

ESTABLISHING SPATIAL TRENDS IN WATER CHEMISTRY AND STABLE ISOTOPES ($\delta^{15}\text{N}$ AND $\delta^{13}\text{C}$) IN THE ELWHA RIVER PRIOR TO DAM REMOVAL AND SALMON RECOLONIZATION[‡]

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ABSTRACT

Two high-head dams on the Elwha River in Washington State (USA) have changed the migratory patterns of resident and anadromous fish, limiting Pacific salmon to the lower 7.9 km of a river that historically supported large Pacific salmon runs. To document the effects of the dams prior to their removal, we measured carbon and nitrogen stable isotope ratios of primary producers, benthic macroinvertebrates, and fish, and water chemistry above, between and below the dams. We found that $\delta^{15}\text{N}$ was significantly higher in fish, stoneflies, black flies, periphyton and macroalgae where salmon still have access. Fish and chloroperlid stoneflies were enriched in $\delta^{13}\text{C}$, but the values were more variable than in $\delta^{15}\text{N}$. For some taxa, there were also differences between the two river sections that lack salmon, suggesting that factors other than marine-derived nutrients are structuring longitudinal isotopic profiles. Consistent with trophic theory, macroalgae had the lowest $\delta^{15}\text{N}$, followed by periphyton, macroinvertebrates and fish, with a range of 6.9, 6.2 and 7.7‰ below, between, and above the dams, respectively. Water chemistry analyses confirmed earlier reports that the river is oligotrophic. Phosphorous levels in the Elwha were lower than those found in other regional rivers, with significant differences among regulated, unregulated and reference sections. The removal of these dams, among the largest of such projects ever attempted, is expected to facilitate the return of salmon and their marine-derived nutrients (MDN) throughout the watershed, possibly altering the food web structure, nutrient levels and stable isotope values that we documented. Published in 2010 by John Wiley & Sons, Ltd.

KEY WORDS: stable isotopes; salmon; dam removal; marine-derived nutrients; food webs

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INTRODUCTION

Dams dramatically alter the connectivity of rivers in multiple spatial dimensions (Petts and Gurnell, 2005). These constraints on connectivity are imposed through restricted lateral movement of the channel within its floodplain, reduced vertical exchange of surface and sub-surface flows, and the altered movement of water, materials and organisms longitudinally along the river continuum (Petts, 1984; Ward and Stanford, 1995; Hart *et al.*, 2002). Dams built without fish passage in particular impede the movement of migratory species that utilize different portions of the watershed or move between freshwater and marine habitats during their life cycle. Such migration barriers have led to innumerable extirpations of diadromous fish populations worldwide (Pringle *et al.*, 2000; Nilsson *et al.*, 2005; Han *et al.*, 2008; Lassalle *et al.*, 2009). In the U.S. Pacific Northwest, dams are one of the major factors implicated in the decline of

numerous anadromous stocks of Pacific salmon and trout (Nehlsen *et al.*, 1991; Lichatowich, 1999; Ruckelshaus *et al.*, 2002).

Reductions in anadromous salmon populations can alter or disrupt multiple pathways within freshwater and riparian food webs (Cederholm *et al.*, 1999; Gende *et al.*, 2002). One consequence that has received much attention recently is the reduction or elimination of marine-derived nutrients (MDN) delivered to freshwater habitats through adult salmon returning from the ocean to spawn in their natal streams and lakes (Larkin and Slaney, 1997; Gresh *et al.*, 2000; Scheuerell *et al.*, 2005). With the majority of their body mass obtained at sea, adult salmon return to freshwater spawning grounds enriched with MDN. These MDN influence the productivity and ecology of freshwater ecosystems via deposition of carcasses, gametes and excretion of waste when salmon complete their semelparous life cycle (see reviews in Kline *et al.*, 1990; Gende *et al.*, 2002; Schindler *et al.*, 2003). Direct consumption of eggs and flesh from carcasses can serve as an important pulse of energy to resident and juvenile anadromous fish populations (Quinn, 2005). Fish carcasses are also reduced by bacteria, invertebrates and fungi (Piorkowski, 1995), or are consumed by scavengers and omnivores (Cederholm *et al.*, 1989). MDN released during

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these processes are important for the productivity of many oligotrophic (nutrient-poor) lakes and streams that support salmon (Kline *et al.*, 1990; Larkin and Slaney, 1997; Naiman *et al.*, 2002). Increased phytoplankton and periphyton production have been observed in the presence of carcasses (Richey *et al.*, 1975; Perrin and Richardson, 1997; Wipfli *et al.*, 1998), as have changes in patterns of invertebrate diversity and density (Piorkowski, 1995; Chaloner and Wipfli, 2002; Chaloner *et al.*, 2002), invertebrate growth rates (Minakawa *et al.*, 2002) and fish growth rates (Bilby *et al.*, 1998; Wipfli *et al.*, 2003). The dispersal of salmon carcasses by scavengers into streamside areas also enriches riparian species—a process further enabled by carcass deposition during flooding and hyporheic nutrient exchanges (Ben-David *et al.*, 1998; Helfield and Naiman, 2001; Drake *et al.*, 2006).

In recent decades, the ability to trace the movement and magnitude of MDN inputs into freshwater and riparian ecosystems has improved with advancements in stable isotope analysis (Fry, 2006). The technique relies upon measuring the isotopic ratio of carbon and nitrogen heavy stable isotopes to their lighter and more common counterparts relative to standards (expressed as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). These ratios differ among freshwater, terrestrial and marine ecosystems and within food webs. Because salmon do not typically feed when they enter freshwater as adults, their tissues retain the isotopic values obtained in the marine environment. Among many other examples, use of this technique has shown that periphyton, invertebrates and fish in salmon-spawning reaches were enriched with MDN relative to reaches above salmon migration barriers (Kline *et al.*, 1990); that salmon carcasses can contribute over 30% of the nitrogen and carbon assimilated by juvenile coho salmon in their freshwater rearing habitats (Bilby *et al.*, 1996); that salmon once contributed 33–90% of the metabolized carbon and nitrogen in grizzly bears in the Columbia River drainage before large-scale salmon migration blockages (Hildebrand *et al.*, 1996); and that riparian plant species may derive over 20% of their foliar nitrogen from salmon nutrients (Helfield and Naiman, 2001).

Although one of the most obvious effects of dams in salmon-bearing rivers is the reduction or elimination of this MDN subsidy to upstream reaches, dams also alter sediment and wood transport, channel migration, water chemistry and other riverine processes (Bunn and Arthington, 2002). These changes may re-structure aquatic food webs and thus indirectly contribute to shifts in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Downstream of dams, habitat simplification from flow regulation and geomorphic changes often results in a loss of niche and species diversity (e.g. Vinson, 2001; Collier, 2002; Munn and Brusven, 2004), which in turn may alter food chain length (Power *et al.*, 1996; Marks *et al.*, 2000). Additionally, regulated sections of dammed rivers experience shifts in

rates of community metabolism (Munn and Brusven, 2004), benthic invertebrate assemblage structure (Morley *et al.*, 2008), relative abundance of large plants and filamentous algae (Bunn and Arthington, 2002) and inorganic content of periphyton (Collier, 2002). Upstream of dams, resident fish may be arranged into different food web configurations than they would in the presence of competing species of anadromous fishes.

The impending removal of two dams on the Elwha River in Washington State provides a unique opportunity to study both the effects of dams and the trophic importance of salmonids and their MDN on freshwater foodwebs and water nutrient levels. Two high-head (>30 m) dams have blocked salmon from accessing all but the lower 7.9 river kilometers (rkm) of the Elwha River watershed for nearly a century, severing the supply of MDN to the middle (between the dams) and upper (above the upper dam) portions of the river. The Elwha River Ecosystem and Fisheries Restoration Act of 1992 (PL 102–495) calls for the restoration of the ecosystem and anadromous fish runs. After years of studying alternatives (Department of the Interior (DOI, 1996)), dam removal is expected to begin in 2011 (Duda *et al.*, 2008). Historically, the river produced large salmon runs which included spring and fall Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), pink (*O. gorbuscha*) and chum salmon (*O. keta*), as well as coastal cutthroat trout (*O. clarki clarki*) and two steelhead (*O. mykiss*) runs. Today, populations are a small fraction of their former size (Pess *et al.*, 2008, Winter and Crain, 2008), are supplemented by hatchery production, and have different assemblage structure compared with the historical fish community (Wunderlich *et al.*, 1994; Brenkman *et al.*, 2008a). Based on water chemistry data collected throughout the Elwha River basin, Munn *et al.* (1999) concluded that the Elwha River and its tributaries are oligotrophic, but estimates of future salmon returns (projections suggest as many as 19 500 and 150 000 spawners 10 and 25 years following dam removal, respectively; Ward *et al.* 2008) could increase annual nitrogen loading by 1275–10 900 kg and phosphorous loading by 210–1350 kg (estimates based on assumptions of Munn *et al.*, 1999 and projected spawners in Ward *et al.*, 2008). The majority of this subsidy will come from mass spawning populations of pink salmon (every other year) and chum salmon, which are expected to be restricted to the lower 16 rkm (Pess *et al.*, 2008).

Our objectives were to establish baseline patterns of water chemistry and $\delta^{15}\text{N}/\delta^{13}\text{C}$ from multiple trophic levels in areas where salmon currently occur and are expected to recolonize following dam removal in the Elwha River. Sampling during summer base flows, we (1) examined how the presence of the dams has shaped the current distribution of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of fish, invertebrate and algae tissues and (2) determined whether water chemistry differed

in dammed and undammed sections of the Elwha River and a reference reach of the adjacent Quinault River. From this baseline, we make predictions about how these patterns in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and water chemistry within the Elwha River may change when the dams are removed. The broader goal of this research is to gain an understanding of the dynamics associated with the re-introduction of anadromous salmonids and the nutrient subsidy provided to their spawning habitats and surrounding ecosystems, which will facilitate an evaluation of the Elwha River recovery, as well as the restoration of other salmon-bearing rivers.

STUDY AREA

The Elwha River watershed in northwestern Washington State (USA) occupies 833 km², with 83% of the area protected within the boundaries of Olympic National Park, a World Heritage Site and International Biosphere Reserve (Figure 1). The river originates from glacier and snow melt in the Olympic Mountains and flows for 72 km until it reaches the Strait of Juan de Fuca, the water body connecting Puget Sound to the Pacific Ocean. The Elwha basin experiences a large

precipitation gradient, with average annual precipitation ranging from 550 cm in the headwaters to approximately 100 cm near the river mouth (Phillips and Donaldson, 1972). The climate is characterized by warm, dry summers and cool, wet winters, with the majority of precipitation falling as snow in higher mountain elevations from October to March. The annual hydrograph is bimodal, as discharge rises with increased precipitation in the winter and again in the spring when warmer temperatures melt snow pack (Duda *et al.*, 2008).

Two dams were built on the Elwha River in 1913 (Elwha Dam at rkm 7.9) and 1927 (Glines Canyon Dam at rkm 21.6) for production of hydroelectric power. Since the mid-1940s, the projects have been operated as run-of-the-river, with irregular exceptions for additional power generation or increased flows for endangered salmon below the dams (Duda *et al.*, 2008). The reservoirs inundate 9 rkm of former fluvial habitat, trap habitat-forming sediments and large woody debris, restrict salmon migration to the lower 7.9 rkm, alter river-floodplain dynamics, and contribute to a slew of ecological changes (see Duda *et al.*, 2008 for additional information on the Elwha River restoration project).

METHODS

Sample collection

During summer low flow periods in 2005 and 2006, we collected samples for water chemistry and stable isotope analysis in mainstem and side channel habitats of the Elwha River from near the river mouth to rkm 59 (elevation range: 0–809 m). We obtained periphyton, macroalgae, benthic invertebrates and water chemistry samples during a companion study documenting pre-dam removal patterns of aquatic invertebrates and periphyton assemblages (Morley *et al.*, 2008), with 43 (2005) and 56 (2006) sample sites distributed across three sections of the Elwha River (below the Elwha dam (hereafter LE = lower Elwha), between the Elwha and Glines Canyon dams (ME = middle Elwha) and above the Glines Canyon dam (UE = upper Elwha)). Water chemistry samples were also collected from a 10-km section of the East Fork Quinault River (QU). The Quinault was selected as a reference basin due to its proximity to the Elwha (Figure 1), location within Olympic National Park and absence of anadromous fish barriers. This river has similar discharge, gradient and watershed area as the Elwha (McHenry and Pess, 2008) and has been used as a reference in studies of floodplain dynamics (Kloehn *et al.*, 2008), invertebrate and periphyton communities (Morley *et al.*, 2008), and other aquatic ecosystem components. All sampling occurred in riffles of mainstem or side channel habitats (except for fish and some macroalgae, see below).

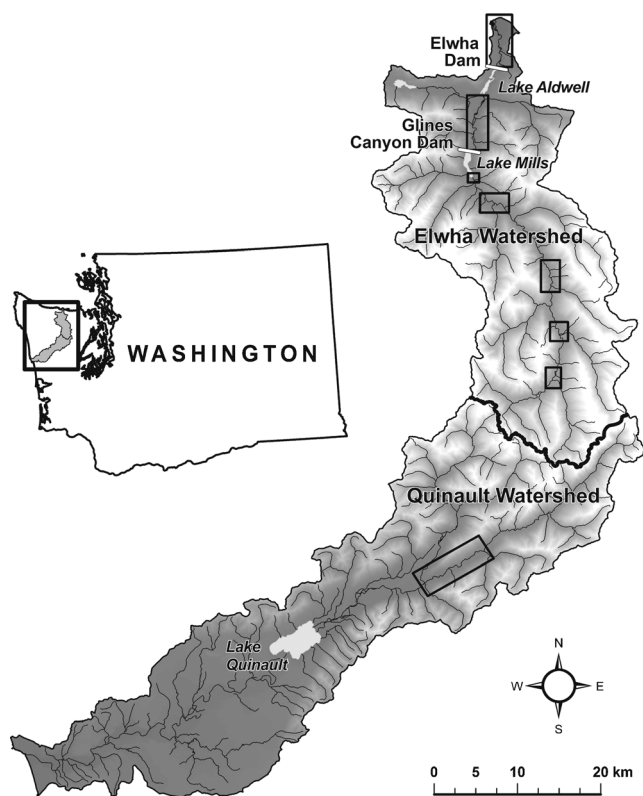


Figure 1. Map of the Elwha River and Quinault River watersheds on the Olympic Peninsula, Washington, with locations of the Elwha and Glines Canyon dams. Floodplain reaches in which multiple sample sites were located are bounded by boxes

Because work in much of UE required extended back-packing trips, we preserved macroalgae, periphyton (the layer of biofilm covering the benthos, which includes algae, bacteria and fungi), and macroinvertebrate samples in 70–75% ethanol (EtOH). Sarakinos *et al.* (2002) and Hobson *et al.* (1997) have shown that EtOH preservation does not appreciably affect stable isotope analyses, although more recent studies contradict this assumption for some taxa, especially aquatic invertebrates. Ventura and Jeppesen (2009), for example, found that $\delta^{15}\text{N}$ from EtOH preserved invertebrate samples was on average 0.39‰ higher than frozen samples, whereas $\delta^{13}\text{C}$ from preserved invertebrates were 1.18‰ lower than frozen samples. We proceeded with stable isotope analysis of preserved samples in light of the fact that the effects of EtOH on stable isotopes were equivocal and we had no choice but to use a preservative for backcountry samples. Yet, we acknowledge that comparisons with other studies that did not use a preservative, prior to application of a correction factor, should be done with caution.

We scrubbed periphyton from five individual cobbles from riffle habitat, pooled into a single sample, and either first preserved in EtOH (backcountry) or filtered directly onto 1- μm pore size 47-mm glass-fibre filters (see Morley *et al.*, 2008). Macroalgae, which consisted primarily of filamentous green algae (*Cladophora* sp.), was collected from submerged rocks or logs in all available habitats at a given site and preserved in EtOH.

We collected benthic invertebrate samples in riffle habitat using a Slack sampler (500 μm mesh, 0.25 m^2 benthic area sampled), a device developed for use in deep, large rivers (Moulton *et al.*, 2002). Samples were preserved in EtOH and identified in the laboratory, where we removed four taxa for stable isotope analysis: a nemourid stonefly classified as a shredder (*Zapada* spp.), the predatory stonefly sub-family Chloroperlinae, a predatory free-living caddisfly (*Rhyacophila* spp.) and a filter feeding dipteran (*Simulium* spp.). We selected these four taxa on the basis of pilot data from 2004 showing that they were relatively widespread and sufficiently abundant across our study sites, and because they represented different taxonomic orders and functional feeding groups (Merritt and Cummins, 1996).

Fish sampling focused on non-anadromous rainbow trout (*O. mykiss*). We collected resident rainbow trout (ranging from approximately 100–350 mm in total length) using a variety of methods: angling within 1–2 rkm floodplain reaches in UE, from fish sacrificed for disease profiles in UE and ME (Brenkman *et al.*, 2008b), and by backpack electrofishing in LE. Due to the potential for lethally sampling threatened steelhead (anadromous *O. mykiss*) in LE, we limited collection in this river section to 12 individuals. To establish background isotope values of MDN delivered by spawning salmon, we also collected tissue samples from recently spawned coho ($n = 2$) and chum ($n = 2$) salmon in LE.

Sample preparation and analysis

For periphyton, acid-washed (10% HCl) filters removed inorganic carbon. We rinsed macroalgae with deionized water and then removed invertebrates and particulate matter. Invertebrate samples were composed of multiple individuals of the same taxon from a given site to ensure adequate biomass for isotope analysis (minimum of 0.4 mg dry weight). For fish, we extracted dorsal muscle plugs (with removal of skin and bone) from the same region for each fish. Dorsal muscle tends to be less variable than other tissues in *O. mykiss* (Pinnegar and Polunin, 1999) and has lower inorganic carbonate and lipid content (which have different fractionation rates than protein-rich muscle tissues (Gannes *et al.*, 1997). Processed tissues were freeze dried (Millrock Technologies, Kingston, NY) until completely desiccated (12–24 h) and then pulverized using a Wig-L-Bug ball-mill grinder (Bratt Technologies, East Orange, NJ). To minimize sample loss from mechanized grinding, we hand-ground invertebrate samples with limited biomass in their vials using a sterilized glass rod.

We analysed homogenized tissues from fish, invertebrates and macroalgae for stable isotopes using an elemental analyser (EA) coupled with isotope ratio mass spectroscopy (IRMS). Periphyton samples were analysed by the University of Alaska Fairbanks isotope laboratory and invertebrates and fish samples were analysed by the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center isotope laboratory. Comparisons of duplicate samples analysed by both laboratories showed high correlations for both $\delta^{13}\text{C}$ (Pearson's $r = 0.995$, $n = 24$) and $\delta^{15}\text{N}$ (Pearson's $r = 0.979$, $n = 24$). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are reported in reference to international isotope standards. At the Alaska laboratory the standards used were peptone for carbon and glycine for nitrogen. At the NOAA isotope laboratory nitrogen values were referenced to atmospheric nitrogen ($\delta^{15}\text{N}$ for atmospheric $\text{N} = 0\text{‰}$) and carbon values were referenced to NBS 19 ($\delta^{13}\text{C}$ of NBS 19 = 1.95‰ (Coplen *et al.*, 2006)). Nitrogen and carbon isotopic values are reported as per mil (‰) as defined by the formula

$$\delta\text{C or } \delta\text{N} = \left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right) \times 1000$$

where R_{Sample} and $R_{\text{Standard}} = \frac{^{13}\text{C}}{^{12}\text{C}}$ or $\frac{^{15}\text{N}}{^{14}\text{N}}$ and the standards were peptone/NBS 19 or air/glycine. Precision for isotope analysis was $\leq \pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ and $\leq \pm 0.2\text{‰}$ for $\delta^{13}\text{C}$.

Water chemistry

We collected water samples in acid washed (10% HCl) bottles for analysis of total nitrogen (TN), total phosphorus (TP), nitrate ($\text{NO}_3^- - \text{N}$), nitrite ($\text{NO}_2^- - \text{N}$), ammonium ($\text{NH}_4^+ - \text{N}$), and soluble reactive P (SRP = $\text{PO}_4^{3-} - \text{P}$). At each site, we rinsed all sampling equipment and bottles with

stream water three times. Samples for dissolved nutrients were filtered in the field using a 0.45 μm (pore-size) syringe filter. Samples were held on ice after collection (backcountry samples were held in river water before being transferred to ice, usually <4–8 h after collection) and frozen in the laboratory prior to analysis by the University of Washington Marine Chemistry Laboratory. TN and TP were analysed using the persulfate digestion method of Valderrama (1981). Modifications of the Armstrong *et al.* (1967), Slawyk and MacIsaac (1972), and Bernhardt and Wilhelms (1967) procedures were used for the analysis of $\text{NO}_3^- - \text{N}/\text{NO}_2^- - \text{N}$, $\text{NH}_4^+ - \text{N}$, and $\text{PO}_4^{3-} - \text{P}$, respectively. All concentrations are reported in $\mu\text{g/L}$.

Statistical analysis

We used *t*-tests to test for differences in taxa-specific stable isotope samples (except fish, which were pooled between habitats but mostly collected in the mainstem) and water chemistry between mainstem and side channel sites within each section-year combination (with a Bonferroni-adjustment of α to reduce the experiment-wide error rate). In all cases, differences between mainstem and side channel habitats were not significant and were subsequently pooled in further analyses. We tested parametric assumptions and applied transformations where appropriate. We used a two-way ANOVA, with section and year as fixed dependent variables, to test for differences in water chemistry and stable isotope values of periphyton, macroalgae and benthic invertebrate taxa. For fish, which were collected across 2 years, we used a one-way ANOVA to test for differences among sites. Because of unequal sample sizes among groups, we used Games-Howell post hoc tests for pairwise comparisons. In cases where transformations did not stabilize variances, we made limited comparisons among factors using 95% bootstrap confidence intervals (bias corrected; Efron, 1987) as implemented in the R (version 2.6.0) package 'boot'. We also used non-parametric two-way tests (ANOVA on ranks; Helsel and Hirsch, 2002). This method uses a transformation of the dependent variable to rank order, across all factors, prior to ANOVA when data are non-normal, unbalanced and/or suffer from heteroscedasticity (see Seaman *et al.*, 1994 for critique). All statistical analyses were run using SPSS software (version 15, SPSS, Chicago, Illinois) with $\alpha = 0.05$, unless otherwise noted.

RESULTS

Stable isotope ratios within taxonomic groups

Macroalgae and periphyton showed differences in isotopic ratios among sections of the Elwha River, but generally had higher variability than the invertebrates and fish, which reduced the ability to detect statistically significant

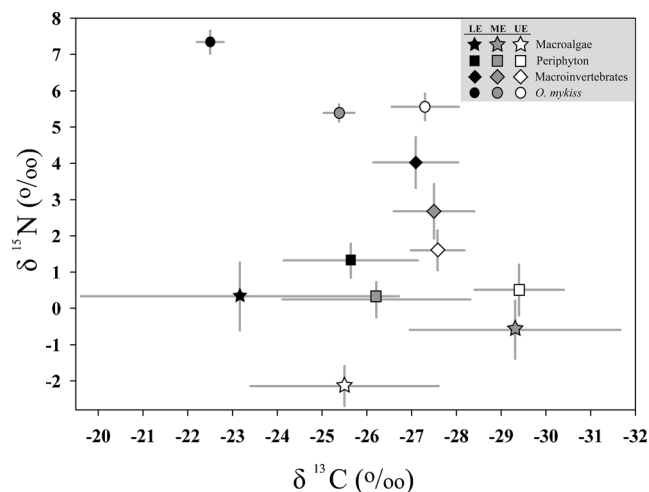


Figure 2. Plots of mean (SD) $\delta^{15}\text{N}$ (ordinate) and $\delta^{13}\text{C}$ (abscissa) values for macroalgae, periphyton, benthic macroinvertebrates and fish collected above (UE), between (ME) and below (LE) two dams in the Elwha River during 2005 and 2006 (combined)

differences. Both types of algae collected from LE had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values compared to sections above the dams (Figure 2). For macroalgae, this difference was only significant for $\delta^{15}\text{N}$ (two way ANOVA on ranks, $F_{2,51} = 11.66$, $p < 0.001$; post hoc $\text{LE} = \text{ME} > \text{UE}$) and there was a difference among years ($F_{1,2} = 17.42$, $p < 0.001$; section $\times$ year interaction not significant; Table I). Periphyton showed a similar pattern for $\delta^{15}\text{N}$ (two-way ANOVA, $F_{2,73} = 5.51$, $P = 0.006$) although with $\text{LE} > \text{ME} = \text{UE}$ (Table I). The differences among sections for $\delta^{13}\text{C}$ periphyton values were significant ($F_{2,73} = 21.92$, $p < 0.001$; $\text{LE} = \text{ME} > \text{UE}$) with no significant difference between years ($p = 0.054$, section $\times$ year interaction not significant; Table I).

Benthic invertebrates in the Elwha River displayed different isotopic ratios according to river section and functional feeding group, although the patterns were not consistent across the four taxa (Figure 3). The predatory stonefly sub-family Chloroperlinae differed among sections (Table I) during both years for $\delta^{15}\text{N}$ (two-way ANOVA, $F_{2,64} = 182.63$, $p < 0.001$, year and section $\times$ year not significant), with the $\text{LE} > \text{ME} > \text{UE}$ (all $p < 0.01$). Values for $\delta^{13}\text{C}$ followed a similar pattern for section ($F_{2,64} = 8.84$, $p < 0.001$) except that UE and ME were not significantly different from each other and the year effect was significant ($p = 0.01$). The shredding stonefly genus *Zapada* showed a similar trend as the Chloroperlinae for $\delta^{15}\text{N}$ ($F_{2,22} = 119.20$, $p < 0.001$), but not for $\delta^{13}\text{C}$ ($F_{2,26} = 0.19$, $p = 0.83$); however, for $\delta^{15}\text{N}$ there was a significant difference between years ($p = 0.01$) and a significant section $\times$ year interaction ($p = 0.002$), likely due to higher variance as a result of fewer numbers of sites at which this taxon was observed. The predatory caddisfly genus *Rhyacophila* was the largest bodied and most

Table I. Differences in carbon (C) and nitrogen (N) stable isotope levels from taxa collected in three sections of the Elwha River, Washington

Taxon	Isotope	Contrast			Post hoc		
		Section	Year	Section × Year	LE	ME	UE
<i>O. mykiss</i>	N	***	—	—	1	2	2
	C	***	—	—	1	2	3
Chloroperlinae	N	***	NS	NS	1	2	3
	C	***	*	NS	1	2	2
<i>Zapada</i> spp.	N	***	**	**	1	2	3
	C	NS	NS	NS	—	—	—
<i>Rhyacophila</i> spp.	N	*** (R)	NS	NS	1	1	2
	C	***	***	NS	1	1	2
<i>Simulium</i> spp. 05	N	***	—	—	1	—	2
	C	***	—	—	2	—	1
<i>Simulium</i> spp. 06	N	***	—	—	1	2	3
	C	NS	—	—	—	—	—
Periphyton	N	**	*	NS	1	2	2
	C	***	NS	NS	1	1	2
Macroalgae	N	*** (R)	***	NS	1	1	2
	C	NS (R)	NS	NS	—	—	—

Tests are two-way ANOVAs, except for fish (one-way) and cases where homogeneity of variances was violated (two-way on ranks (denoted as R in table), see text). If ANOVA was significantly different (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), the rank order among sections is provided (higher rank = higher stable isotope enrichment), with differences among sections tested with a Games-Howell post hoc test. Two sites that have the same value are not significantly different.

widespread insect of those we sampled. Both $\delta^{15}\text{N}$ (two-way ANOVA on ranks, $F_{2,76} = 14.01$, $p < 0.001$) and $\delta^{13}\text{C}$ (two-way ANOVA, $F_{2,76} = 8.70$, $p < 0.001$) values were significantly lower in UE (LE = ME > UE, $P_s < 0.001$), but with a significant year effect for $\delta^{13}\text{C}$ ($F_{2,76} = 26.11$, $p < 0.001$). Finally, we were unable to perform a two-way ANOVA for the dipteran genus *Simulium* due to low sample size in ME ($n = 2$). Thus, we analysed years separately with a t -test between UE and LE in 2005, which indicated that $\delta^{15}\text{N}$ in LE tissues were significantly higher than in UE tissues (t -test, $t = 17.03$, $df = 11$, $p < 0.001$). A one-way ANOVA for *Simulium* tissues from 2006 showed that $\delta^{15}\text{N}$ was significantly different for all sections (one-way ANOVA, $F_{2,20} = 35.28$, $p < 0.001$; LE > ME > UE, $P_s < 0.03$), whereas $\delta^{13}\text{C}$ was not significantly different ($p = 0.08$).

O. mykiss in LE were enriched in both ^{13}C and ^{15}N relative to sites in ME and UE (Figure 2). Fish in LE had higher average $\delta^{15}\text{N}$ (7.35‰ SD = ± 0.64 ‰) than fish collected in ME (5.39 ± 0.48 ‰) and UE (5.56 ± 0.74 ‰) (one-way ANOVA, $F_{2,219} = 39.5$, $p < 0.001$; Table I). Values for $\delta^{13}\text{C}$ also showed that LE sites (−22.5‰ SD = ± 0.60 ‰) were enriched relative to ME (−25.4‰ SD = ± 0.68 ‰), which in turn were higher than UE (−27.5‰ SD = ± 1.5 ‰) ($F_{2,221} = 106.3$, $p < 0.001$; Table I). Although based upon a small sample size, chum and coho salmon carcasses sampled in the lower river had $\delta^{13}\text{C}$ (−19.6 and −20.5 for chum and coho, respectively) and $\delta^{15}\text{N}$ (13.3 and 11.5) isotopic signatures similar to values reported for other adult salmonids in the Pacific Northwest (Bilby *et al.*, 2001; Chaloner *et al.*, 2002; Honea, 2005) and Alaska (Satterfield and Finney, 2002; Johnson and Schindler, 2009).

Stable isotope ratios among taxonomic groups

In terms of relative differences in isotope values among different taxa within a given river section, we did not observe striking differences above and below the dams. Of the taxa we surveyed, mean $\delta^{15}\text{N}$ values were consistently lowest for macroalgae and highest for *O. mykiss*, with $\delta^{15}\text{N}$ ranges among taxonomic group averages spanning 6.9‰ for LE, 6.2‰ for ME and 7.7‰ for UE. In LE and ME, average periphyton $\delta^{15}\text{N}$ was approximately 1‰ higher than macroalgae, followed by a 1–2‰ increase in the filter-feeding *Simulium* and the shredder *Zapada*, another 1–3‰ increase in the predatory Chloroperlinae and *Rhyacophila*, and 1.3–3.3‰ greater for *O. mykiss*. This pattern generally follows the predicted 2–4‰ increase in $\delta^{15}\text{N}$ by trophic level (Vander Zanden and Rasmussen, 2001; Fry, 2006). The relationships among taxonomic groups were slightly different in UE. Periphyton $\delta^{15}\text{N}$ values were 2.9‰ higher than macroalgae and 0.2–0.5‰ higher than *Simulium* and *Zapada*. Unlike LE and ME, the two invertebrate predators Chloroperlinae and *Rhyacophila* completely overlapped in

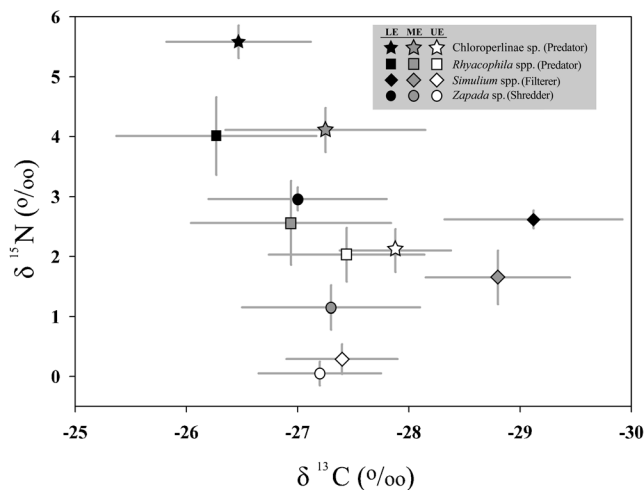


Figure 3. Plots of mean (SD) $\delta^{15}\text{N}$ (ordinate) and $\delta^{13}\text{C}$ (abscissa) values for four benthic macroinvertebrate taxa collected above (UE), between (ME) and below (LE) two dams in the Elwha River during 2005 and 2006 (combined)

$\delta^{15}\text{N}$ values, and *Simulium* and *Zapada* were more similar to each other than elsewhere in the Elwha. Overall, variability of $\delta^{15}\text{N}$ within river sections was low for *O. mykiss* and benthic invertebrate taxa, and greatest for periphyton and macroalgae—particularly in LE and ME. Relationships between different taxa were less consistent across river sections for $\delta^{13}\text{C}$, with the observed range of average values among taxa compressed in ME (2.2‰) and UE (3.9‰) relative to LE (6.3‰). For LE and ME, *Simulium* had the lowest $\delta^{13}\text{C}$ values and *O. mykiss* the highest, but there was no consistent ordering of intermediate taxa. Periphyton and macroalgae were both highly variable and overlapped with remaining invertebrate taxa, which were themselves very similar in $\delta^{13}\text{C}$ values. In UE, $\delta^{13}\text{C}$ values were highest for macroalgae and lowest for periphyton, with fish and invertebrate taxa intermediate and very similar to each other.

Water chemistry

Nutrient concentrations in the Elwha and Quinault Rivers ranged from 2.0 to 39.8 $\mu\text{g/L}$ for DIN (nitrate + nitrite + ammonium) and 1.1–4.4 $\mu\text{g/L}$ for $\text{PO}_4^{3-} - \text{P}$ across sections and years (Table II). Water chemistry samples did not differ between mainstem and side channel sites of most section-year combinations for water chemistry variables (*t*-tests, all $p > 0.001$ after Bonferroni correction) and were pooled for testing differences among sections and between years. As all nutrients except total Nitrogen (TN) had unequal variances (Levene's test, $P_s < 0.02$), our two-way ANOVAs should be interpreted with caution and in conjunction with graphical representations based on bootstrapped confidence intervals

(Figure 4). Levels of TN and TP did not differ significantly between years or among sections (Figure 4 and two-way ANOVA, $P_s > 0.17$). Dissolved inorganic nitrogen (DIN) was higher in QU than in UE, ME and LE during both years (Figure 4, two-way ANOVA: Section $p < 0.001$, Year $p = 0.99$, Section $\times$ Year $p = 0.10$, Games-Howel post hoc test $p < 0.05$). Phosphate was higher in the two unregulated sections (UE and QU) than LE and ME (Figure 4, two-way ANOVA: section $p < 0.001$, year $p < 0.001$, section $\times$ year $p < 0.03$, Games-Howel post hoc test $\text{LE} = \text{ME} < \text{QU} < \text{UE}$). However, there were differences between years and a significant section $\times$ year interaction, with values in the unregulated sections higher in 2005 than in 2006.

DISCUSSION

Stable isotope ratios were similar between habitat types (mainstem and side channels), but differed by river section and among taxa. Across multiple trophic levels, we generally found higher stable isotope ratios of nitrogen below the lower dam (LE) compared with two sections above the dams (ME and UE) that lacked salmon (Figure 2). The patterns differed among invertebrate functional feeding groups (Figure 3), with predators having higher nitrogen isotope ratios than shredders and filter feeders within each river section. This result is consistent with trophic shifts of isotope ratios seen in other studies (McCutchan *et al.* 2003) and is likely a reflection of the differences in food sources among these groups. However, the differences in stable isotope ratios were not always explained by whether salmon had

Table II. Average nutrient levels (number of sites, SD) of water samples collected in the Elwha and Quinault rivers from mainstem and side channel riffles (pooled).

Year	Lower Elwha	Middle Elwha	Upper Elwha	Quinault
Total nitrogen ($\mu\text{g/L}$)				
2005	137.6 (12, 77.3)	117.4 (9, 111.0)	48.9 (10, 69.1)	128.4 (12, 86.9)
2006	118.3 (13, 90.0)	116.4 (13, 53.0)	116.6 (17, 56.0)	105.7 (12, 59.1)
2-way ANOVA: Section $p = 0.17$; Year $p = 0.69$				
Total phosphorous ($\mu\text{g/L}$)				
2005	13.6 (12, 1.2)	11.6 (9, 1.3)	13.9 (10, 1.4)	13.4 (12, 2.7)
2006	13.0 (12, 8.2)	13.0 (13, 8.2)	12.7 (17, 2.1)	10.1 (12, 2.7)
2-way ANOVA: Section $p = 0.62$; Year $p = 0.42$				
Dissolved inorganic nitrogen ($\mu\text{g/L}$)				
2005	15.2 (12, 27.9)	2.0 (9, 1.6)	15.7 (10, 7.0)	39.8 (12, 18.2)
2006	20.6 (13, 24.3)	14.1 (13, 11.2)	8.1 (17, 5.4)	29.8 (12, 20.8)
2-way ANOVA: Section $p < 0.001$, Year $p = 0.99$, Section $\times$ Year $p = 0.10$ Post hoc (Tukey's HSD):				
$\text{LE} = \text{ME} = \text{UE} < \text{QU}$				
Phosphate ($\mu\text{g/L}$)				
2005	2.1 (12, 1.0)	1.4 (9, 0.4)	4.4 (10, 1.0)	3.6 (12, 1.2)
2006	1.1 (13, 0.9)	1.3 (13, 1.2)	3.3 (17, 0.5)	1.8 (12, 0.9)
2-way ANOVA: Section $p < 0.001$; Year $p < 0.001$; Section $\times$ Year $p < 0.03$ Post hoc (Tukey's HSD):				
$\text{LE} = \text{ME} < \text{QU} < \text{UE}$				

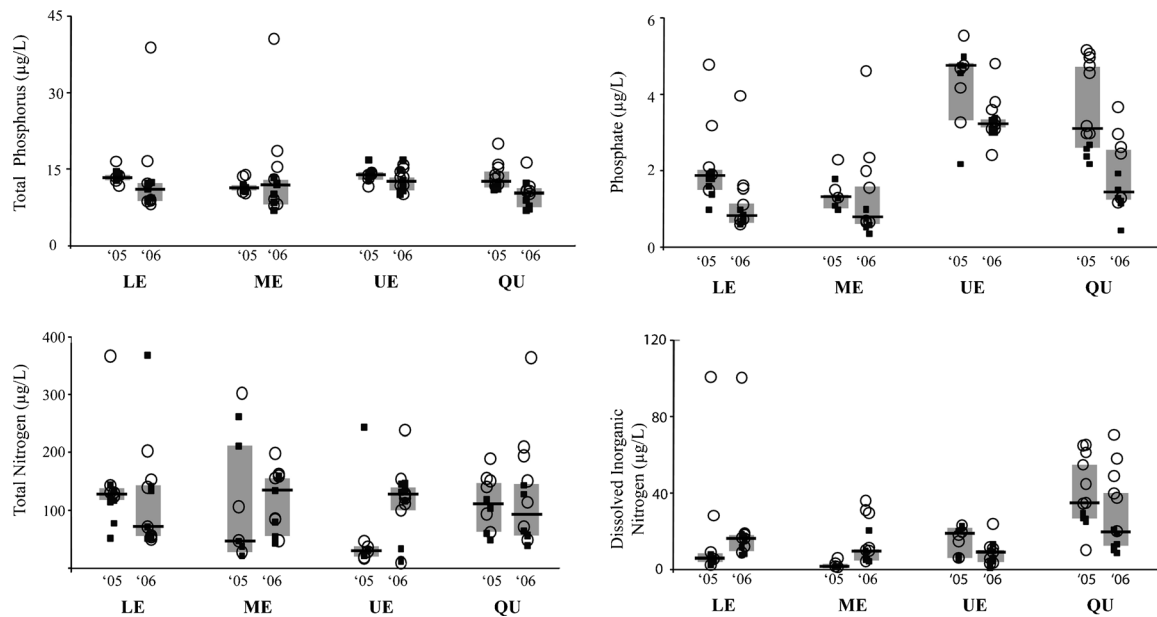


Figure 4. Plots showing water sample concentrations (µg/L) of total nitrogen, total phosphorous, dissolved inorganic nitrogen (DIN) and phosphate collected from 43 (2005) and 56 (2006) sites above (UE), between (ME) and below (LE) two dams in the Elwha River, Washington and from the adjacent Quinault River (QU). Open circles and filled squares denote side channels and mainstem sites (respectively) with 95% bootstrapped confidence intervals (bias corrected (Efron, 1987)) shown as shaded boxes and the median shown as a black bar

access to a section of the river. The Elwha River dams have blocked salmon and their marine-derived nutrient subsidy from migrating past rkm 7.9 for over 97 years. Despite dramatic reductions in salmon population sizes over historical estimates (up to 90%; Pess *et al.*, 2008; Winter and Crain, 2008), salmon still occur in LE. Our data suggest that in areas where salmon still have access, enriched stable isotope values, especially for fish and predatory invertebrate taxa, could be MDN from current salmon populations and/or the legacy of MDN from previous annual salmon returns. Our observation that stable isotope values in ME were often more similar to values below, rather than above, the dams may also be explained in part by legacy effects, but we cannot rule out the role of other factors.

In addition to the availability of MDN via anadromous fishes, other factors likely contributed to present distributions of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios throughout the Elwha River. These include processes that affect the availability and movement of heavy and light isotopes within foodwebs. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values may be affected by the composition of primary producers, isotope fractionation rates across trophic levels, and foodweb interactions. At the base of the food chain, changes in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for macroalgae and periphyton may reflect shifts in growth rate, water velocity, watershed area or other abiotic factors (Macleod and Barton, 1998; Finlay, 2001; Trudeau and Rasmussen, 2003) rather than the presence or absence of salmon. Similarly, the composition of the riparian forest also changes along the

length of the Elwha River. Of particular note is the higher relative abundance in LE and ME of nitrogen-fixing red alder (*Alnus rubra*) (the authors, unpublished data), which contributes a consistently narrow range of $\delta^{15}\text{N}$ values (-1.5 to -0.5‰) independent of MDN (Scott *et al.*, 2008). The presence of riparian alder may also affect $\delta^{15}\text{N}$ values of aquatic taxa by increasing the total pool of available nitrogen and thus increasing fractionation rates between trophic levels (Adams and Sterner, 2000). For $\delta^{13}\text{C}$, it is thought that periphyton $\delta^{13}\text{C}$ values and watershed area are positively correlated due to lower fractionation rates in larger productive rivers where carbon dioxide is more limiting (Finlay 2001). As the relative importance of autochthonous versus allochthonous food resources shifts along the river continuum, so too will consumer trophic position—due to changes in the food base and the presence or absence of competing species. Such changes are likely reflected in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. In addition, denitrification, a microbial process that reduces nitrate to gaseous forms of N, can increase the availability of ^{15}N , particularly in finer riparian soils in spawning streams (Pinay *et al.*, 2003). This may be the case in ME where ratios are higher relative to the UE. Denitrification-mediated increases in isotopic ratios can be misconstrued as a marine-derived nutrient effect (Pinay *et al.*, 2003).

We found that the Elwha River is oligotrophic (see also Munn *et al.*, 1999), with low levels of nutrients essential for biological productivity. Relative to other rivers in the Pacific

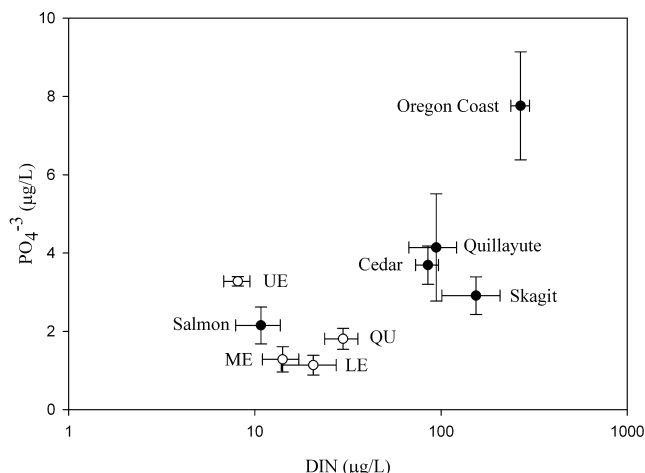


Figure 5. A comparison of PO_4^{3-} and DIN concentrations in the Elwha and Quinnault Rivers (open circles; this study) and other regional rivers (closed circles). All samples were collected from riffle habitats in salmon-bearing rivers. Data from the Cedar River were collected above an impassable salmon barrier. Water chemistry samples for all studies were obtained by collecting grab samples from riffles in summer (July–September) and were analysed by the University of Washington Oceanography Marine Chemistry Lab. Data for the Skagit River ($n=6$) and Quillayute ($n=5$) rivers, WA were collected by Morley *et al.* (2005). Data for the Salmon River, ID ($n=10$) were collected by Sanderson *et al.* (2009). Data for the Oregon coast (2001, $n=10$) and the Cedar River, WA (2002, $n=41$) are unpublished and were collected by Phil Roni (NWFSC) and Peter Kiffney (NWFSC), respectively

Northwest, nutrient concentrations within the Elwha and Quinnault River systems were low (Figure 5). Concentrations for both PO_4^{3-} – P and DIN were consistent with those observed in the Salmon River, Idaho, which has also experienced reductions in marine-derived nutrients as a result of the Columbia River dams (Sanderson *et al.*, 2009). DIN concentrations in the Quillayute, Skagit (Morley *et al.*, 2005) and Cedar rivers (P. Kiffney, NOAA, unpublished data) are approximately an order of magnitude higher than in the Elwha; yet PO_4^{3-} – P concentrations were similar. Higher nutrient concentrations in these systems could be due to higher relative abundance of salmon populations. In the case of the Cedar and Skagit rivers, urbanization and agriculture may also be contributing factors.

We observed contrasting trends in phosphorus and nitrogen concentrations among regulated and unregulated reaches of the Elwha. PO_4^{3-} – P concentrations were significantly higher in unregulated reaches (QU and UE) than in regulated reaches (LE and ME), suggesting an impact of the dams on nutrient dynamics in this system. Phosphorus, which occurs primarily in particulate form in aquatic systems, can be trapped by reservoirs, thereby reducing the availability of this nutrient downstream of dams (Kelly, 2001 and references therein). Phosphorus supply to downstream reaches is further reduced by uptake of dissolved phosphorus

by algal communities within reservoirs (Elser and Kimmel, 1985). Inputs of phosphorus to rivers are generally very low ($<0.1 \text{ kg P ha}^{-1} \text{ yr}^{-1}$) (Withers and Jarvie, 2008); therefore, the reduction in phosphorus inputs to downstream reaches has important implications for primary production and food web dynamics in general. Alternatively, significantly lower PO_4^{3-} – P concentrations in LE and ME could be due to higher biological demand for inorganic phosphorus as a result of significantly higher biomass in these sections (Morley *et al.* 2008). Uptake by biota, as well as increased interactions between dissolved phosphorus with sediments, results in a shift from dissolved to particulate phosphorus, particularly in lowland river reaches (Withers and Jarvie, 2008). The shift from dissolved to particulate phosphorus may be the reason for our inability to detect significant differences in TP among the reaches. In addition, because these reaches can interact substantially with their floodplains, particulate phosphorus inputs may be higher due to inputs of riparian leaf litter and soil (Kelly, 2001). However, inputs of particulate phosphorus are more likely to be important during high flow events.

In contrast to phosphorus, we saw no significant differences between DIN concentrations in regulated and unregulated reaches of the Elwha. In general, the availability of dissolved nitrogen in aquatic ecosystems tends to be highly variable due to a number of in-stream processes including assimilation by heterotrophic and autotrophic organisms, nitrification and denitrification (Peterson *et al.*, 2001). Furthermore, the amount of nitrogen in aquatic systems can vary depending on the abundance and distribution of species such as alder, which facilitate high rates of N fixation (Scott *et al.*, 2008). Alder is prevalent in both regulated and unregulated reaches of the Elwha River and is likely contributing to spatial variability of N inputs into the watershed. While we can speculate about the mechanisms driving observed trends in phosphorus and nitrogen, our primary research goal was to establish baseline conditions in nutrient concentrations prior to dam removal. Because we did not collect corollary explanatory variables, we have limited ability to make inferences about the mechanisms that might be responsible for the differences among river sections. Additional studies that examine the factors noted above, in addition to possible differences due to transient storage and hyporheic flows (Ensign and Doyle, 2006), are warranted.

Considering the oligotrophic nature of the Elwha, MDN delivered by salmon to reaches previously impacted by the dams could provide an important subsidy for aquatic food-webs in this system. Low levels of primary and secondary productivity are typical of many coastal streams in the Pacific Northwest. Thus, even modest inputs of nutrients and carbon from relatively few anadromous fish may be important in stimulating primary production and maintaining

trophic productivity (Larkin and Slaney, 1997). For example, Schuldt and Hershey (1995) found short-term increases in phosphorous concentration and periphyton biomass by experimentally placing 3 mesh bags of eight salmon carcasses (average weight of 56 kg) in a small, experimental stream. In the Salmon River, British Columbia, inorganic nutrient manipulations, which were designed to simulate nutrient delivered by carcasses, have not only led to increases in algal biomass but also subsequent increases in benthic invertebrate biomass, and weight and abundance of various fish species (Slaney *et al.*, 2003; Wilson *et al.*, 2003). Similarly, direct consumption of carcass flesh and eggs can lead to higher juvenile salmonid growth rates in natural and artificial stream channels stocked with salmon carcasses (Bilby *et al.*, 1998; Wipfli *et al.*, 2003). Alternatively, it follows that small reductions in the numbers of anadromous fish could significantly alter ecosystem processes and reduce foodweb productivity, thus contributing to a negative feedback loop (Larkin and Slaney, 1997; Bilby *et al.*, 2001; Scheuerell *et al.*, 2005). Associated decreases in parr and smolt sizes can reduce overwinter and marine survival, resulting in decreased adult returns and further reducing stream productivity (Bilby *et al.*, 1996; Ward and Slaney, 1988).

Our study was primarily designed to examine differences between river sections relative to current transport of MDN via anadromous fishes. Although stable isotope analysis provides a useful tool for tracking interactions between multiple species (Vander Zanden *et al.*, 2006), our monitoring efforts were focused on a limited set of taxa, potential food sources and feeding guilds, thus reducing our ability to explicitly delineate food web interactions. Nonetheless, our data still provide a useful starting point for formulating hypotheses on the effects of dams and dam removal on foodweb interactions. For instance, we postulated that decreased floodplain heterogeneity in river sections below the dams (LE and ME) would result in a less diverse food base (*sensu* Power *et al.*, 1996), with fewer ecological niches among consumers reflected in greater overlap of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values relative to UE. Instead, we observed a compressed range of values above the dams. This likely reflects both the 97-year absence of isotopically enriched salmon tissues and a shift in the resource base at higher elevations. Not only is the channel narrower in UE but also it experiences a more dynamic disturbance regime manifested in higher bed mobility rates producing younger, on average, floodplain stand ages (Kloehn *et al.*, 2008). Additional sampling, in time and space, focused upon available organic matter sources would be valuable for evaluating future changes in foodweb interactions. Similarly, expanded sampling of invertebrates, fishes and other aquatic and riparian taxa is critical for building a more predictive foodweb model that will help us understand ecological response to dam removal in the Elwha River.

The degree to which increased MDN subsidies could affect foodwebs following dam removal will vary in time and space, as salmon recolonization is not expected to be spatially uniform and could take decades (Brenkman *et al.*, 2008a; Pess *et al.*, 2008). Habitats currently above the dams will likely receive different assemblages of recolonizing fish, depending upon life history attributes, status of source populations, and differences in swimming ability between species that stay lower in watersheds (e.g. pink salmon) with those that migrate farther distances (e.g. Chinook salmon). In addition, the release of large volumes of sediment is expected to have a large short-term impact on benthic communities (Morley *et al.*, 2008), which may restructure food web dynamics over the long term (e.g. Harding *et al.*, 1998) and possibly confound detection of changes related to increased MDN. Similarly, release of sediments from the reservoirs could increase nutrient levels (Chen and Jia, 2008), but the degree to which they would be retained in the system is unknown. Yet, dam removal in the Elwha River is expected to provide access to relatively pristine spawning and rearing habitat currently above the impassable dams. Estimates of future salmon returns (projections suggest as many as 150 000 spawners following full restoration; Department of the Interior (DOI), 1996; Ward *et al.*, 2008) could substantially increase annual nitrogen and phosphorous loading. We hypothesize that the return of salmon and their marine derived-nutrient subsidy to ME and UE will have both direct and indirect effects (e.g. Scheuerell *et al.*, 2007; Moore and Schindler 2008; Honea and Gara 2009; Janetski *et al.*, 2009) on nutrient status and trophic structure, which should be traceable using stable isotope ratios compared with the values that we describe herein.

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REFERENCES

- Adams TS, Sterner RW. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. *Limnology and Oceanography* **45**: 601–607.
- Armstrong FAJ, Stearns CR, Strickland JDH. 1967. The measurement of upwelling and subsequent biological processes by means of the Technicon autoanalyser and associated equipment. *Deep Sea Research* **14**: 381–389.
- Ben-David M, Hanley TA, Schell DM. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* **83**: 47–55.
- Bernhardt H, Wilhelms A. 1967. The continuous determination of low level iron, soluble phosphate and total phosphate with the autoanalyzer. *Technicon Symposia* **1**: 385–389.
- Bilby RE, Fransen BR, Bisson PA. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 164–173.
- Bilby RE, Fransen BR, Bisson PA, Walter JK. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1909–1918.
- Bilby RE, Fransen BR, Walter JK, Cederholm CJ, Scarlett WJ. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* **261**: 6–14.
- Brenkman SJ, Pess GR, Torgersen C, Kloehn KK, Duda JJ, Corbett SC. 2008a. Predicting recolonization patterns and interactions between potamodromous and anadromous salmonids in response to dam removal in the Elwha River, Washington State. *Northwest Science* **82** (Special Issue): 91–106.
- Brenkman SJ, Mumford SL, House M, Patterson C. 2008b. Establishing baseline information on the geographic distribution of fish pathogens endemic in Pacific salmonids prior to dam removal and subsequent recolonization by anadromous fish in the Elwha River, Washington. *Northwest Science* **82** (Special Issue): 142–152.
- Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**: 492–507.
- Cederholm CJ, Houston DB, Cole DL, Scarlett WJ. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1347–1355.
- Cederholm CJ, Kunze MD, Murota T, Sibatani A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* **24**: 6–15.
- Chaloner DT, Martin KM, Wipfli MS, Ostrom PH, Lamberti GA. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 1257–1265.
- Chaloner DT, Wipfli MS. 2002. Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. *Journal of the North American Benthological Society* **21**: 430–442.
- Chen F, Jia G. 2008. Spatial and seasonal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of particulate organic matter in a dam-controlled subtropical river. *River Research and Applications* **25**: 1169–1176. DOI: 10.1002/rra.1225
- Collier KJ. 2002. Effects of flow regulation and sediment flushing on instream habitat and benthic invertebrates in a New Zealand river influenced by a volcanic eruption. *River Research and Applications* **18**: 213–226.
- Coplen TB, Brand WA, Gehre M, Gröning M, Meijer HAJ, Toman B, Verkouteren RM. 2006. New guidelines for ^{13}C measurements. *Analytical Chemistry* **78**: 2439–2441.
- Department of the Interior (DOI). 1996. Elwha River ecosystem restoration implementation, final environmental impact statement. NPS D-271A. Department of the Interior, National Park Service, Olympic National Park, Port Angeles, WA.
- Drake DC, Smith JV, Naiman RJ. 2006. Salmon decay and nutrient contributions to riparian forest soils. *Northwest Science* **79**: 61–71.
- Duda JJ, Freilich JE, Schreiner EG. 2008. Baseline studies in the Elwha River ecosystem prior to dam removal: introduction to the special issue. *Northwest Science* **82** (Special Issue): 1–12.
- Efron B. 1987. Better bootstrap confidence intervals. *Journal of the American Statistical Association* **82**: 171–200.
- Ensign SH, Doyle MW. 2006. Nutrient spiraling in streams and river networks. *Journal of Geophysical Research* **111**: G04009. DOI:10.1029/2005JG000114
- Elser JJ, Kimmel BL. 1985. Nutrient availability for phytoplankton production in a multiple-impoundment series. *Canadian Journal of Fisheries and Aquatic Science* **42**: 1359–1370.
- Finlay JC. 2001. Stable carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology* **82**: 1052–1064.
- Fry B. 2006. *Stable Isotope Ecology*. Springer: New York.
- Gannes LZ, O'Brien DM, Martinez del Rio C. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* **78**: 1271–1276.
- Gende SM, Edwards RT, Willson MF, Wipfli MS. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* **52**: 917–928.
- Gresh T, Lichatowich J, Schoonmaker P. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* **25**: 15–21.
- Han M, Fukushima M, Kameyama S, Fukushima T, Matsushita B. 2008. How do dams affect freshwater fish distributions in Japan? Statistical analysis of native and nonnative species with various life histories. *Ecological Research* **23**: 735–743.
- Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EDB III. 1998. Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences* **95**: 14843–14847.
- Hart DD, Johnson TE, Bushaw-Newton KL, Horwitz RJ, Bednarek AT, Charles DF, Kreeger DA, Velinsky DJ. 2002. Dam removal: challenges and opportunities for ecological research and river restoration. *BioScience* **52**: 669–681.
- Helfield JM, Naiman RJ. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream habitat. *Ecology* **82**: 2403–2409.
- Helsel DR, Hirsch RM. 2002. *Statistical Methods in Water Resources*. Elsevier: Amsterdam.
- Hildebrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* **74**: 2080–2088.
- Hobson KA, Gibbs HL, Gloutney ML. 1997. Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. *Canadian Journal of Zoology* **75**: 1720–1723.
- Honea JM. 2005. Effect of salmon spawning on seasonal changes in structure and function of stream macroinvertebrate communities. *PhD Dissertation*, University of Washington, Seattle, WA.

- Honea JM, Gara RI. 2009. Macroinvertebrate community dynamics: strong negative response to salmon redd construction and weak response to salmon-derived nutrient uptake. *Journal of the North American Benthological Society* **28**: 207–219.
- Janetski DJ, Chaloner DT, Tiegs SD, Lamberti GA. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* **159**: 583–595.
- Johnson SP, Schindler DE. 2009. Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research. *Ecological Research* **24**: 855–863.
- Kelly VJ. 2001. Influence of reservoirs on solute transport: a regional-scale approach. *Hydrological Processes* **15**: 1227–1249.
- Kline TC Jr, Goering JJ, Mathisen OA, Poe PH, Parker PL. 1990. Recycling of elements transported upstream by runs of Pacific salmon: 1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in Sashin Creek, southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 136–144.
- Kloehn KK, Beechie TJ, Morley SA, Coe HJ, Duda JJ. 2008. Influence of dams on river-floodplain dynamics in the Elwha River, Washington. *Northwest Science* **82** (Special Issue): 224–235.
- Larkin GA, Slaney PA. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonids production. *Fisheries* **22**: 16–24.
- Lassalle G, Crouzet P, Rochard E. 2009. Modelling the current distribution of European diadromous fishes: an approach integrating regional anthropogenic pressures. *Freshwater Biology* **54**: 587–606.
- Lichatowich J. 1999. *Salmon Without Rivers*. Island Press: Washington, DC.
- MacLeod NA, Barton DR. 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1919–1925.
- Marks JC, Power ME, Parker MS. 2000. Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos* **90**: 20–27.
- McCutchan JH, Lewis WM, Kendall C, McGrath CC. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102**: 378–390.
- McHenry ML, Pess GR. 2008. An overview of monitoring options for assessing the response of salmonids and their aquatic ecosystems in the Elwha River following dam removal. *Northwest Science* **82** (Special Issue): 29–47.
- Merritt RW, Cummins KW (Eds). 1996. *An Introduction to the Aquatic Insects of North America*, 3rd edn. Kendall Hunt: Dubuque, IA.
- Minakawa N, Gara RI, Honea JM. 2002. Increased individual growth rate and community biomass of stream insects associated with salmon carcasses. *Journal of the North American Benthological Society* **21**: 651–659.
- Moore JW, Schindler DE. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology* **77**: 275–284.
- Morley SA, Duda JJ, Coe HJ, Kloehn KK, McHenry ML. 2008. Benthic invertebrates and periphyton in the Elwha River basin: current conditions and predicted response to dam removal. *Northwest Science* **82** (Special Issue): 179–198.
- Morley SA, Garcia PS, Bennett TR, Roni P. 2005. Juvenile salmonid (*Oncorhynchus* spp.) use of constructed and natural side channels in Pacific Northwest Rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 2811–2821.
- Moulton SR, Kennen JG, Goldstein RM, Hambrook JA. 2002. Revised protocols for sampling algal, invertebrate, and fish communities as part of the National Water-Quality Assessment Program. *U.S. Geological Survey Open-File Report 02-150*, Reston, VA.
- Munn MD, Black RW, Haggland AL, Hummling MA, Huffman RL. 1999. An assessment of stream habitat and nutrients in the Elwha River basin: implications for restoration. *US Geological Survey Water-Resources Investigations Report 98-4223*, Tacoma, WA.
- Munn MD, Brusven MA. 2004. The influence of Dworshak Dam on epilithic community metabolism in the Clearwater River, U.S.A. *Hydrobiologia* **513**: 121–127.
- Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**: 399–417.
- Nehlsen W, Williams JE, Lichatowich JA. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* **16**: 4–21.
- Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–408.
- Perrin CJ, Richardson JS. 1997. N and P limitation of benthos abundance in the Nechako River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 2574–2583.
- Pess GR, McHenry ML, Beechie TJ, Davies J. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Science* **82** (Special Issue): 72–90.
- Peterson BJ, Wollheim WM, Mulholland PJ, Webster JR, Meyer JL, Tank JL, Marti E, Bowden WB, Valett HM, Hershey AE, McDowell WH, Dodds WK, Hamilton SK, Gregory S, Morrall DD. 2001. Control of nitrogen export from watersheds by headwater streams. *Science* **292**: 86–90.
- Petts GE. 1984. *Impounded Rivers: Perspectives for Ecological Management*. John Wiley and Sons: New York.
- Petts GE, Gurnell AM. 2005. Dams and geomorphology: research progress and future directions. *Geomorphology* **71**: 27–47.
- Phillips EL, Donaldson WR. 1972. Washington climate for Clallam, Grays Harbor, Jefferson, Pacific, and Wahkiakum counties. *Cooperative Extension Service publication EM 3708*, Washington State University, Pullman, WA.
- Pinay G, O'Keefe T, Edwards R, Naiman RJ. 2003. Potential denitrification activity in the landscape of a western Alaska drainage basin. *Ecosystems* **6**: 336–343.
- Pinnegar JK, Polunin NVC. 1999. Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13**: 231–255.
- Piorkowski RJ. 1995. Ecological effects of spawning salmon on several southcentral Alaskan streams. *Ph.D. Dissertation*, University of Alaska, Fairbanks, AK.
- Power ME, Dietrich WE, Finlay JC. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental Management* **20**: 887–895.
- Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical-temperate comparisons. *Bioscience* **50**: 807–823.
- Quinn TP. 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press: Seattle, WA.
- Richey SC, Perkins MA, Goldman CR. 1975. Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a subalpine stream. *Journal of the Fisheries Research Board of Canada* **32**: 817–820.
- Ruckelshaus MH, Levin P, Johnson JB, Kareiva PM. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* **33**: 665–706.
- Sanderson BL, Coe HJ, Tran CD, Macneale KH, Harstad DL, Goodwin AB. 2009. Nutrient limitation of periphyton in Idaho streams: results from nutrient diffusing substrate experiments. *Journal of the North American Benthological Society* **28**: 832–845.
- Sarakinos HC, Johnson ML, Vander Zanden MJ. 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology* **80**: 381–387.
- Satterfield FR IV, Finney BP. 2002. Stable isotope analysis of Pacific salmon: insight into trophic status and oceanographic conditions over the last 30 years. *Progress in Oceanography* **53**: 231–246.

- Scheuerell MD, Levin PS, Zabel RW, Williams JG, Sanderson BL. 2005. A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Science* **62**: 961–964.
- Scheuerell MD, Moore JW, Schindler DE, Harvey CJ. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshwater Biology* **52**: 1944–1956.
- Schindler DE, Scheuerell MD, Moore JM, Gende SM, Francis TB, Palen WJ. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* **1**: 31–37.
- Schuldt JA, Hershey AE. 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society* **14**: 259–268.
- Scott EE, Perakis SS, Hibbs DE. 2008. $\delta^{15}\text{N}$ patterns of Douglas-fir and red alder riparian forests in the Oregon coast range. *Forest Science* **54**: 140–147.
- Seaman JW, Walls SC, Wide SE, Jaeger RG. 1994. Caveat emptor: rank transformation methods and interactions. *Trends in Ecology and Evolution* **9**: 261–263.
- Slaney PA, Ward BR, Wightman JC. 2003. Experimental nutrient addition to the Keogh River and application to the Salmon River in coastal British Columbia. *American Fisheries Society Symposium* **34**: 111–126.
- Slawyk G, MacIssac JJ. 1972. Comparison of two automated ammonium methods in a region of coastal upwelling. *Deep Sea Research* **19**: 521–524.
- Trudeau V, Rasmussen JB. 2003. The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. *Limnology and Oceanography* **48**: 2194–2199.
- Valderrama JC. 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. *Marine Chemistry* **10**: 109–122.
- Vander Zanden JM, Chandra S, Park S, Vadeboncoeur Y, Goldman CR. 2006. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 2608–2620.
- Vander Zanden JM, Rasmussen JB. 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography* **46**: 2061–2066.
- Ventura M, Jeppesen E. 2009. Effects of fixation on freshwater invertebrate carbon and nitrogen isotope composition and its arithmetic correction. *Hydrobiologia* **632**: 297–308.
- Vinson MR. 2001. Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecological Applications* **11**: 711–730.
- Ward L, Crain P, Freymond B, McHenry M, Morrill D, Pess G, Peters R, Shaffer JA, Winter B, Wunderlich B. 2008. Elwha River Fish Restoration Plan-Developed Pursuant to the Elwha River Ecosystem and Fisheries Restoration Act, Public Law 102-495. *NOAA Technical Memorandum NMFS-NWFSC-90*, U.S. Department of Commerce; 168.
- Ward BR, Slaney PA. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1110–1122.
- Ward JV, Stanford JA. 1995. The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research and Management* **10**: 159–168.
- Wilson GA, Ashley KI, Land RW, Slaney PA. 2003. Experimental enrichment of two oligotrophic rivers in south coastal British Columbia. *American Fisheries Society Symposium* **34**: 149–162.
- Winter BD, Crain P. 2008. Making the case for ecosystem restoration by dam removal in the Elwha River, Washington. *Northwest Science* **82** (Special Issue): 13–28.
- Wipfli MS, Hudson JP, Caouette JP. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Science* **55**: 1503–1511.
- Wipfli MS, Hudson JP, Caouette JP. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* **132**: 371–381.
- Withers PJA, Jarvie HP. 2008. Delivery and cycling of phosphorus in rivers: a review. *Science of the Total Environment* **400**: 379–395.
- Wunderlich RC, Winter BD, Meyer JH. 1994. Restoration of the Elwha River ecosystem. *Fisheries* **19**: 11–19.