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Abstract

The impending removal of two dams on the Elwha River in Washington State offers a unique opportunity to study ecosystem restoration at a watershed scale. We examine how periphyton and benthic invertebrate assemblages vary across regulated and unregulated sections of the Elwha River and across different habitat types, and establish baseline data for tracking future changes following dam removal. We collected multiple years of data on physical habitat, water chemistry, periphyton, and benthic invertebrates from 52 sites on the Elwha River and a reference section on the Quinault River, a neighboring basin. We found that substrate in regulated river sections was coarser and less heterogeneous in size than in unregulated sections, and summer water temperature and specific conductivity higher. Periphyton biomass was also consistently higher in regulated than unregulated sections. Benthic invertebrate assemblage structure at sites above both dams was distinct from sites between and below the dams, due in large part to dominance of mayfly taxa compared to higher relative abundance of midges and non-insect taxa at downstream sites. Following dam removal, we anticipate that both periphyton and benthic invertebrate abundance and diversity will temporarily decrease between and below dams as a result of sediment released from behind the reservoirs. Over the long-term, increased floodplain heterogeneity and recolonization by anadromous fish will alter benthic invertebrate and periphyton assemblages via increases in niche diversity and inputs of marine-derived nutrients. The extended timeline predicted for Elwha River recovery and the complexities of forecasting ecological response highlights the need for more long-term assessments of dam removal and river restoration practices.

Introduction

Primary and secondary producers serve vital roles in the structure and function of aquatic ecosystems. In medium and large rivers in particular (≥ 4th order), primary production by periphyton is a major food source for higher trophic levels (Thorp and Delong 1994, 2002). Secondary producers (e.g., aquatic invertebrates) serve as a direct food source for most fish and strongly influence nutrient cycling and primary productivity (Merritt and Cummins 1996, Wallace and Webster 1996). As periphyton and invertebrates are directly associated with the benthos, they are likely to be profoundly influenced by both the presence and removal of dams (Bednarek 2001, Doyle et al. 2005, Thomson et al. 2005). Periphyton are also particularly sensitive to nutrient availability, which may itself be strongly influenced by dams via sorption to fine sediments stored in reservoirs and the blockage of anadromous fish and associated subsidies of marine-derived nutrients (Dent et al. 2002, Gende et al. 2002, Stanley and Doyle 2002). The rapid response and recovery that periphyton and benthic invertebrates typically display to disturbance are also well suited to monitoring efforts seeking to capture ecological response trajectories to dam removal (Blinn et al. 1998, Shannon et al. 2001, Doyle et al. 2005).

Dams dramatically affect rivers and aquatic biota by altering hydrology, sediment transport, nutrient cycling, temperature regimes, and the movement of organisms (Petts 1984). The degree of impact on aquatic communities depends on the type and function of the dam as well as the specific characteristics of the affected watershed (Ward and Stanford 1995, Hart et al. 2002). The most obvious effect of river regulation is the conversion of lotic to lentic environments. The formation of reservoirs

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results in a shift from aquatic communities adapted to free-flowing, erosional habitats to those suited to depositional environments (Petts 1984). For the most part, these lentic environments comprise a small proportion of available habitat; therefore a majority of studies have focused on larger scale impacts on aquatic communities downstream of dams (Ligon et al. 1995). For periphyton, less mobile substrate, increased temperatures, and higher nutrients in tailwaters often lead to the proliferation of filamentous green algae, thus changing the quality and quantity of food resources available to secondary producers (Blinn et al. 1998, Munn and Brusven 2004, Chester and Norris 2006). Benthic invertebrate diversity below dams often decreases, with corresponding shifts in taxonomic and functional composition relative to unregulated sections within the same river (Munn and Brusven 1991, Vinson 2001). In regulated rivers with extreme and non-seasonal flow fluctuation, exposure can also dramatically reduce standing stocks of both periphyton and benthic invertebrates downstream of impoundments (Gislason 1985, McKinney et al. 1999).

Although much has been written on the deleterious effects of dams on biotic and abiotic processes, relatively few studies have documented the effects of dam removal (Hart et al. 2002). Existing studies typically concern low-head dam (< 10 m) removal responses of geomorphology and chemistry (Stanley and Doyle 2002, Orr et al. 2006, Velinsky et al. 2006) or fish (Kanehl et al. 1997, Smith et al. 2000, Burdick and Hightower 2006). Studies that have examined dam removal responses lower in the food web are often designed to capture localized effects by focusing on changes in community structure in formerly impounded areas or habitats immediately downstream of the dismantled dam (but see Pollard and Reed [2004] and Sethi et al. [2005]). We are interested in capturing the potentially subtler, but more spatially extensive changes that occur across the larger river network as a result of dam removal. Two large dams (> 30 m in height) on the Elwha River in Washington State are scheduled to be removed over the next decade (DOI 1996, Duda et al. 2008). We examined existing benthic community structure to begin a long-term study of the response of invertebrates and periphyton to dam removal and river recovery.

Although the dams on the Elwha are of moderate size (reservoir capacities < 50 x 10^6 m^3), no dam removal of this scale has yet been undertaken (Gregory et al. 2002, Nilsson et al. 2005). Moreover, two dams will be removed simultaneously. Dam removal on the Elwha River is also significant in its potential to restore anadromous salmonid populations. Historically, 10 native anadromous fish stocks were found in the Elwha River. Due to habitat loss and hatchery intervention, current salmon populations are reduced by more than 90% with dramatic shifts in species composition (Wunderlich et al. 1994, Pess et al. 2008). As 83% of the Elwha Watershed is located within Olympic National Park (ONP), this restoration effort affords a greater opportunity for true recovery, with fewer confounding factors complicating interpretation of response (i.e., drastically different land-use than before dam construction). Although the two dams were built in the early 1900s to generate hydroelectric power, they have been operated as run-of-the river since the 1940s. Thus, hydrologic alteration is not severe, with minor attenuation of flood flows and moderate depression of low flows (Pohl 2004).

We hypothesize that the two primary mechanisms by which the Elwha River dams have affected periphyton and invertebrate assemblages are the obstruction of sediment and wood transport to the lower and middle sections (nearly 18 million cubic meters of sediment are stored in the reservoirs; DOI 1996), and the blockage of anadromous fish passage between and above the dams (Wunderlich et al. 1994). Not only has lack of fish passage contributed greatly to major decline in total fish populations, it has also eliminated the upstream transport of marine-derived nutrients from anadromous fish spawning in historically oligotrophic headwaters (Munn et al. 1996, 1999). Associated changes in river bed characteristics and nutrient availability are likely to have had both direct and indirect effects on benthic invertebrates and periphyton. Heat storage in the two reservoirs has also increased late summer and early fall water temperatures in regulated sections of the river (Wunderlich et al. 1994).

Our primary objectives are to improve understanding of how the Elwha dams have shaped current periphyton and benthic invertebrates assemblages, and to establish baseline data that will better enable us to track changes following dam removal. Assessment of most river restoration actions are limited by sparse pre-project data (Pess et al. 2005), and this is particularly the case for

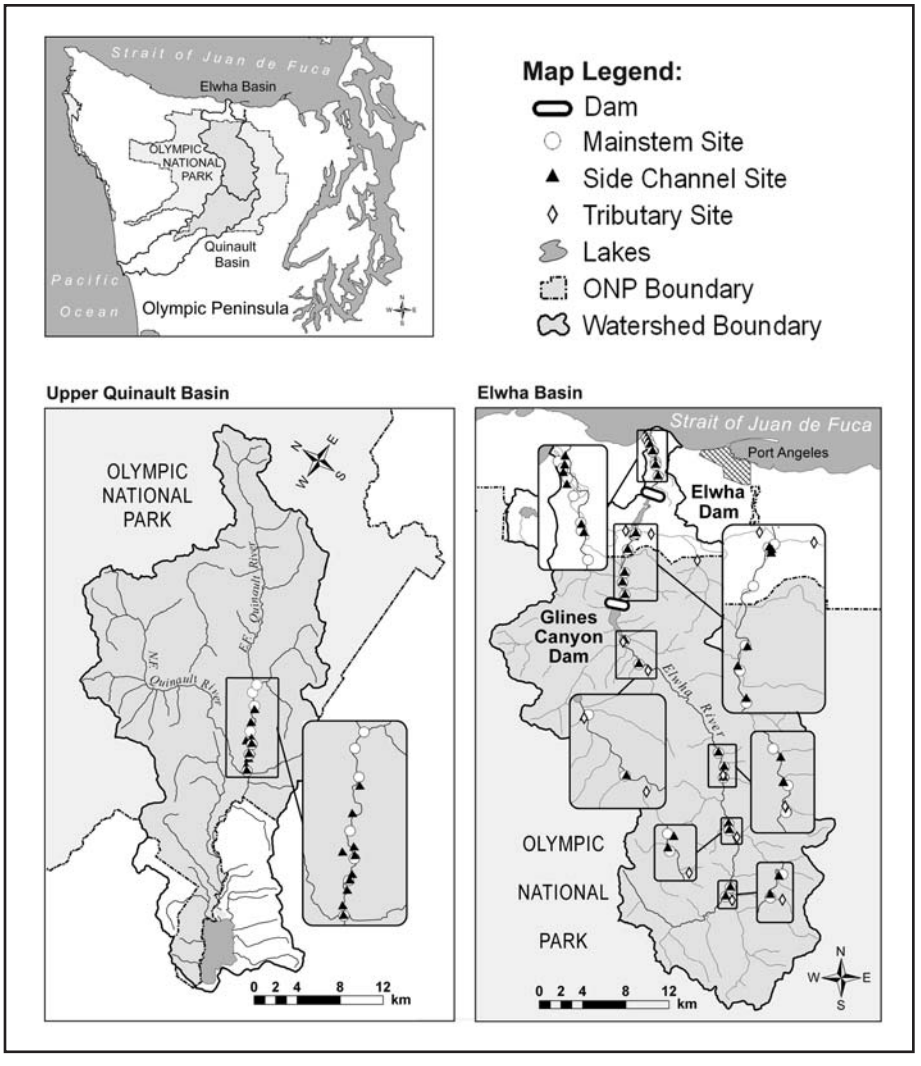

Figure 1. Study region, indicating locations of the Elwha and Quinault River Basins on the Olympic Peninsula of Washington State. Study sites sampled from 2004-2006 are plotted by habitat type. Insets magnify floodplain sections and are intended to minimize the overlap among map symbols.

dam removal, a relatively new restoration strategy (Doyle et al. 2005). Here, we address the following questions: (1) How do benthic invertebrate and periphyton assemblages in regulated and unregulated sections of the Elwha River compare to each other and to the unregulated Quinault River, (2) Are there major differences in benthic invertebrates and periphyton across different habitats types (mainstem, side channels, and tributaries), and (3) How will benthic invertebrates and periphyton respond to dam removal in both the short- and long-term?

Methods

Study Region and Site Selection

The 6th order Elwha River (833 km^2 drainage area) originates in the mountains of the Olympic Peninsula in Washington State, flows northward for 72 km, and empties into the Strait of Juan de Fuca at the Lower Elwha Klallam Reservation, 6 km west of the City of Port Angeles (Figure 1). The Elwha (32 m high) and Glines Canyon (64 m high) dams form three distinct sections of the Elwha: the lower river from the mouth to the Elwha Dam

(8 km long, elevation 0–30 m, hereafter referred to as LE), the middle river (ME) between the two dams (14 km long, elevation 60-120 m), and the upper river (UE) from Glines Canyon Dam to the headwaters (50 km long, elevation 170-1300 m). All of UE and approximately half of the ME subbasins are contained within ONP, with LE flowing through a mosaic of largely forested private, state, and tribal lands. For further background on the Elwha River and the history of the two dams, see Duda et al. (2008). Our sampling also included a 10-km section of the East Fork Quinault River (QU, elevation 118-179 m) as a reference system due to its similarity to the pre-dammed Elwha in sediment regime and anadromous fish populations (McHenry and Pess 2008). QU, located entirely within ONP, drains an area of 210 km^2 immediately southwest of the Elwha Basin.

We collected benthic invertebrate and periphyton samples from the Elwha and Quinault Rivers from 2004–2006 during the summer (late July–early September), a typical index period that coincides with high taxa richness, low flow variability, and good site accessibility. The distribution of monitoring sites was non-random. Within the Elwha River basin, sites spanned 57 rkm and were located a minimum of every 2 rkm except in UE, where steep river canyons separated four distinct alluvial floodplains (Figure 1). Specific sampling locations within a given 2 km reach were selected to coincide with side channel complexes and tributary junctions, such that multiple habitat types (mainstem=MS, side channel=SC, and tributary=TR) could be sampled in proximity. Nearly all MS sample sites had a spatially paired SC site nearby. All study sites were also located at least 2 rkm from either dam to avoid localized effects. We used 52 unique sites across the Elwha Basin, 25 of which were sampled in all three years, and 45 sampled in both 2005 and 2006. We collected similar data from 12 sites in QU in 2005 and 2006.

Sampling Parameters and Protocols

We collected benthic invertebrate samples from riffle margins using a Slack sampler (500 µm mesh, 0.25 m^2 frame; Moulton et al. 2002). Based on Munn et al. (1996) and statistical power analyses of pilot data, five Slack samples were collected from each site and subsequently pooled for analysis. At MS sites, where riffle length often exceeded 100 m, samples were distributed evenly over the length of a single riffle; samples were collected over five consecutive riffles at most SC and TR sites. Sample location within a given riffle or multiple riffles was randomized. A sub-sample of 600 invertebrates per sample were identified to the lowest practical taxonomic level (typically species or genus) and converted to density based on sample area and the proportion of each sample processed.

At each site, we sampled periphyton from five rock cobbles collected adjacent to each of the invertebrate samples. Periphyton was scrubbed and rinsed from each cobble, pooled into one sample, homogenized, and filtered onto two 47 mm glass-fiber filters (1 µm pore size) for analysis of chlorophyll *a* concentration and ash-free dry mass (AFDM). Chlorophyll *a* specifically measures the algal component of periphyton whereas AFDM is a measure of total periphyton biomass which includes algae, fungi, bacteria and microzoans (Steinman and Lamberti 1996). We extracted chlorophyll *a* from filters with acetone and measured the absorbance of the resulting supernatant using fluorometry (Marker et al. 1980). AFDM was calculated following the gravimetric method (Steinman and Lamberti 1996). Chlorophyll *a* concentration and AFDM weights were converted to biomass per unit area (mg/cm^2 for AFDM, and µg/cm^2 for chlorophyll *a*) based on total rock surface area sampled at each site (Dall 1979).

One set of water chemistry samples was collected at the downstream end of each sample reach immediately prior to benthic invertebrate and periphyton sampling in LE and ME. In UE, backcountry samples were collected on a single day, held on ice, and returned to the front country on horseback. All samples were kept frozen until they were analyzed for concentrations of total phosphorous (TP), total nitrogen (TN), phosphate (PO_4), nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), and silicate (SiO_4) using the continuous flow Alpkem RFA/2 system. This nutrient dataset will be presented elsewhere in relation to stable isotope monitoring.

We characterized the stream bed within each Slack sample frame by a visual estimate of percent coverage across five substrate classes (silt, sand, gravel, cobble, and boulder) and assigned an embeddedness rating of 1-5 based on the proportion and extent of substrate covered in sand or silt (Platts et al. 1983). Temperature and specific

conductivity at each invertebrate sample were measured using a YSI model 85 multimeter, and water depth and velocity recorded using a Global Water flow probe. We averaged values for each parameter across the five invertebrate sample locations at each site. We measured wetted width, gradient, and bank-full width using an Impulse laser range finder. Particle size distribution across the entire sample riffle(s) was characterized by pebble counts (Wolman 1954), from which we calculated D_{50} (median particle size) and D_{84}:D_{16} (diameter at which 84% of pebbles are smaller divided by the diameter at which 16% of pebbles are smaller, a measure of particle size variability). Canopy closure was measured using a modified convex spherical densiometer and averaged across 18 readings per sample site (Lazorchak et al. 2000). We determined elevation, total drainage area, and rkm at each site by using ArcInfo 9.1 GIS software to overlay a 1:24,000 scale hydrography layer with 30 m resolution digital elevation models. Hydrologic data was downloaded from the USGS National Water Information System webpage from the real-time flow gages on the Elwha River at rkm 14 in ME, and on the Quinault River 20 km downstream from our reference section.

Statistical Analyses

For habitat data, we provide descriptive information on all parameters collected, but focus our statistical analyses on a subset of 7 variables that we expected to differ by habitat type and river section and that were uncorrelated: two measures of site-scale substrate (D_{50} and D_{84}:D_{16}), two measures of sample-scale substrate (percent gravel + fines (silt and sand) and embeddedness), specific conductivity, water temperature, and mean canopy closure. For comparisons of habitat types, we analyzed spatially paired MS and SC sites (9 pairs in 2004, 19 in 2005, and 21 in 2006) and tested for statistical differences with 2-tailed paired t-tests. We excluded TR sites from the habitat comparisons as none were sampled in either LE or QU. Where significant differences existed between MS and SC sites, we analyzed the log ratio of paired values (MS:SC) with a 1-way ANOVA to determine if habitat difference varied as a function of river section, testing for differences between means with Tukey's HSD test. To examine differences in study variables by river section we also used a 1-way ANOVA, pooling MS and SC sites if no significant differences were detected by habitat type (paired t-test, $P > 0.05$), and focusing only on MS sites if habitat-type differences were detected.

We conducted two analyses on periphyton data: (1) 2-way ANOVA's to test for differences in chlorophyll *a* and AFDM by river section, habitat type, and their interaction for each year, and (2) backward stepwise multiple linear regression to examine the relationships between periphyton (AFDM and chlorophyll *a*) and measures of physical habitat (canopy cover, embeddedness, temperature, velocity, depth), water chemistry (conductivity, dissolved inorganic nitrogen [DIN = $NO_3 + NO_2 + NH_4$], PO_4, and SiO_4) and elevation. Due to limited sample size, data from 2004, TR sites, and QU were not included in the analyses. For both the ANOVA's and regression analysis, model residuals were examined for approximate normality, independence, and equality of variance and data were log or square root transformed as appropriate. With the exception of the periphyton regression analysis, each year (2004-2006) was analyzed separately. Physical habitat and periphyton analyses were done using the statistical software packages R version 2.6.0 and SYSTAT version 12.

We used both univariate and multivariate statistics to analyze benthic invertebrate data. We used a 3-way ANOVA to examine differences in density, taxa richness, and diversity by river section, habitat type, and sample year. To analyze patterns of community structure and relate this structure to measured environmental variables associated with each sample site, we used a suite of complementary multivariate techniques, available in the PRIMER statistical software package (version 6, Clarke and Gorley 2006). We square-root transformed the species by sample data matrix (hereafter referred to as the invertebrate matrix), to reduce the effects of right-skew and matrix wide non-detections and to down-weight the influence of common taxa with relatively high abundances (Clarke and Warrick 2001, McCune and Grace 2002). Treating each year separately, we created triangular resemblance matrices of pair-wise similarities between all sites based upon the transformed density of species using the Bray-Curtis distance, the most appropriate choice for species by sample data (Clarke et al. 2006).

We used non-metric multidimensional scaling (nMDS) to graphically analyze the patterns of

invertebrate community structure by section and habitat type and tested for differences among groups using analysis of similarities (ANOSIM). nMDS is an iterative ordination procedure where the distance between points (representing sample sites) most accurately represents the pair-wise similarities in the triangular resemblance matrix. A stress value is calculated that represents the goodness-of-fit between the ordination and the ranked similarities. ANOSIM is a non-parametric analog to analysis of variance (Clarke and Warrick 1994) that tests for compositional differences among groups of sites based upon the ratio of rank similarities found in the resemblance matrix and computes a statistic, R, that takes a value between 1 (within group sites are more similar to each other than any sites from other groups) and 0 (similarities among sites does not differ by groups). We ran a 2-way crossed ANOSIM, with section and habitat type as factors, and used a permutation test (999 iterations) to develop a null distribution that allowed calculation of exact *P* values.

We next used the SIMPER procedure (Clarke and Warrick 2001) to determine the taxonomic groups driving the dissimilarity among factors (river section and habitat type) that were significantly different according to ANOSIM tests. We aggregated the data by summing relative densities of taxa into 9 groups (Ephemeroptera, Plecoptera,Trichoptera, Coleoptera, Diptera, Chironomidae, Odonata, Lepidoptera, and all non-insect taxa), computed an average dissimilarity between groups (based upon Bray-Curtis distance), and then computed the average taxonomic group percentage contribution to this dissimilarity. Exploring differences in invertebrate assemblages among sites, treatment levels, or environmental gradients using multivariate statistics can be more interpretable at higher taxonomic levels, without large departures in sensitivity when compared with lower taxonomic levels (Bailey et al. 2001).

To relate ordinations of measured environmental factors (physical habitat, water chemistry, periphyton biomass, and elevation) at each site to ordinations of invertebrate assemblage data, we ran the BIO-ENV procedure in PRIMER (Clarke and Ainsworth 1993). Resemblance matrices based upon environmental variables were calculated

TABLE 1. Mean values (±1 SD) for physical habitat parameters collected at MS, SC, and TR sites on LE, ME, UE, and QU from 2004-2006. Depth and velocity were measured at the location from which benthic invertebrates and periphyton were collected (riffle margins), and are not representative of the entire channel. Dashes indicate that no data were collected.

	Lower Elwha		Middle Elwha			Upper Elwha			Quinault	
	MS	SC	MS	SC	TR	MS	SC	TR	MS	SC
2004	**n=3**	**n=2**	**n=3**	**n=3**	**n=0**	**n=5**	**n=5**	**n=4**	**n=0**	**n=0**
Gradient (%)	1.3(1.0)	2.0(0.7)	1.7(1.4)	1.7(1.0)	-	1.2(0.3)	1.4(0.7)	1.9(0.5)	-	-
Bankfull Width (m)	130(69)	18(9)	65(24)	24(6)	-	91(38)	36(23)	42(23)	-	-
Wetted Width (m)	33(14)	5(1)	47(11)	12(1)	-	32(6)	14(8)	8(2)	-	-
Depth (cm)	26(9)	15(13)	37(35)	31(23)	-	19(3)	19(3)	20(3)	-	-
Velocity (m/s)	0.8(0.3)	0.7(0.5)	0.8(0.5)	0.9(0.3)	-	0.5(0.1)	0.6(0.1)	0.7(0.1)	-	-
2005	**n=7**	**n=5**	**n=5**	**n=4**	**n=3**	**n=9**	**n=8**	**n=5**	**n=4**	**n=8**
Gradient (%)	1.3(0.7)	0.7(0.5)	1.6(1.1)	1.4(0.8)	2.2(0.7)	1.3(0.8)	1.1(0.7)	1.7(0.6)	0.4(0.2)	0.8(0.4)
Bankfull Width (m)	70(26)	18(5)	64(33)	22(9)	17(3)	51(37)	27(17)	22(14)	78(26)	19(8)
Wetted Width (m)	37(12)	10(6)	41(10)	10(4)	8(2)	25(6)	11(7)	9(3)	20(7)	4(1)
Depth (cm)	38(31)	20(11)	53(29)	40(19)	13(2)	21(15)	23(22)	17(2)	20(2)	10(10)
Velocity (m/s)	1.5(0.8)	0.6(0.4)	1.2(0.9)	1.3(1.1)	0.5(0.1)	0.6(0.4)	0.5(0.2)	0.5(0.1)	0.5(0.2)	0.6(0.6)
2006	**n=6**	**n=7**	**n=6**	**n=7**	**n=3**	**n=9**	**n=8**	**n=5**	**n=6**	**n=6**
Gradient (%)	1.2(0.9)	1.1(0.4)	1.0(0.5)	1.4(0.5)	2.5(0.7)	1.0(0.4)	1.5(0.7)	1.9(0.7)	0.8(0.5)	1.1(0.5)
Bankfull Width (m)	92(39)	22(8)	73(23)	15(6)	13(4)	45(17)	26(18)	26(13)	54(8)	21(9)
Wetted Width (m)	42(14)	11(6)	38(14)	8(5)	9(2)	32(9)	12(11)	11(3)	21(6)	5(2)
Depth (cm)	26(6)	33(40)	25(3)	15(10)	18(4)	20(5)	18(7)	18(4)	37(23)	11(4)
Velocity (m/s)	0.6(0.1)	0.7(0.2)	0.5(0.2)	0.4(0.2)	0.5(0.1)	0.4(0.1)	0.4(0.1)	0.6(0.2)	0.7(0.5)	0.4(0.2)

using Euclidian distance on log (x+1) transformed data that were normalized (mean = 0, sd = 1) to eliminate differences in measurement scale. The BIO-ENV routine is iterative, as different subsets of the environmental data are used until the rank correlation between matrices (invertebrate and environmental) is maximized. We ran the stepwise procedure (BVSTEP) with 6 initial variables and 500 random starts on 2005 and 2006 data. As our 2004 datasets were less complete (fewer sample sites in LE and ME, and no chlorophyll or water chemistry data for UE), we did not include this year in the BIO-ENV analyses. Finally, we ran a Principle Components Analysis (PCA) on the environmental variable sub-sets from BIO-ENV that best matched the invertebrate matrices.

Results

Physical habitat

Physical habitat parameters did not change greatly across the three years of the study (Table 1). Of the seven physical habitat parameters tested, only substrate was significantly different by habitat type. At the site scale, median particle size diameter (D_{50}) was significantly smaller in SC than in MS sites in 2005 (paired t-test, n = 19, $P < 0.01$) and 2006 (n = 21, $P < 0.05$) but not in 2004 (n = 9, $P = 0.07$). At the sample scale, there was a higher percentage of gravel and fines in SC than at corresponding MS sites in 2004 (n = 9, $P < 0.05$), but not in subsequent years. Based on ANOVA of the log ratio of MS:SC, differences in the percent of gravel and fines were significantly more pronounced in ME than in UE. The differences in D_{50} between MS and SC sites did not differ by river section in either year ($P > 0.05$, ANOVA). We pooled MS and SC sites in subsequent analyses of physical habitat differences by river section, with the exception of D_{50} and percent gravel + fines, which were significantly different by habitat type.

In general, substrate composition of LE and ME sites was distinct from UE, with QU sites between these two groups (Figure 2). This trend was consistent across years, although not statistically significant in all cases. The greatest difference in median particle size diameter (D_{50}) was observed between UE and ME (Tukey's HSD, $P < 0.05$ for 2005 and 2006), with LE and QU falling between this range. Particle size variability (D_{84}:D_{16}) was significantly higher in UE than LE in all three years, and also higher than ME and QU in 2005 ($P < 0.05$). At the sample scale, a higher percentage of gravel and fines were observed in all years at UE and QU compared to LE and ME. However, these differences were only statistically significant between UE and ME in 2005, and between QU and ME in 2006 ($P < 0.05$). Embeddedness was signifi-

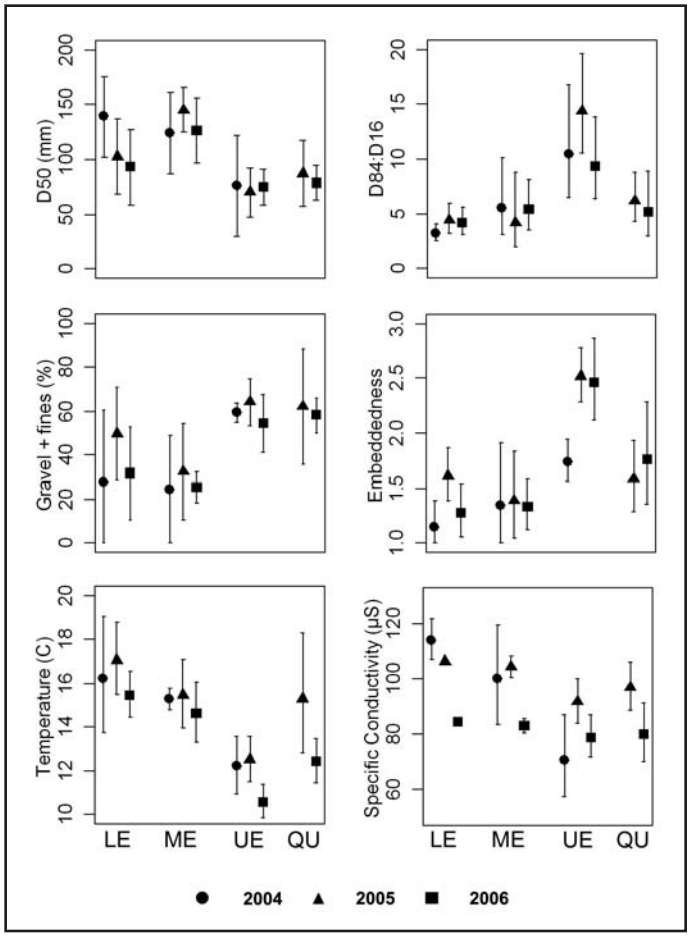

Figure 2. Habitat parameter mean values by river section and sample year plotted with 95% CI derived from log transformed data. For D_{50} and gravel + fines, data are plotted for MS sites only; all other plots combine MS and SC sites by river section. See Table 1 for sample size.

cantly higher in UE compared to LE in all three years, and also higher than ME and QU in 2005 and 2006 ($P < 0.01$). UE sites were significantly cooler than LE and ME in all sample years and also cooler than QU in 2006 ($P < 0.001$). Specific conductivity was significantly lower in UE than LE in 2004 and 2005 and also lower than ME in 2005 ($P < 0.01$). Specific conductivity in QU fell between these two ranges. Although canopy was consistently more open in UE compared to LE or ME, with QU in the middle—differences were not significant.

Periphyton

Mean chlorophyll *a* and AFDM concentrations across years, sections, and habitats ranged from 0.013 to 5.5 μg cm^{-2} and 0.056 to 0.73 $mgcm^{-2}$, respectively (Table 2). In general, trends in chlorophyll *a* and AFDM were similar to those found for physical habitat variables, with LE and ME grouping separately from UE (Table 2). QU was more similar to LE and ME than to UE. There were also differences between MS and SC habitat, but this trend varied both by section and by year. In 2004, habitat type had no effect on either chlorophyll *a* or AFDM; however AFDM was significantly higher (MS and SC combined) in LE and ME than in UE (2-way ANOVA, $P < 0.01$). We did not examine variation in chlorophyll *a* by river section as this parameter was not collected from UE or QU in 2004. In 2005, there were no significant differences in AFDM among habitats or sections but chlorophyll *a* concentrations were higher in QU relative to UE and significantly higher in SC's relative to MS's in all sections except ME ($P < 0.01$). In 2006, AFDM and chlorophyll *a* concentrations in LE, ME, and QU were significantly higher than in UE, but the only significant difference between SC and MS sites was in QU, where AFDM and chlorophyll *a* concentrations were significantly higher in MS relative to SC ($P < 0.01$).

A stepwise multiple linear regression analysis showed that water chemistry and a sub-set of physical habitat parameters best predicted periphyton variables. Temperature, velocity, conductivity, and elevation were not identified as significant variables in either model ($P > 0.10$). Models including PO_4, SiO_4, DIN, and depth explained 53% of the variation in AFDM density across all years and habitats ($P < 0.001$). Similarly, PO_4, SiO_4, DIN, along with canopy and embeddedness, explained 53% of the variation in chlorophyll *a* concentrations ($P < 0.001$). Both chlorophyll *a* and AFDM were positively correlated with DIN and SiO_4, but negatively correlated with PO_4. AFDM was positively correlated with depth. Chlorophyll *a* was positively correlated with canopy but negatively correlated with embeddedness.

Benthic Invertebrates

We identified a total of 244 benthic invertebrate taxa at our study sites. Of these, 119 were unique to Elwha River sites, 7 were unique to Quinault

TABLE 2. Mean values for chlorophyll *a* (μgcm^{-2}) and periphyton AFDM ($mgcm^{-2}$) (±1 SD) for MS, SC, and TR habitats in LE, ME, UE, and QU from 2004-2006. Dashes indicate that no data were collected.

		Lower Elwha		Middle Elwha			Upper Elwha			Quinault	
		MS	SC	MS	SC	TR	MS	SC	TR	MS	SC
Chl a	2004	1.9 (1.7)	5.5 (4.2)	1.0 (0.39)	2.8 (3.6)	-	-	-	-	-	-
	2005	0.12 (0.066)	0.18 (0.024)	0.090 (0.038)	0.073 (0.043)	0.097 (0.027)	0.029 (0.015)	0.064 (0.033)	0.056 (0.048)	0.018 (0.006)	0.23 (0.20)
	2006	0.13 (0.10)	0.17 (0.11)	0.23 (0.20)	0.22 (0.11)	0.098 (0.024)	0.013 (0.006)	0.018 (0.012)	0.062 (0.064)	0.20 (0.14)	0.85 (0.41)
AFDM	2004	0.51 (0.41)	0.59 (0.32)	0.40 (0.23)	0.18 (0.11)	-	0.056 (0.011)	0.066 (0.025)	0.093 (0.021)	-	-
	2005	0.22 (0.056)	0.27 (0.053)	0.21 (0.21)	0.18 (0.079)	0.19 (0.015)	0.13 (0.037)	0.19 (0.075)	0.16 (0.050)	0.11 (0.019)	0.36 (0.27)
	2006	0.29 (0.078)	0.34 (0.20)	0.73 (0.38)	0.36 (0.23)	0.14 (0.032)	0.074 (0.012)	0.072 (0.037)	0.13 (0.097)	0.28 (0.15)	0.56 (0.25)

River sites, and 118 were common between the two basins. Across all sample sites, mean taxa richness was 41 (22-69), mean density 2,861 individuals/m^2 (576-14,318), and mean Shannon diversity (H′) was 2.53 (1.67-3.18) (Table 3). To test for differences among sections, years, and habitats, we excluded TR sites and 2004 data to achieve a balanced design. A 3-way ANOVA showed UE was significantly less diverse (H′) than LE, ME, and QU ($P < 0.001$, Games-Howell post-hoc all $P < 0.01$). Habitat type, year, and all 2-way and 3-way interactions were not significant. Species richness differed among sections ($P < 0.001$; EM>QU=EL>EU, $Ps < 0.04$) and between habitats (SC>MS, $P = 0.04$), but not between years. Invertebrate density was similar among sections and between habitats and years ($Ps > 0.13$). The top three most numerically abundant taxa by river section were: oligochaetes, the blackfly genus *Simulium*, and the chironomid Polypedium in LE; oligochaetes, the mayfly *Baetis tricaudatus*, and the stonefly *Zapada cinctipes* in ME; three mayfly taxa in UE: *Baetis bicaudatus, Drunella doddsi*, and *Rhithrogena* spp., and the mayflies *Baetis tricaudatus* and *Cinygmula* spp. and the chironomid *Orthocladius* spp. in QU.

Benthic invertebrate community structure differed among the three Elwha River sections, with nMDS plots showing clear separation between UE and both ME and LE (Figure 3). This pattern was consistently expressed during all three years. Stress values of nMDS ordinations were 0.10, 0.15, and 0.15 for 2004, 2005, and 2006 (respectively) and within the range of interpretable results suggested by Clarke and Ainsworth (1993). When QU was added as a reference river in 2005, those sites were located between regulated and unregulated sections of the Elwha in nMDS plots.

TABLE 3. Mean values (±1 SD) for benthic invertebrates parameters at MS, SC, and TR sites on LE, ME, UE, and QU from 2004-2006. Dashes indicate that no data were collected.

	Lower Elwha		Middle Elwha			Upper Elwha			Quinault	
	MS	SC	MS	SC	TR	MS	SC	TR	MS	SC
2004	**n=3**	**n=2**	**n=3**	**n=3**	**n=0**	**n=5**	**n=5**	**n=4**	**n=0**	**n=0**
Density (x $10^3/m^2$)	7.0(3.0)	1.5(0.0)	3.5(1.1)	2.5(1.3)	-	2.3(1.1)	3.7(2.1)	2.7(0.5)	-	-
Total Taxa (No.)	31(3.1)	35(4.2)	31(1.2)	31(6.7)	-	28(5.1)	28(5.6)	31(5.7)	-	-
EPT Taxa (No.)	14(1.3)	17(0.09)	15(2.2)	18(3.6)	-	15(2.6)	16(2.4)	16(1.9)	-	-
Ephemeroptera (%)	15(6.0)	15(7.3)	34(15)	49(10)	-	69(17)	72(19)	75(18)	-	-
Plecoptera (%)	10(3.6)	23(6.2)	7.5(5.2)	11(5.4)	-	7.7(6.4)	10(12)	3.4(3.5)	-	-
Trichoptera (%)	15(6.9)	5.3(0.4)	14(9.6)	12(4.0)	-	0.81(0.4)	1.2(0.7)	4.5(2.9)	-	-
Chironomidae (%)	41(7.4)	21(14)	21(8.6)	14(4.9)	-	6.3(5.2)	3.7(4.2)	7.9(7.5)	-	-
2005	**n=7**	**n=5**	**n=5**	**n=4**	**n=3**	**n=9**	**n=8**	**n=5**	**n=4**	**n=8**
Density (x $10^3/m^2$)	2.8(2.0)	2.5(1.3)	2.4(1.9)	2.5(1.0)	2.1(0.3)	2.2(0.6)	2.5(1.0)	2.6(1.1)	2.8(1.5)	5.8(4.1)
Total Taxa (No.)	36(5.7)	38(7.5)	37(6.8)	47(5.7)	46(4.9)	31(7.0)	34(6.3)	36(7.5)	34(5.2)	41(5.5)
EPT Taxa (No.)	16(2.8)	18(1.6)	21(5.2)	24(3.4)	26(3.1)	17(2.6)	19(2.7)	21(4.1)	17(1.3)	21(3.4)
Ephemeroptera (%)	17(8.8)	19(8.9)	33(12)	33(20)	65(20)	77(16)	69(21)	79(10)	65(19)	40(15)
Plecoptera (%)	11(7.7)	21(11)	13(7.5)	8.5(4.3)	8.5(8.5)	7.5(2.7)	12(5.8)	2.8(2.6)	11(4.2)	18(14)
Trichoptera (%)	6.5(3.9)	6.4(3.4)	8.8(7.8)	9.8(4.0)	6.9(3.1)	1.6(0.9)	1.9(0.9)	4.1(1.1)	1.8(1.1)	3.1(1.9)
Chironomidae (%)	28(19)	26(18)	32(15)	28(14)	8.3(4.1)	8.3(12)	12(13)	7.6(6.2)	8.4(11)	22(14)
2006	**n=6**	**n=7**	**n=6**	**n=7**	**n=3**	**n=9**	**n=8**	**n=5**	**n=6**	**n=6**
Density (x $10^3/m^2$)	2.9(2.4)	2.2(1.6)	2.3(1.3)	4.1(4.7)	1.6(0.7)	2.1(2.0)	2.1(0.9)	2.6(2.4)	2.2(1.3)	3.8(2.4)
Total Taxa (No.)	37(4.3)	40(6.7)	46(10)	44(5.4)	50(6.9)	31(10)	37(8.6)	41(7.7)	42(4.2)	39(5.6)
EPT Taxa (No.)	16(2.8)	18(2.7)	21(6.5)	22(3.6)	27(3.8)	17(5.0)	21(5.6)	20(3.3)	21(1.2)	22(5.9)
Ephemeroptera (%)	22(10)	19(7.3)	27(14)	34(23)	64(18)	73(22)	73(20)	79(8.7)	35(17)	41(13)
Plecoptera (%)	8.7(5.9)	14(7.6)	4.3(1.8)	15(12)	8.2(6.9)	6.8(3.1)	5.6(3.4)	2.1(1.1)	12(4.4)	15(7.9)
Trichoptera (%)	6.3(4.5)	7.8(5.7)	2.8(1.5)	4.6(3.9)	6.7(2.9)	6.5(12)	3.1(2.1)	4.5(1.6)	2.1(1.7)	4.1(2.5)
Chironomidae (%)	33(18)	30(13)	46(15)	28(24)	7.6(3.9)	5.2(3.7)	9.7(11)	7.4(4.4)	30(20)	26(18)

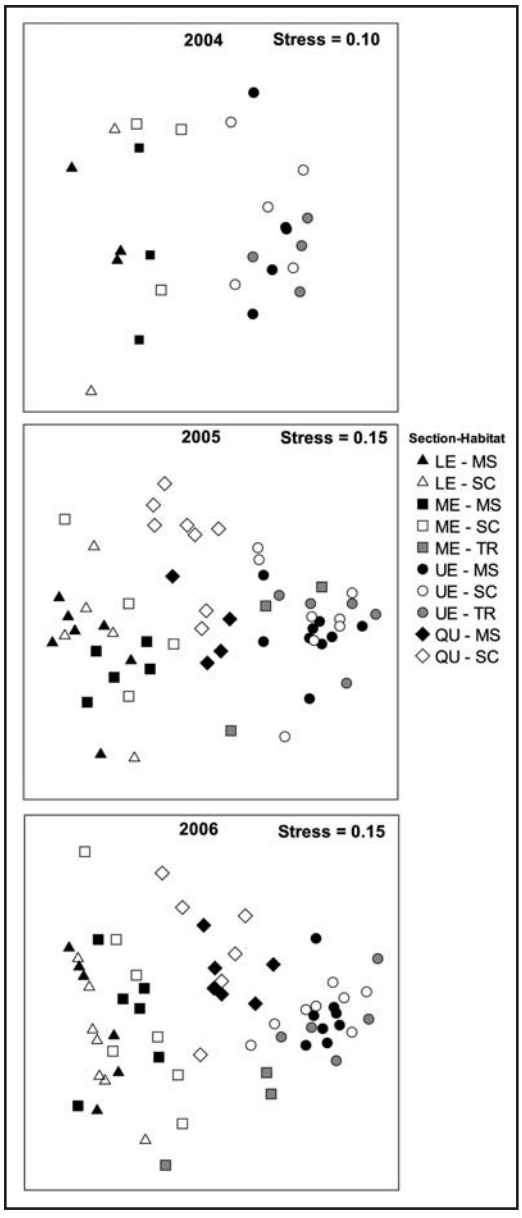

Figure 3. Non-metric multidimensional scaling (nMDS) plots of benthic invertebrate community composition data (√ transformed) collected from MS (filled), SC (open) and TR (shaded) habitats in LE (triangles), ME (squares), UE (circles) and QU (diamonds).

Two-way ANOSIM procedures, calculated separately for each year, confirmed the differences among river sections in invertebrate assemblage structure. To meet the criteria of a 2-way crossed design, we removed tributary sites from this analysis (no tributaries were sampled in LE or QU). In each year, there was a significant difference of section (Global $R_{2004} = 0.83$, $R_{2005} = 0.78$, and $R_{2006} = 0.76$, all $P = 0.001$), but not between MS and SC sites (Table 4). Evaluating pair-wise comparisons between sections, we found significant differences between UE and LE ($R > 0.99$ in all years) and between UE and ME ($R > 0.92$, $P = 0.001$ in all years). ME and LE assemblages were significantly different in 2005 and 2006 ($R = 0.31$ and $R = 0.26$, $P = 0.01$ in both years) but not in 2004. QU sites were different from all sections of the Elwha and most similar to ME (*R's* > 0.60; Table 4).

To determine the taxonomic groups most responsible for the differences among sections using SIMPER, we pooled MS and SC sites and excluded TR sites. Chironomids (midges) and Ephemeroptera (mayflies) were two groups of invertebrates that consistently differentiated pairs of sections, especially UE from ME and LE, across all years and section combinations (Table 5). In general, differences among sections were most explained by the dominance of mayflies in UE compared with other sections, as well as higher abundances of midges in ME and LE. These groups also were the top ranked taxa in discriminating between Elwha and Quinault sections (Table 5). The ratio of mayflies:midges (untransformed densities, MS and SC sites combined) in EU was, on average, 24.6 times higher than LE and 10.1 times higher than ME (2-way ANOVA, Section: $P < 0.001$; Year: $P = 0.38$; Year x Section: $P = 0.50$).

The BIO-ENV routine found a high rank correlation between biotic and environmental resemblance matrices in both 2005 (8 variable solution, Spearman's $\rho = 0.66$, $P = 0.001$) and 2006 (5 variable solution, Spearman's $\rho = 0.71$, $P = 0.001$). Elevation, PO_4, AFDM, water temperature, and embeddedness were environmental variables selected in the best models of 2005 and 2006, with NH_4, D_{84}:D_{16}, and conductivity selected as additional variables from 2005 data. A PCA using the significant variables from 2005 explained 59 % of the variation within the first two Principle components. In 2006, using 3 fewer variables, the PCA explained 78% of the variation within the first two principle components (Figure 4).

TABLE 4. Results of 2-way crossed ANOSIM with section (LE, ME, UE, QU) and habitat (MS, SC) as factors. Exclusion of tributaries, which were not present in all sections, did not demonstrably change the results. The significance of Global R values and pair-wise comparisons were computed with 999 permutations and exact statistics are given as ≤ 0.01 (*) and ≤ 0.001 (**). Pair-wise comparisons were computed only when the global test was significant and dashes indicate that data were not collected in both river sections for a given year.

			Pair-wise Comparisons					
Year	Factor	Global R	LE-ME	LE-UE	ME-UE	QU-ME	QU-UE	QU-LE
2004	Section	0.83**	0.18	1.0**	0.93**	-	-	-
	Habitat	-0.1						
2005	Section	0.78**	0.31**	0.99**	0.96**	0.60**	0.78**	0.77**
	Habitat	0.08						
2006	Section	0.76**	0.26*	1.0**	0.92**	0.63**	0.77**	0.84**
	Habitat	0.05						

TABLE 5. Pairwise similarity percentages (SIMPER) results comparing benthic invertebrate assemblage structure in LE, ME, UE, and QU over 3 years. Higher values indicate greater dissimilarity between sections. Relative densities of species were summed into higher taxonomic groups and results provided are of taxa contributing up to 90% of the dissimilarity between pairs of river sections (thus, Odonata and Lepidoptera are not included). For each taxonomic group the % dissimilarity contribution (***C***), the direction (***D***, where ▲ = first listed of section-pair has higher average abundance, ▼ = second listed of section-pair has higher abundance), and the within-year rank (***R***) are given.

Comparison		**LE-ME**			**LE-UE**			**ME-UE**	
Year	2004	2005	2006	2004	2005	2006	2004	2005	2006
Ave. Dissimilarity	30.5	29.2	31.8	48.4	40.6	37.7	34.0	30.2	32.8
Taxa Contributing	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*
Ephemeroptera	8.9▼6	20.8▼2	18.3▼2		29.8▼1	33.6▼1	17.4▲3	31.3▼1	29.6▼1
Plecoptera	19.9▲2	11.4▲5	11.9▲4	17.3▲3	8.9▲5		10.7▲6	11.4▲5	11.0▲4
Trichoptera	13.3▲4	8.8▼6	8.7▲6	17.3▲3	8.0▲6	7.3▲6	18.7▲2	11.5▲4	
Coleoptera	12.1▲5			10.2▲5		8.9▲4			7.4▲6
Non-insect	15.7▲3	15.4▼3	14.6▲3	17.6▲2	14.8▲3	14.6▲3	17.0▲4	12.2▲3	12.9▲3
Diptera		13.4▲4	9.4▲5	8.6▼6	10.9▲4	7.9▲5	13.6▼5	7.7▲6	7.6▲5
Chironomidae	21.3▲1	21.9▲1	29.0▼1	23.6▲1	19.6▲2	20.8▲2	19.0▲1	20.7▲2	25.0▲2
Comparison		**QU-ME**			**QU-UE**			**QU-LE**	
Year	2004	2005	2006	2004	2005	2006	2004	2005	2006
Ave. Dissimilarity	-	30.6	29.1	-	32.8	30.9	-	33.9	30.2
Taxa Contributing	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*	*C-D-R*
Ephemeroptera	-	24.6▲1	17.3▲2	-	19.6▲2	21.7▼2	-	29.2▲1	23.3▲2
Plecoptera	-	17.6▲3	17.2▲3	-	18.1▲3	14.9▲4	-	13.9▲4	11.6▲4
Trichoptera	-	8.2▼6		-	17.4▲6	6.2▲6	-	7.4▲6	8.2▲6
Coleoptera	-		6.9▼6	-			-		
Non-insect	-	10.5▲5	12.6▲4	-	13.8▲5	16.2▲3	-	10.0▲5	12.6▲3
Diptera	-	13.9▲4	10.0▲5	-	14.7▲4	10.0▲5	-	15.2▲3	10.0▲5
Chironomidae	-	20.2▲2	29.3▲1	-	22.0▲1	26.9▲1	-	20.4▲2	26.8▲1

Discussion

Physical habitat, periphyton, and benthic invertebrate parameters did not vary greatly by habitat type, but were different between regulated and unregulated sections of the Elwha River. Parameters for the unregulated East Fork Quinault River were most often in-between values observed for LE and ME (regulated) and UE (unregulated). This pattern was consistent across years, although results were not always statistically significant. In 2004, the first year of this study, our statistical power was limited by low sample size in LE and ME. Hydrologic conditions were also strikingly different across the three years of the study, which may have contributed to some of the variability in our results. While 2004 was one of the wettest years on record, 2005 was one of the driest, and 2006 a relatively typical water year. Sampling across such different water years better reflected inter-annual variability—something we will need to account

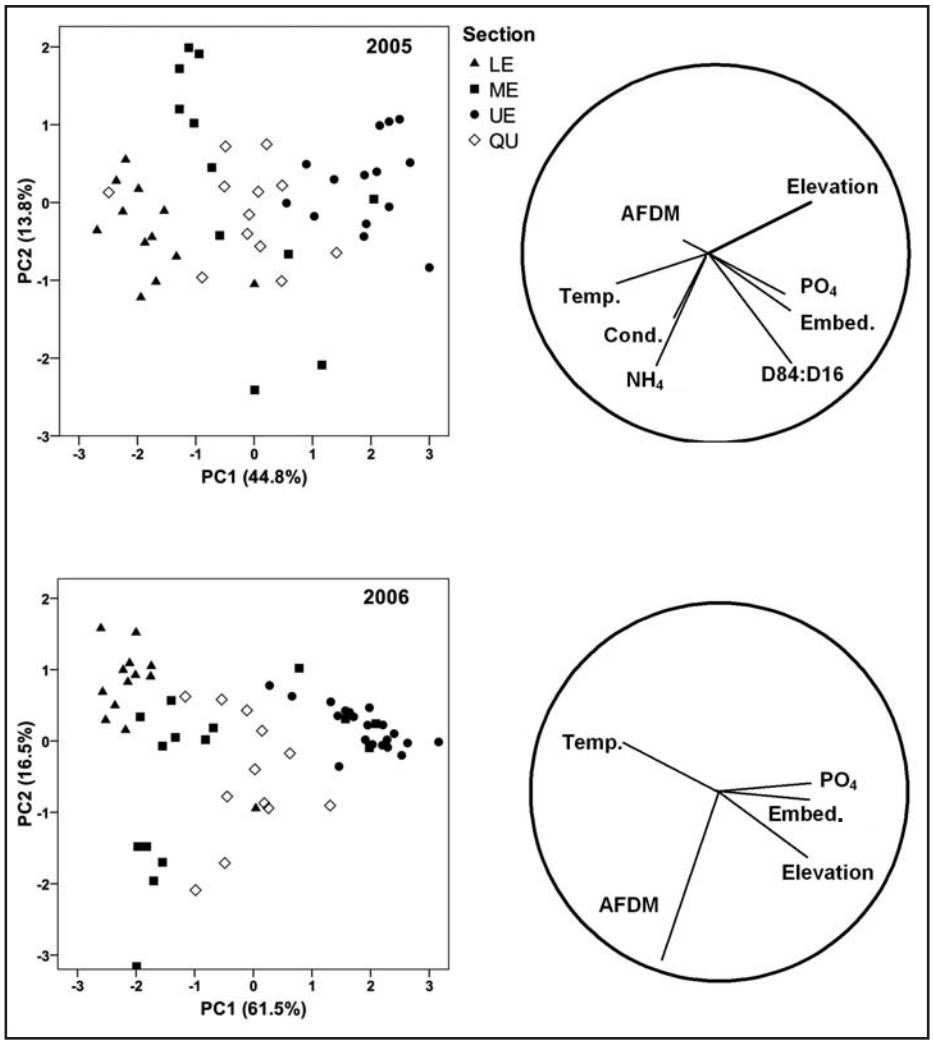

Figure 4. Principle component analysis (PCA) of the best environmental variables (Log [x+1] transformed and normalized) found to explain the structure of benthic invertebrates by section in 2005 (top) and 2006 (bottom) using BIO-ENV routine (see text). Eigen vectors in circular plot reflect variable loadings (direction and magnitude) on each axis.

for in interpreting dam removal response over the long-term. Another factor complicating data interpretation was the span of 57 rkm and 800 m in elevation across our 52 study sites. In the absence of comparable data collected prior to the construction of the Elwha dams, partitioning differences between regulated and unregulated river sections according to relative influence of impoundment versus natural longitudinal gradients is challenging (Vannote et al. 1980, Thorp et al. 2006). Recognizing this limitation, our primary goal was to document the spatial and temporal patterns in Elwha River benthic communities prior to dam removal, so that these data can be used as a baseline to track future changes associated with dam removal.

In terms of channel substrate, LE and ME were very similar to each other and typically distinct from UE, with the QU reference section between these two groups. Substrate was larger in LE and ME, less heterogeneous in size, composed of a smaller proportion of gravel and fine sediments, and less embedded than in UE. Although the bed was coarsest in ME, particle size heterogeneity was lowest in LE. Our results agree with Pohl's

(2004), who observed the largest particle size and lowest bed mobility in ME and concluded that this section between the two dams was the most armored and least dynamic in terms of sediment movement. Although substrate in LE was still larger than would be expected near the mouth of an unregulated river, lower overall gradient and sediment from eroding glacial bluffs and terraces in LE likely contribute to smaller median particle size as compared to ME. Summer water temperatures were cooler in UE compared to both LE and ME, observations confirmed by temperature loggers deployed throughout the basin (M. McHenry, Elwha Tribe, unpublished data). Although Wunderlich et al. (1994) report that the presence of the dams has increased summer and fall temperature in ME and LE due to reservoir warming, we would also expect water temperature to be cooler at the higher elevations of UE. Canopy cover was not statistically different between sections, but was most open for each sample year in UE, where riparian vegetation is less mature in the more active floodplain of this unregulated section (Pohl 2004, Kloehn et al. 2008).

Periphyton biomass (AFDM and chlorophyll *a)* differed between regulated and unregulated sections as well as between habitat types. Section differences were not unexpected as other studies have documented higher biomass in regulated relative to unregulated sections within the same river (Blinn et al. 1998, Munn and Brusven 2004, Chester and Norris 2006). Although we did not analyze periphyton samples for taxonomic composition, we suspect that higher biomass in LE and ME reflected the higher relative abundance of filamentous algae as compared to UE. Li (1990) also observed dominance by filamentous algae below the dams and dominance by diatoms and other algae in UE. The prevalence of filamentous algae below dams is often related to increased water temperature, higher water clarity, and decreased bed movement (Munn and Brusven 2004). Differences between SC and MS sites were less consistent but still present across years, with higher biomass at SC sites compared to MS. Although canopy was more closed in SC's than in MS sites, we hypothesize that more light penetrates to the benthos due to lower turbidity and depth. Variation in periphyton biomass was best predicted by water chemistry. Chlorophyll *a* and AFDM were positively correlated with dissolved inorganic nitrogen and silicate. This was not unexpected as the Elwha River generally has low nitrogen and phosphorus concentrations (Munn et al. 1999) and silicate is required by diatom species. Although regression analysis indicated that there was a negative relationship between periphyton biomass and phosphate, we do not believe this to be a causal relationship but an artifact of differences between river sections (phosphate concentrations were significantly higher in UE relative to LE and ME).

The structuring of benthic communities according to abiotic and biotic filters expressed at multiple spatial scales has been pointed out by many authors (reviewed by Wiens 2002). We found consistent patterns of invertebrate assemblage structure along ecological and anthropogenic gradients. These relationships are summarized in the PCA plots that were derived from the environmental factors that most closely matched the structure of benthic invertebrate assemblages (Figure 4). Temperature and elevation clearly separated UE sites from LE and ME sites, a gradient that likely existed prior to dam construction. However, the magnitude of these temperature differences is affected by release of warmer water from the reservoirs, especially during the summer (Wunderlich et al. 1994). Temperature differences can exert control over invertebrate communities below dams, through altering temperature dependent developmental cues as well as bioenergetics (Benke et al. 1988, Vinson 2001). Differences in substrate size and levels of embeddedness clearly have changed as a result of disrupted sediment transport below the dams. Substrate differences among sections significantly loaded on the primary axis differentiating sections (Figure 4). Overall, our findings are similar to those reported by Munn et al. (1996) from comparable benthic invertebrate sampling conducted a decade earlier on the Elwha River. These researchers detected no major differences in invertebrate metrics amongst different habitat types, but did see major taxonomic shifts between regulated and unregulated sections. Specifically, a high percentage of chironomids were present at LE sites compared to numerical dominance by mayfly taxa at UE sites, but no overall change in total taxa richness across river sections.

Although our observation of major shifts in taxonomic composition from mayfly-dominated UE to a prevalence of chironomids and non-insects in LE is consistent with findings from other studies of regulated rivers (Munn and Brusven

1991, Vinson 2001), we were surprised to observe higher invertebrate diversity in regulated sections. Because the Elwha River dams are operated as run-of-the-river, hydrological alteration has not been as severe as in other river systems with large hydroelectric dams. Despite the presence of the Elwha Dam, the LE floodplain is still fairly dynamic, with a diversity of SC age, fine sediment contributions from eroding bluffs and terraces, and bed mobility rates more similar to UE than ME (Pohl 2004, Kloehn et al. 2008). In ME, numerous tributary inputs may dampen the effects of regulation by partially "re-setting" the system (Ward and Stanford 1995). Higher invertebrate diversity in regulated sections may also be a reflection of greater food availability. We observed higher periphyton biomass in LE and ME compared to UE, and more mature riparian vegetation in regulated sections may also contribute greater quantities of allochthonous food sources (Kloehn et al. 2008). Lower water temperatures and a higher proportion of diatomaceous algae (as opposed to the filamentous algae that dominates in LE and ME) likely contribute to the high relative abundance of mayfly taxa in UE (Li 1990). The nearly century-long absence in ME and UE of anadromous salmon -- ecologically important species in Pacific Northwest rivers -- is likely also a factor in invertebrate differences observed across Elwha River sections (Gende et al. 2002).

The short-term response of periphyton and benthic invertebrate assemblages following dam removal will be primarily driven by sediment transport from the reservoirs to river sections below the dams. There currently exists nearly 18 million m^3 of sediment in the deltas of Lake Mills and Lake Aldwell, a substantial portion of which will be mobilized and transported downstream during and following dam removal. Current predictions suggest that the river will return to normal turbidity levels in 3-5 years, depending upon flow conditions during the period following dam removal (DOI 1996, Randle et al. 1996). UE (representing the largest portion of the river basin) will be relatively unaffected by this high intensity disturbance event – and thus will likely serve as a source of invertebrate recolonizers in affected sections below the dams. We anticipate that both periphyton and benthic invertebrate abundance and diversity in LE and ME will temporarily decrease as a result of increased occurrence of finer, more mobile substrates which will bury stream cobbles, limit photosynthesis via increased turbidity, and decrease the efficiency of filter-feeding organisms (Wood and Armitage 1997). Benthic invertebrates from the aquatic insect orders Ephemeroptera, Plecoptera, and Trichoptera are expected to be most affected by increased fine sediments, possibly decreasing over the long-term in LE (Waters 1995, Minshall et al. 2001, Shaw and Richardson 2001). Other generalist taxa with high dispersal ability and an affinity for fine-grained substrates (e.g., chironomids, oligochaetes, burrowing mayflies) are expected to recover quickly and replenish the local benthic standing crop (Zuellig et al. 2002). In general, we expect that species with high dispersal ability, short life cycles (i.e., multivoltine taxa), and generalist feeding habits will move into affected habitats quickly. A dearth of long-term data sets (Jackson and Füreder 2006), makes it difficult to predict whether the sediment mediated effects of dam removal will quickly dissipate, or become a long-term ecological legacy maintained for decades (e.g., Harding et al. 1998, Vinson 2001). In addition to light and substrate limiting periphyton production in the short-term, a potential decrease in anadromous fish populations due to increased straying (Pess et al. 2008) may indirectly affect periphyton assemblages via a temporary reduction in marine-derived nutrient inputs.

Evidence from other studies that have looked at the short-term response of benthic invertebrates and periphyton to dam removal varies, due in part to differences in the quantity of sediment stored behind dams and the hydrologic and geomorphic context of the study river. Studies of low-head dam removal in Wisconsin streams and rivers detected no major changes to benthic invertebrate assemblages in study reaches downstream of removed dams (Stanley et al. 2002, Pollard and Reed 2004; but see Sethi et al. 2005); however, much less sediment was transported in these systems than is predicted to occur in the Elwha basin. Significant reductions in benthic invertebrate abundance and periphyton biomass were reported downstream of a small dam removed from a Pennsylvania stream, but no major taxonomic shifts in either assemblage were detected (Thomson et al. 2005). Given the smaller scale of existing dam removal studies, benthic invertebrate and periphyton response to dam removal on the Elwha River may be better predicted by drawing on the results of numerous studies that have documented the deleterious effects of major sediment inputs on river biota (see Waters

[1995] and Wood [2004] for review). Experimental floods conducted below large hydroelectric dams may also provide clues to short-term biological response on the Elwha River. During the 1996 test flood on the Colorado River, Shannon et al. (2001) report dramatic reductions in periphyton and invertebrate standing crops due to benthic scour, but with recovery occurring in < 7 months. Floods below Punt de Gall Dam in Switzerland also resulted in temporary reductions in periphyton biomass, benthic respiration, and benthic invertebrate abundance and taxonomic richness, although effects were only significant for the largest flood, and did not affect all invertebrate taxa (Jakob et al. 2003, Uehlinger et al. 2003).

Once the most pronounced sediment effects have dissipated, we anticipate that the long–term (decades) response of benthic invertebrate and periphyton to dam removal will be shaped by changes in habitat heterogeneity in LE and ME and recolonization by anadromous fish in ME and UE. Reconnection of sediment and wood supply below the dams will result in a more dynamic floodplain: new channels will be created or widened due to bed aggradation and lateral migration, with concurrent changes in riparian species and age class composition (Kloehn et al. 2008). We predict that the creation of a shifting mosaic of habitat patches with different hydrologic, substrate, and riparian characteristics will ultimately increase benthic invertebrate and periphyton diversity over the long-term in ME and LE via increased niche diversity (Ward et al. 1999, Amoros and Bornette 2002, Latterell et al. 2006). The recolonization of salmon in ME and UE could have both positive and negative effects on periphyton and benthic invertebrates. Salmon carcasses, gametes, and waste can represent a large flux of marine-derived nutrients into freshwater ecosystems (Wipfli et al. 1998, Gende et al. 2002), which could provide an important nutrient subsidy to the oligotrophic Elwha (Munn et al. 1999). Yet, salmon also can dramatically modify benthic habitat via bioturbation of their spawning grounds (Moore et al. 2004) and transport marine contaminants into freshwater foodwebs (Gregory-Eaves et al. 2007). The effects of returning salmon on the different sections of the Elwha River will also vary due to species specific differences in recolonization (Pess et al. 2008).

The projected effects of dam removal on periphyton and benthic invertebrate assemblages will also vary by habitat type. River floodplains are complex systems where the mainstem channel constitutes but a fraction of available habitat (Ward and Stanford 1995, Pess et al. 2005, Thorp et al. 2006). For this reason, and also because dam removal response may be quite different across the floodplain, we recommend focusing monitoring efforts on more than one habitat type. Although for the most part we did not detect major differences in benthic invertebrates or periphyton between MS and SC habitats across the Elwha basin, these habitats may respond very differently to dam removal. SC's with less hydrologic connectivity to the MS will be less affected by the sediment pulse, and thus may maintain a higher level of invertebrate diversity than MS habitats following dam removal and river recovery. The highest levels of sediment are expected in the MS, followed by surface connected SC's. The least affected areas of ME and LE will be TR's and groundwater influenced SC's. Salmon recolonization rates in ME and LE will also differ by habitat type, depending on life history adaptations of different species (Pess et al. 2008).

To date, existing studies to date on the effects of dam removal concern low-head dams. While these smaller structures are more numerically abundant, they also typically affect smaller streams and rivers, and exert less severe geomorphic and ecological alterations (Poff and Hart 2002, Doyle et al. 2005). There are over a thousand dams in the US of a similar size to those on the Elwha River, and a number are being considered for removal over the next decade, including the Condit Dam (36 m high) on the White Salmon River in Washington State, the Savage Rapids Dam (13 m) on the Rogue River in Oregon, and the Matilija Dam on Matilija River in California (51 m) (Gregory et al. 2002, Graf 2003). All of these projects face management questions similar to those on the Elwha River regarding the severity and longevity of sediment impacts and the projected timelines for fish recolonization and ecosystem recovery. This study helps to address this data gap by establishing a framework for long-term benthic monitoring to track invertebrate and periphyton responses to high-head dam removal. By documenting the methods and results of baseline ecological data collection for the Elwha River, we hope to improve consistency in monitoring protocols and consequently comparability of pre- and post-removal datasets. The extended timeline predicted for Elwha River

recovery highlights the need for more long-term assessments of dam removal and river restoration practices in general.

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