation between cover types and trout densities may, in part, be spurious and the result of competition with other species, or an artefact of their ability to occupy higher-velocity habitats (Bisson *et al.* 1988).

Although conducted in a remote wilderness river, the riverscape approach proved to be logistically feasible in the Elwha River. Surveys necessarily occurred during a short timeframe (< 1 week) to

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Table 2. Model selection results and parameter estimates for factors associated with trout density (count km^{-1}) in the Elwha River basin. Models for each length class were the best ranked (i.e. most plausible; $\Delta AICc < 4$) of competing models; p is the number of parameters. The ratio of Akaike weights (w_i/w_j) indicates the plausibility of the best-fitting model (w_i) compared with other models (w_j)

Length Class	Model (coefficient* ± SE)	Intercept	Log likelihood	p	$\Delta AICc$	Akaike weight (w_i)	R^2	w_i/w_j
All	WetWid(0.247 ± 0.07), BO_IS (−0.123 ± 0.04), Hab. Area(< 0.001 ± < 0.001)	−4.00	−117.63	4	0.00	0.43	0.73	1.000
	BO_IS (−0.086 ± 0.04), LWDArea(−0.001 ± < 0.001), Hab.Area(< 0.001 ± < 0.001)	−1.69	−118.74	4	2.23	0.14	0.71	3.050
> 10–20cm	Hab.Area(0.002 ± 0.0003), BO(0.66 ± 0.17), OH_IS(1.47 ± 0.46)	−53.24	−203.84	4	0.00	0.73	0.74	1.000
> 20–30 cm	Section(−7.99 ± 2.90), BO(0.74 ± 0.081), BO_IS(−0.86 ± 0.14)	25.54	−172.31	4	0.00	0.39	0.77	1.000
	Hab.Area (< 0.001 ± < 0.001), BO (0.66 ± 0.097), BO_IS (−0.73 ± 0.16)	−6.10	−172.38	4	0.14	0.36	0.77	1.072
	BO (0.64 ± 0.12),BO_IS (−0.82 ± 0.16) WetWid. (0.53 ± 0.25)	−6.25	−173.77	4	2.93	0.09	0.76	4.328
> 30 cm	LWDArea (< 0.001 ± < 0.001), Hab. Area (−0.0012 ± < 0.001), BO_IS (−0.086 ± 0.039)	−1.69	−117.63	4	0.00	0.43	0.73	1.000
	Hab.Area (< 0.001 ± < 0.001), BO_IS (−1.23 ± 0.039), WetWid. (0.25 ± 0.068)	−4.00	−118.74	4	2.23	0.14	0.71	3.049

*#LWD = number of large woody debris jams; LWDArea = total LWD area (m^2); Hab.Area = total channel-unit area (m^2); Section = LE, ME, UE; Ave.Depth = average channel-unit depth (m); SACO Abund. = abundance of bull trout; GR = percent gravel; BO = percent boulder; SA_SI = percent sand + percent silt; OH_IS = percent overhanging vegetation (in stream); BO_IS = percent boulder habitat (in stream); WetWid. = average wetted width (m).

Table 3. Model selection results and parameter estimates for factors associated with bull trout density (count km^{-1}) in the Elwha River basin. Models for each size category were the best ranked (i.e. most plausible; $\Delta AICc < 4$) of competing models; p is the number of parameters. The ratio of Akaike weights (w_i/w_j) indicates the plausibility of the best-fitting model (w_i) compared with other models (w_j)

Length class	Model (coefficient* ± SE)	Intercept	Log likelihood	p	$\Delta AICc$	Akaike weight (w_i)	R^2	w_i/w_j
All	Section (4.30 ± 1.54), GR(0.17 ± 0.035), Hab.Area(< 0.001 ± < 0.001),	−21.54	−129.87	4	0.00	0.58	0.45	1.000
	#LWD(−0.24 ± 0.12), GR(0.21 ± 0.043), Hab.Area(< 0.001 ± < 0.001)	−5.98	−131.74	4	3.74	0.09	0.40	6.488
> 30 cm	Section(4.01 ± 1.44), GR(0.16 ± 0.032) Hab.Area(< 0.001 ± < 0.001)	−21.45	−127.02	4	0.00	0.50	0.47	1.000
	#LWD(−0.28 ± 0.11), GR(0.21 ± 0.039), Hab.Area(< 0.001 ± < 0.001)	−6.68	−127.94	4	1.84	0.20	0.45	2.509

*#LWD = number of large woody debris jams; Hab.Area = total channel-unit area (m^2); GR = % gravel; Section = LE, ME, UE.

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minimise the effects of fish movements within the river. Conversely, the narrow timeframe of the surveys provides only a snapshot of river fish assemblages during summer low flows and limits any evaluation of population trends over time. Such an evaluation would require more intensive and repeated sampling to account for the high inter-annual and temporal variability in fish abundances (Brenkman & Connolly 2008; Dauwalter *et al.* 2009). Because sampling occurred only during summer low flows, key salmonid species such as adult coho and chum salmon and winter steelhead were missed, which typically enter the river in autumn. The snorkel methods were also ineffective at sampling benthic species (e.g. sculpins) and juvenile bull trout that are typically observed more at night (Thurow *et al.* 2006). Despite these limitations, the approach was relatively low in cost ($60 000 US per year) and provided multi-scale fish and habitat data in a remote wilderness river.

It was also not possible to survey the reservoirs (8.5 km) and portions of canyons with white water rapids ($\approx$ 8.8 km). Rainbow trout and bull trout exist in each reservoir, and alternate sampling techniques, such as hydroacoustics, would be required to estimate their abundances. It is likely that some adfluvial bull trout moved upriver in the late summer and were detected during the snorkel surveys, particularly in the river above Lake Mills. The unsurveyed portions of white-water rapids in remote portions of canyons pose major challenges to any fish sampling technique. These canyons will serve as important migratory corridors and staging areas for salmonids that recolonise the upper portions of the watershed after dam removal.

Conclusions

The historic dam removal project in the Elwha River will provide an unprecedented opportunity for salmon recovery. One of the most important aspects of the project is the recolonisation of multiple salmonid species into pristine habitats protected within Olympic National Park. This study provides an important landscape-scale context for understanding the changes expected to occur in fish assemblage structure after dam removal, including: (1) upstream and downstream recolonisation by salmonids; (2) resumption of anadromy by upper river bull trout, rainbow trout and cutthroat trout populations; and (3) increased species richness in portions of the river upstream of the dams. A combination of the riverscape perspective and more traditional site-based, discontinuous fisheries surveys will likely be required to understand recolonisation at multiple temporal and spatial scales. In the light of the many upcoming dam removal projects in the western United States, increased monitoring efforts that focus on the collection of spatially continuous fish and habitat data should prove valuable for evaluating the effectiveness of dam removal at restoring anadromous salmonids and the riverscapes in which they reside.

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