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Short communication

The rapid return of marine-derived nutrients to a freshwater food web following dam removal

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ABSTRACT

Dam removal is increasingly being recognized as a viable river restoration action. Although the main beneficiaries of restored connectivity are often migratory fish populations, little is known regarding recovery of other parts of the freshwater food web, particularly terrestrial components. We measured stable isotopes in key components to the freshwater food web: salmon, freshwater macroinvertebrates and a river specialist bird, American dipper (*Cinclus mexicanus*), before and after removal of the Elwha Dam, WA, USA. Less than a year after dam removal, salmon returned to the system and released marine-derived nutrients (MDN). In that same year we documented an increase in stable-nitrogen and carbon isotope ratios in American dippers. These results indicate that MDN from anadromous fish, an important nutrient subsidy that crosses the aquatic–terrestrial boundary, can return rapidly to food webs after dams are removed which is an important component of ecosystem recovery.

1. Introduction

Over 16 million dams impact the geophysical and ecological integrity of rivers worldwide (Lehner et al., 2011). In the United States (US), it is estimated that fluvial processes in every watershed greater than 2000 km^2 have been affected by dams (Graf, 2001). Although dams provide socio-economic benefits, such as 16% of water for the global food supply and 19% of the world's electricity (WCD, 2000), they disrupt food web dynamics, modify and obstruct critical habitat, fragment populations, and alter species life history (e.g. Scudder, 2005). Such environmental costs along with aging infrastructure have led to removal of >1000 dams in the US (O'Connor et al., 2015). Dam removals present a unique opportunity to examine ecosystem responses and recovery (Service, 2011).

One of the greatest ecological costs of dams is the disruption of migratory connectivity for anadromous fish that migrate from oceans to rivers. In western North America, dams have had profound effects on Pacific salmon (*Oncorhynchus spp.*) populations, and the river ecosystems of which they are a key component (Bunn and Arthington, 2002). Salmon acquire >90% of their biomass in pelagic waters, accumulating large amounts of marine-derived nitrogen, phosphorous, and carbon (Kline et al., 1990; Willson and Halupka, 1995). These marine-derived nutrients (MDNs) are deposited in mostly oligotrophic freshwater systems when salmon return to natal streams to spawn and die (Hocking and Reimchen, 2002; Naiman et al., 2002). As a result, large pulses of MDN become available to terrestrial and aquatic food webs, affecting juvenile salmon growth (Wipfli et al., 2003), primary productivity (Bellmore et al., 2014), consumer densities (Christie et al., 2008), and life histories of terrestrial organisms (Tonra et al. *in review*). Although MDN effects on freshwater food webs have been much studied (*reviewed in* Janetski et al., 2009), empirical data on the speed at which MDN returns to freshwater and terrestrial food webs following dam removal is lacking.

In 2012, the first stage in the largest dam removal in history was completed with removal of the 32 m tall Elwha Dam on the Elwha River, WA, US, providing returning salmon access to upstream habitats for the first time in a century. Anadromous fish immediately began colonizing upstream of the former Elwha Dam, with redds of multiple species documented in mainstem, floodplain, and tributary habitats (McMillan and Moses, 2011; McHenry et al., 2015). By 2013, 85% of redds (McHenry et al., 2015) and >4000 Chinook salmon (*O. tshawytscha*) spawners (Denton et al., 2014) were located upstream of the Elwha Dam.

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We examined patterns in MDN pre- and post-dam removal using stable isotopes in samples collected from three stream-obligate taxa: spawning salmon; an avian consumer, the American dipper, (*Cinclus mexicanus*); and an aquatic invertebrate prey of dippers. We hypothesized that increased MDN input following dam removal would be reflected in increased stable isotope ratios in dippers and their prey sampled before and after dam removal.

2. Methods

2.1. Study site and dam removal

The Elwha and Glines Canyon dams (8.0 and 21.8 km from the mouth, respectively) were constructed without fish passage structures, limiting in-river migrations by anadromous fish to 7.9 km of river downstream of Elwha Dam since 1912. Our study was conducted along mainstem and tributary mouths of the Elwha River (48.081079 N, −123.571796 W; Fig. 1). The Elwha Dam was removed between September 2011 and April 2012, but Glines Canyon Dam removal was not completed until September 2014. Therefore habitat upstream of this dam was not accessible to salmon during our study. In addition to natural recolonization of multiple salmon species, during the autumn of 2011 708 adult coho salmon (*O. kisutch*) and 65 adult steelhead (*O. myskiss*) were transported from the capture locations downstream of Elwha dam to mainstem and tributary release locations between the two dams. This action was taken to mitigate exposure to high sediment conditions in the river and to assist recolonization; however, 55% of the coho equipped with radio-transmitters returned to their capture location downstream of the dam site (McMillan and Moses, 2011).

2.2. Measuring MDN

Animal tissues grown in marine environments are enriched with heavy stable isotopes of carbon (^{13}C) and nitrogen (^{15}N; Bilby et al., 1996). MDN enters food webs indirectly when primary producers access enriched nitrogen provided by salmon, resulting in high stable-nitrogen isotope ratios (δ^{15}N) and base-level stable-carbon isotope ratios δ^{13}C in consumer tissues (Ben-David et al., 1998), or directly when consumers feed on salmon tissues (e.g. carcasses, eggs), resulting in both enriched δ^{15}N and δ^{13}C in consumer tissues (Bilby et al., 1996). In this way, δ^{13}C and δ^{15}N can be used to measure both indirect and direct pathways for MDN enrichment of consumers.

With the exception of pre-removal *Rhyacophila* (see Duda et al., 2011 for details), all stable isotope analyses were completed at the

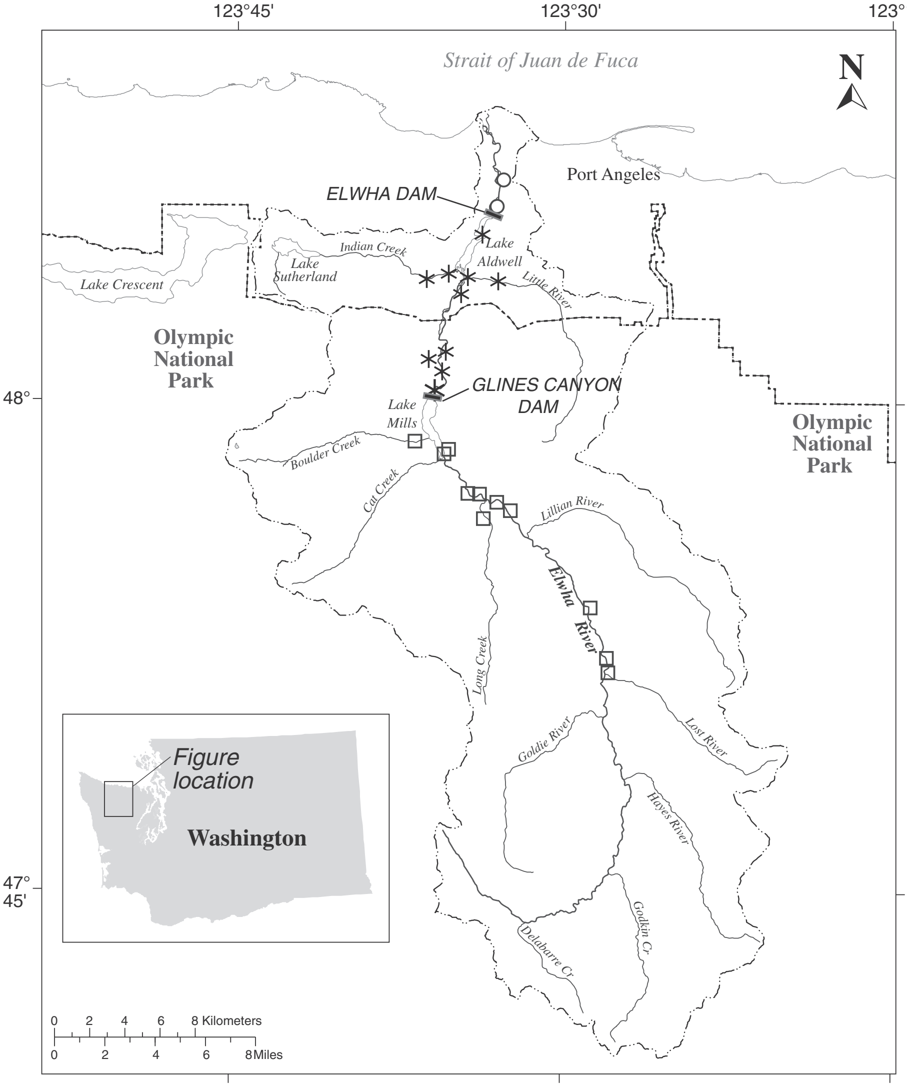

Fig. 1. Map of study area along the Elwha River, WA, USA. Circles indicate American dipper territories in areas never obstructed to salmon, stars denote territories in the middle Elwha which was opened to salmon following removal of the Elwha Dam, and squares denote territories in the upper Elwha, which was blocked to salmon throughout the study period by the since removed Glines Canyon Dam.

Smithsonian Stable Isotope Mass Spectrometry Laboratory in Suitland, MD. We combusted samples in an elemental analyzer (Thermo TC/EA; Thermo Scientific, Waltham, Massachusetts, US) prior to introducing them into an isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage). All C:N ratios were <3.5, therefore we did not perform a fat extraction (Post et al., 2007), but feather samples were washed in a 2:1 chloroform:methanol solution to remove surface oils. Two in-house standards (acetanalide and urea) were run for every 10 samples. Stable isotope values are expressed in δ units as parts per thousand (‰) deviations from international standards PDB (carbon) and air (nitrogen) by the following equation:

$$\delta X = \{[(R_{unknown} - R_{standard}) - 1] \times 1000\},$$

where X is the isotope of interest and R is the corresponding ratio (^{13}C:^{12}C or ^{15}N:^{14}N). Samples were repeatable within ±0.2‰ based on repeated measurements of standards.

2.3. Salmonids

To measure MDN in Elwha salmonids we sampled muscle tissue from 10 adults each of Chinook, coho, and pink (*O. gorbuscha*) salmon in 2013. The Lower Elwha Klallam Tribal hatchery provided coho and pink salmon carcasses immediately following spawning. Tissues from post-spawned Chinook salmon were collected in the Elwha River during 2013 late-summer spawning surveys. From each individual, we dissected a dorsal muscle tissue plug (excluding skin and bone) from the area posterior to the dorsal fin, and freeze dried and homogenized tissue prior to stable isotope analysis.

2.4. American dipper

American dippers are aquatic songbirds and top-level consumers of freshwater aquatic prey (Willson and Kingery, 2011). Dippers primarily eat macroinvertebrates, but when available, will consume fish eggs and small fish (the former almost exclusively during the non-breeding season; Willson and Kingery, 2011). Dippers in this region utilize MDN, and salmon obstructions negatively impact life history parameters, such as the number of breeding attempts (Tonra et al. *in review*). We analyzed dipper $\delta^{13}C$ and $\delta^{15}N$ from feathers and blood. To correct for differences in diet-tissue discrimination between tissues, we used linear corrections ($R^2 = 0.84$ and 0.77 for $\delta^{13}C$ and $\delta^{15}N$, respectively). Corrections were developed using blood and feathers grown by 67 dependent young dippers captured within 5 days of fledging between 2011 and 2013, both from the Elwha and neighboring rivers. Given the age of these individuals, both tissue types were grown over the same time frame. We corrected all feather values to blood values using the formulas:

$$\delta^{13}C_{blood} = 0.888 * \delta^{13}C_{feather} - 3.825 \tag{1}$$

$$\delta^{15}N_{blood} = 0.789 * \delta^{15}N_{feather} + 0.276 \tag{2}$$

Based on timing of feather molt, we generated a time series of stable isotope values over 7 sampling periods: 2010 combined, and 2011–2013 breeding and nonbreeding periods. Outside of adventitious regrowth due to loss, feathers in dippers could have been grown during two different time periods: the breeding season (young of the year and yearling breeders who have retained natal feathers from the previous year), or the early part of the non-breeding season (annual molt in older birds). We did not have specific age data for adults sampled in the 2011 breeding season. Thus, since we could not distinguish between feather growth periods (i.e. breeding for yearling birds, or non-breeding for older), we considered feather stable isotope values to represent values for both breeding and nonbreeding periods combined in 2010. For other years, we only included feathers from older birds (aged based on capture in previous years, or plumage characters) collected in the breeding season to represent stable isotope values from the previous nonbreeding period. Blood stable isotope values were considered to represent the season in which they were collected. To verify that values from feathers grown during annual molt could be combined with values of blood sampled in late September–October of the same non-breeding period, we compared paired feather and blood values within eight adult birds of known previous season origin, sampled in 2012 and 2013 and did not find significant differences ($\delta^{13}C$: $F_{1,14} = 1.86$, $P = 0.19$; $\delta^{15}N$: $F_{1,14} = 2.68$, $P = 0.12$). Values from 2010–2011 represent pre-removal conditions and 2012–13 post-removal values. Sample sizes can be found in Fig. 2.

2.5. Macroinvertebrates

To examine an indirect route of MDN uptake we analyzed pre- and post-removal stable isotopes in a macroinvertebrate prey of dippers, *Rhyacophila* spp. (a predatory caddisfly), upstream of the Elwha Dam. This family was selected because based on previous Elwha research, *Rhyacophila* $\delta^{15}N$ varies based on access to MDN (Duda et al., 2011) and we had sufficient sample sizes for both time periods. Pre-dam removal samples were taken in Summer 2004–2006, and post-removal samples in Summer 2012–2013. All *Rhyacophila* spp. samples were collected from riffle habitats following protocols of Morley et al. (2008), preserved in ethanol, freeze dried, and homogenized. Detail on sampling locations can be found in Duda et al. (2011).

2.6. Stable isotope changes

We tested the prediction that stable isotopes would be enriched following dam removal with linear mixed models using the “lmer” package in R (R Core Development Team, 2014). In dippers, we examined changes in $\delta^{13}C$ and $\delta^{15}N$ between the upper (i.e. upstream of Glines Canyon Dam) and middle Elwha (between dams). Our models included river section (upper vs. middle) as a fixed factor and individual as a random factor, to account for repeatedly sampled individuals. We included two temporal variables (time period (1–7), pre- vs. post-removal) as fixed factors and tested for interaction between these variables and river section. For *Rhyacophila*, we examined models with pre- vs. post-dam removal as a fixed factor, and sampling site as a random factor. To assess variable significance we used likelihood ratios between full and reduced models. We collected tissue samples from dippers utilizing the lower Elwha, in which salmon were never obstructed, to acquire “undammed” reference values.

We used an isotope mixing model to estimate contribution of MDN to nitrogen isotopic content of dipper tissues (Koshino et al., 2013):

$$\%\,\text{enrichment} = 100 * (\delta X_{se} - \delta X_c)/((\delta X_s + (TL \times \delta X_e)) - \delta X_c \tag{3}$$

where, δX_{se} is the value of dippers in areas with salmon (i.e. post recolonization), δX_c is the mean isotopic value for dippers in areas without salmon ($\delta^{15}N = 4.58$), δX_s is the mean isotopic value of salmon (mean for all Elwha species sampled: $\delta^{15}N = 13.89$), δX_e is the isotope enrichment factor for nitrogen (3.4‰; Minagawa and Wada, 1984), and TL is the trophic level correction factor (2 for carnivore). As we were interested in measuring marine enrichment, and negative enrichment is not logical, negative values were treated as zeros (i.e. lack of enrichment).

3. Results

Marine derived nutrients have already made their return to the Elwha River as demonstrated by spawning salmon stable isotope ratios (Table 1), which were greater than in other consumers measured. For $\delta^{13}C$ in dippers, no temporal trend was evident in the relationship between the upper and middle Elwha (time period: $\chi^2_1 = 0.03$, $P = 0.87$; time period * section: $\chi^2_1 = 0.15$, $P = 0.70$, Fig. 2A; coefficients

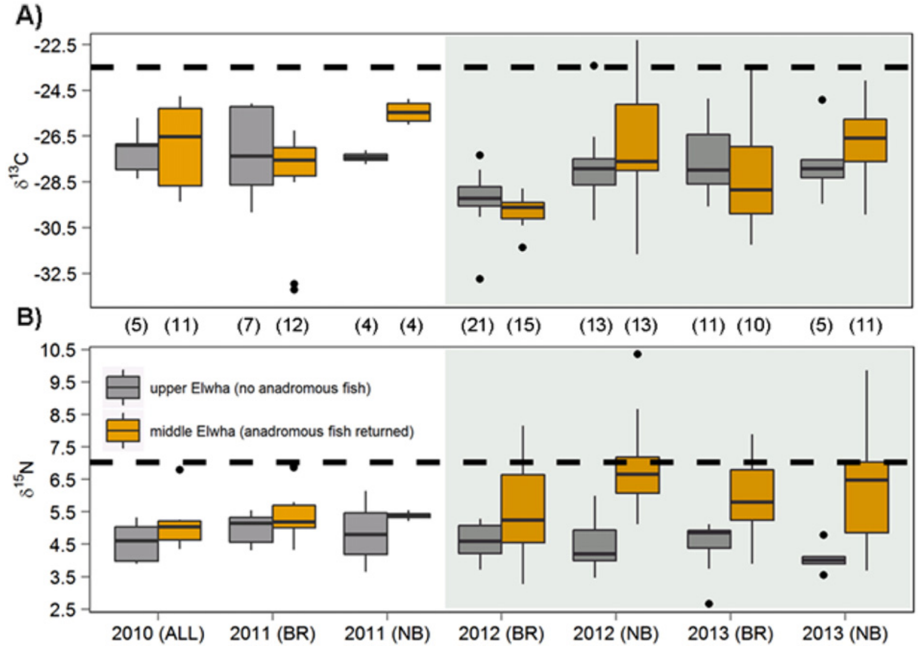

Fig. 2. Box plots of values for A) stable-carbon and B) stable-nitrogen isotopes from the upper and middle Elwha River, WA, USA across 7 sampling periods (BR = breeding, NB = non-breeding; 76 and 66 isotope samples from tissues grown in 2010–2013 by 45 individual dippers per section in the middle and upper Elwha, respectively). Dashed line indicates the mean value (based on 13 samples from 10 dippers between 2010 and 2013) for each stable isotope ratio from dippers in the lower Elwha (mean ± SE; δ^{13}C: −24.23 ± 0.50; δ^{15}N: 7.03 ± 0.46), which has remained open to anadromous fish. Shaded area depicts time periods following removal of the Elwha Dam. Numbers in parentheses are sample sizes.

for all fixed effects in dipper models can be found in Appendix A). δ^{13}C increased post-dam removal, but the removal itself could not explain variation in δ^{13}C between sections (pre/post removal: $\chi^2_1 = 5.77$, $P = 0.02$; pre/post removal ∗ section: $\chi^2_1 = 0.33$, $P = 0.57$). However, limiting the dataset to the dipper non-breeding season revealed δ^{13}C was elevated in the middle Elwha in 2011 (when some spawning coho were translocated above the Elwha Dam; McMillan and Moses, 2011), and both post-dam removal years ($\chi^2_1 = 14.38$, $P < 0.001$). We compared 31 *Rhyacophila* samples from 18 middle Elwha sites pre-removal to 23 samples from 15 sites post-removal. *Rhyacophila* δ^{13}C did not increase following dam removal ($\chi^2_1 = 1.11$, $P = 0.29$; pre-removal mean ± SE: −27.19 ± 0.33; post-removal: −28.36 ± 0.65).

δ^{15}N became more enriched over time in the middle, compared to the upper, Elwha (time period ∗ section: $\chi^2_1 = 10.33$, $P = 0.001$; Fig. 2B). This relationship corresponds to the dam removal and subsequent re-colonization by salmon (pre/post-dam removal ∗ section: $\chi^2_1 = 8.06$, $P = 0.005$). In fact, over the course of the study, δ^{15}N in the middle Elwha dippers became more similar to those in the lower Elwha ($adjR^2 = 0.49$, n = 7, $P = 0.05$) while diverging from the upper Elwha ($adjR^2 = 0.63$, n = 7, $P = 0.02$). In contrast to δ^{13}C, these effects remain even when controlling for season (2010 excluded; time period ∗ river section: $\chi^2_1 = 8.60$, $P = 0.003$; pre/post-dam removal ∗ river section: $\chi^2_1 = 6.19$, $P = 0.01$). Based on our mixing model, since removal of the Elwha Dam, dippers are acquiring 10.40 ± 1.23%, and as much as 36%, of their nitrogen from MDN (n = 49). *Rhyacophila* δ^{15}N did not change following dam removal ($\chi^2_1 = 0.74$, $P = 0.39$). Although there was a marked increase in the mean δ^{15}N (pre-removal mean ± SE: 2.42 ± 0.26; post-removal: 3.30 ± 0.27), our analysis showed that this effect was strongly site-dependent (ΔAIC with and without random site effect = 15.98).

Table 1
Means and standard errors (SE) for stable-carbon and -nitrogen ratios in muscle tissue of three species of salmon spawning in the Elwha River, Washington, USA.

Species	n	δ^{13}C Mean	δ^{13}C SE	δ^{15}N Mean	δ^{15}N SE
Chinook	10	−16.90	0.50	15.85	0.23
Coho	10	−18.20	0.38	14.16	0.27
Pink	10	−20.88	0.28	11.69	0.37

4. Discussion

Our results reveal that components of aquatic–terrestrial food webs have the capacity to be restored quite rapidly despite being dammed for over 100 years. Immediately following removal of the Elwha Dam salmon returned to the middle Elwha, bringing tissues enriched in ^{13}C and ^{15}N. MDN, as measured through enriched stable isotopes, were transferred to a higher-order terrestrial consumer, the American dipper. Human assisted migration of several hundred coho and steelhead salmon may have made small contributions to this transfer. However, this effect is in all likelihood dwarfed by the effects of naturally colonizing salmon of multiple species (e.g. Denton et al., 2014) that naturally migrated past the former dam, especially when considering the relatively high 'fallback' rates of salmon transported upstream of Elwha dam site to their capture locations below the dam (McMillan and Moses, 2011) and the order of magnitude larger abundance estimates of natural colonizers (Denton et al., 2014). We found support for both direct and indirect transfer of MDN to dippers, through consuming salmon tissues and through bottom-up enrichment, respectively. During non-breeding, it appears that there was a direct pathway of MDN to dippers, as both ^{13}C and ^{15}N were enriched. This is likely from consumption of salmon eggs, which is not observed during the dipper breeding season (Tonra et al. *in review*). High δ^{15}N in dipper tissues during breeding, in the absence of high δ^{13}C, suggests the indirect pathway. However, we did not find corresponding increases in a single prey species of dippers, *Rhyacophila* spp. One reason for this is that dippers are receiving enriched ^{15}N from consuming salmon fry, which can incorporate large amounts of ^{15}N from feeding directly on carcasses (Bilby et al., 1996). Dippers in this region have been found to consume more fish in areas open to salmon spawning (Tonra et al. *in review*). In addition, it is possible that enrichment came through other macroinvertebrates besides *Rhyacophila*.

As the number of dams removed in the U.S. has grown, research has shown that rivers and their migratory fish populations can respond quickly (O'Connor et al., 2015). Our research highlights how restoration of highly interactive species like salmon (Helfield and Naiman, 2001), provide nutrient subsidies, and these can have positive impacts on terrestrial plant (e.g. Helfield and Naiman, 2001) and animal (e.g. Sabo and Power, 2002) populations. What remains to be seen is the time frame over which species and ecosystem respond to returning subsidies. For instance, dippers adopt life history strategies with greater lifetime reproductive success in areas with intact salmon migrations or greater abundance of salmon (Gillis et al., 2008; Green et al., 2015; Tonra et al. *in review*). Continued monitoring will reveal the rate at which these strategies are adopted by individuals in areas with returning MDN.

Dam removals have the capacity for expansive benefits to terrestrial and aquatic organisms, highlighting the importance of interdisciplinary baseline studies across taxonomic groups prior to future removal projects (Service, 2011). Studies like ours demonstrate that these systems have enormous resiliency to recover many aspects of their ecological function. The return of nutrient subsidies on their own does not signify recovery however, as effects on the structure and function of the biotic community must follow. Future studies, in addition to monitoring returns of migratory fish, should quantify both aquatic and terrestrial cascading effects, as full recovery of river ecosystems will not be realized until interactions among fish and other parts of the food web are reestablished.

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Appendix A

Coefficients and 95% confidence intervals (C.I.) for linear mixed models describing variation in stable isotopes above and below the Glines Canyon Dam both during 7 sampling periods, and before and after removal of the Elwha Dam, Elwha River, Washington, U.S.A.

	$\delta^{13}C$		$\delta^{15}N$	
Fixed effect	Estimate	95% C.I.	Estimate	95% C.I.
Sample period	−0.03	−0.33–0.26	−0.91	−0.24–0.06
Above/below dam	−0.002	−1.70–1.70	−0.09	−1.01–0.83
Sample period × above/below dam	0.07	−0.30–0.44	0.32	0.13–0.52
Before/after removal	1.10	−0.02–2.19	0.24	−0.34–0.81
Above/below dam	0.31	−0.46–1.10	1.61	1.18–2.04
Before/after removal × above/below dam	−0.41	−1.84–1.01	−1.11	−1.87–−0.34

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