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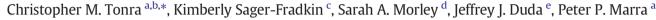
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Short communication

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

ABSTRACT



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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 km² 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

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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.

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

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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 (¹³C) and nitrogen (¹⁵N; 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

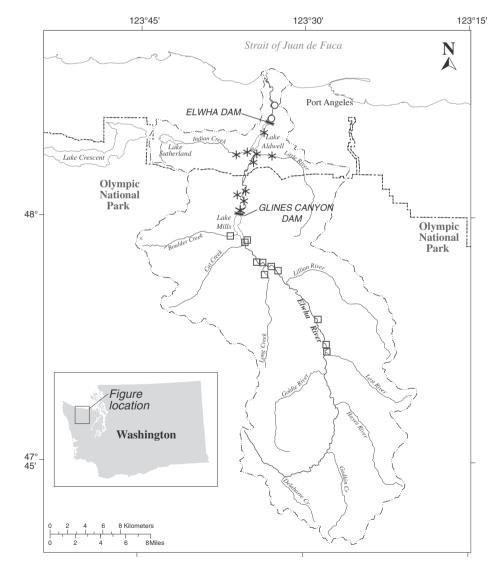


Fig. 1. Map of study area along the Elwha River, WA, USA. Circles indicate American dipper territories in areas never obstructed to salmon, stars denote territories in the middle Elwha which was opened to salmon following removal of the Elwha Dam, and squares denote territories in the upper Elwha, which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

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