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Article in *Environmental Biology of Fishes* · September 2017

DOI: 10.1007/s10641-017-0676-0

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Re-awakening dormant life history variation: stable isotopes indicate anadromy in bull trout following dam removal on the Elwha River, Washington

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Received: 10 March 2017 / Accepted: 18 September 2017 / Published online: 22 September 2017
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Abstract Migratory species take advantage of multiple habitats during their life cycle to optimize growth, survival, and reproduction. However, migration also makes them vulnerable to habitat degradation and exploitation in each habitat, and loss of connection between habitats. Partially migratory species (i.e., migration is facultative rather than obligate) can persist after loss of connectivity and may then resume migration after the habitats are reconnected. We analyzed stable isotopes of carbon and nitrogen to investigate the possible use of marine habitats for foraging by bull trout, *Salvelinus confluentus*, in years immediately after removal of impassable hydroelectric dams on the Elwha River, Washington State,

USA. Juveniles in the Elwha River estuary were similar in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to those in the estuary of the free-flowing Dungeness River nearby, and the values of fish from the estuaries were higher than those of juveniles collected in the river, consistent with use of marine food sources. Adult bull trout collected in each of the rivers had values indicating extensive reliance on marine prey - similar to those of adult Pacific salmon that had spent several years at sea. Taken together, these data demonstrate that the Elwha River bull trout, almost entirely landlocked for a century, are rapidly resuming anadromy and that the marine prey contribute substantially to their trophic ecology and likely their growth. More broadly, the results reveal the importance of connectivity for migratory fishes, their ability to resume anadromy once the connection between habitats is restored, and the population resilience that partial migration provides for them.

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Keywords Anadromy · Char, dam removal, partial migration · Salmonid · Stable isotopes

Introduction

Migratory animals take advantage of temporally predictable opportunities for feeding and reproduction in discrete habitats (Baker 1978; Dingle and Drake 2007), with important consequences for growth, life history, and reproductive success of individuals (Roff 1988), the dynamics of the population (Morales et al. 2010), and the associated components of the ecosystem (Bauer

and Hoyer 2014). Migration involves the integration of many aspects of the organism including morphology, physiology, and energetics, and so is central to the basic biology of the species that undertake these journeys (Bowlin et al. 2010). However, the benefits of migration can be compromised by habitat degradation, loss of connectivity, or exploitation in any of the critical habitats or corridors between them (Bairlein 2016). These problems are particularly acute for fishes constrained by rivers.

Many fishes migrate between habitats within fresh water (Lucas and Baras 2001; Brönmark et al. 2014; Avigliano and Volpedo 2016), and others are diadromous, migrating regularly between freshwater and marine environments, including alosids (e.g., Wynne et al. 2015), salmonids (Quinn 2005; Jonsson and Jonsson 2011), and many other families (McDowall 1988). Dams that sever the connection between habitats needed to complete the life cycle can have serious consequences for riverine migrants and diadromous fishes, including extirpation (Nehlsen et al. 1991), or isolation of populations below and above dams. However, the early part of the twenty-first century has seen the removal or modification of dams, including many in the United States (O'Connor et al. 2015) and Europe (e.g., Sweden: Lejon et al. 2009; France: Lasne et al. 2015; Norway: Fjeldstad et al. 2012). Environmental improvement including restoring migratory fish populations is often an explicit goal of these efforts (Bednarek 2001; Hart et al. 2002; Pohl 2002).

Removal or modification of dams has benefitted a number of migratory fishes (Pess et al. 2014), including sea lamprey, *Petromyzon marinus* (Hogg et al. 2013), shortnose sturgeon, *Acipenser brevirostrum* (Wippelhauser et al. 2015), American eel, *Anguilla rostrata* (Hitt et al. 2012), and multiple species in some cases (Lake et al. 2012; Raabe and Hightower 2014). Recently, several dams have been removed or modified in the Pacific Northwest region of the United States, motivated in large part by the need to restore salmonid populations. Condit Dam on the White Salmon River, Washington was removed (Hatten et al. 2016), and Landsburg Dam on the Cedar River, Washington was modified to allow upstream colonization by Pacific salmon (Anderson et al. 2015). However, the largest dam removal project in the United States was the removal of two dams on the Elwha River in Washington to restore ecosystem processes and recover migratory

salmonids (Pess et al. 2008; Winter and Crain 2008). These dam removal projects provide opportunities to examine the resumption of anadromy by species that had been landlocked for decades. This capacity is important because it will likely affect the density and size distribution of the partially migratory species.

The Elwha River drains 833 km² and flows 72 km from glaciers and snow fields 1372 m above sea level into the Strait of Juan de Fuca. Elwha Dam, built in 1912 at river km 7.9 blocked fish passage and created Lake Aldwell reservoir (Fig. 1). Construction of Glines Canyon Dam in 1925 at river km 21.6 created another reservoir, Lake Mills (Pess et al. 2008). The dams converted a free-flowing river (mean annual discharge 42 m³/s) that supported all species of salmonids native to the region into a short lower river, accessible to the ocean but lacking tributaries, and two reservoirs with rivers and tributaries above them, isolated from each other and from the lower river. Elwha Dam was fully removed by the spring of 2012 and Glines Canyon Dam was removed by fall of 2014 and the river is now undergoing rapid changes in geomorphology as the stored sediment is transported and redistributed (East et al. 2015; Warrick et al. 2015). In addition to these changes in the river itself, the sediment-starved estuary is now growing rapidly (Foley et al. 2015; Gelfenbaum et al. 2015). Restoration of salmonid abundance will depend, most obviously, on spatial expansion to upriver habitats by species with obligate anadromous life histories that had been confined to the section of river downstream of the Elwha dam: Chinook, *Oncorhynchus tshawytscha*; chum, *O. keta*; pink, *O. gorbuscha*; and coho salmon, *O. kisutch*. However, equally important is the resumption of anadromy by species that had been entirely or largely land-locked upstream of each dam, including sockeye salmon, *O. nerka*; rainbow trout, *O. mykiss*; cutthroat trout, *O. clarkii*; and bull trout, *Salvelinus confluentus* (Brenkman et al. 2008).

Bull trout are listed as Threatened under the U.S. Endangered Species Act but are less extensively studied than are Pacific salmon and trout. Bull trout display fluvial, adfluvial, and anadromous migration patterns (Brenkman et al. 2007; Dunham et al. 2008; Paragamian and Walters 2011). Anadromous and nonanadromous bull trout can co-occur and both forms can produce anadromous progeny (Brenkman et al. 2007). In the Elwha River, all evidence indicates that they were very scarce below Elwha Dam, likely because this area lacks tributaries suitable for spawning, but they

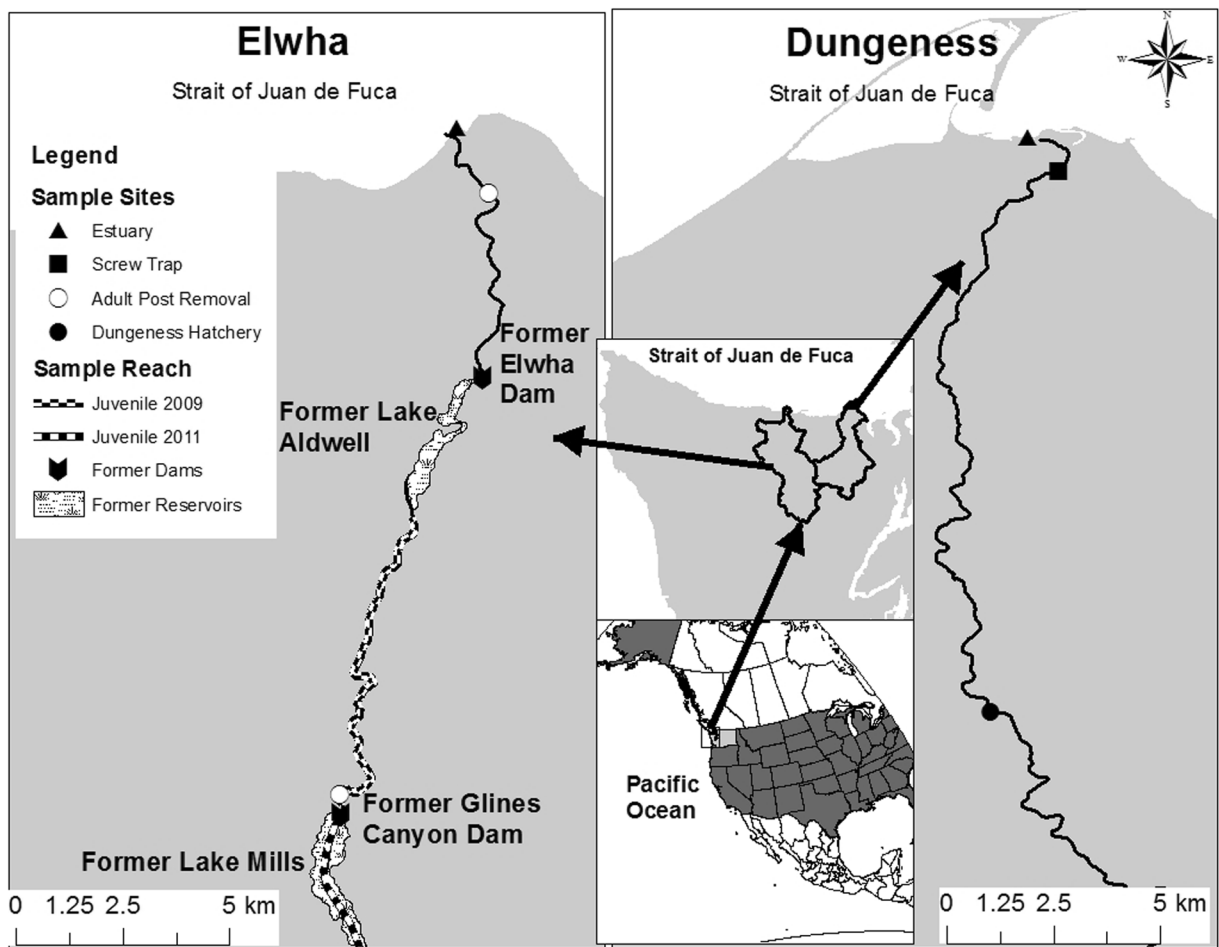


Fig. 1 Map of the Elwha and Dungeness rivers, in northwestern Washington (black lines), showing the locations where bull trout were collected, and the sites where the dams and associated reservoirs were located in the Elwha River

persisted upstream of the dams prior to their removal (Brenkman et al. 2008, 2012; Pess et al. 2008). Specifically, six snorkel surveys in the 7.9 km reach below Elwha Dam between 1995 and 2004 observed, on average, only nine adult bull trout, and in five of the six years fewer than ten were seen (Brenkman et al. 2008). Additional surveys in 2007 and 2008 again revealed very low densities below the dam (Brenkman et al. 2012), and some of these might have passed over the dam during high water. In the years during and following dam removal, beach seining in the Elwha River estuary to assess the fish community yielded juvenile bull trout (R. Paradis, Lower Elwha Klallam Tribe, unpublished data) but it was uncertain whether these were fluvial fish briefly entering the small and evolving estuary or fish taking advantage of marine foraging opportunities. Sampling in the lower river to determine the species composition of adult salmonids also yielded adult bull

trout but it was not known whether they had been feeding in marine waters or were resident in the river.

The overall goal of this study was to determine whether the Elwha River bull trout population, almost entirely restricted to habitat upstream of the Elwha Dam for a century, has resumed anadromy as a common life history pattern, including reaches of the river that were previously inaccessible. Such confirmation would indicate that the marine resources may contribute to growth rates of individuals and, indirectly, increase the population’s viability through numerical and spatial expansion and increased life history diversity (McElhany et al. 2000). The approach was to compare the stable isotope values of fin tissue samples taken prior to and after dam removal from juvenile and adult Elwha River bull trout to determine whether they were making use of marine resources, as would be indicated by enrichment of ^{15}N and ^{13}C . We also compared the samples from the Elwha

River with ones from bull trout in the Dungeness River as a reference because it is proximate to the Elwha River (approximately 30 km east), free-flowing, and has a self-sustaining bull trout population. We did not attempt to estimate the diets of bull trout in marine and freshwater environments from the data but, rather, sought the kind of abrupt shift in isotope values detected by comparing smolts to adults in Atlantic salmon, *Salmo salar* (Dixon et al. 2012) and sockeye salmon (Kline et al. 1993). Specifically, $\delta^{13}\text{C}$ tends to be enriched in marine compared to freshwater systems (Doucett et al. 1999), as does $\delta^{15}\text{N}$, though the latter is strongly affected by trophic position as well (Vander Zanden and Rasmussen 1999; Post 2002). Consequently, the combination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been used to distinguish between resident and anadromous salmonids (Doucett et al. 1999; Ciancio et al. 2008). In addition, we used length frequency distributions of juvenile bull trout in the Elwha River and in the estuary to estimate the age at which they first entered marine waters. Such information is an important aspect of anadromy and will allow comparison to other anadromous bull trout populations (e.g., the Skagit River, Washington: Zimmerman and Kinsel 2010).

Given the complex, flexible, and poorly understood ecology of bull trout in coastal rivers, our analyses were designed to test multiple hypothesized sources of variation in isotope values. In addition to possible variation between the Elwha and Dungeness rivers, and before and after dam removal, we needed to consider the effects of fish size because larger fish can feed at higher trophic levels, strongly affecting $\delta^{15}\text{N}$. There might also be seasonal variation in isotope values (Morley et al. 2016). In rivers of Puget Sound, Washington juvenile and adult bull trout generally move downstream to estuarine and nearshore habitats in spring and a return in early-mid summer, though some fish occupy the estuary in fall as well (Beamer et al. 2004; Hayes et al. 2011) and not all are anadromous. Consequently, if all juveniles spent equal amounts of time in the Elwha River estuary then there would be no seasonal difference in isotope values but if they spent the summer there, then a seasonal increase in marine values might be detected, and we tested these alternative hypotheses. In addition, adult bull trout spawn in fall and then prey heavily on salmon eggs and juveniles in rivers where they are available (Lowery and Beauchamp 2015). Therefore, samples taken in late fall might differ from those in the summer because salmon eggs and tissue are

enriched (Scheuerell et al. 2007; Jaecks and Quinn 2014), and this hypothesis was also tested. Finally, we obtained stable isotope values for other anadromous and non-anadromous salmonids in the Elwha River.

Materials and methods

Field sampling

Bull trout sampling was opportunistic with respect to the present study and constrained to non-invasive, non-lethal methods by their federally threatened status and limited distribution. Nevertheless, a total of 223 fish were sampled including a wide range in sizes and months of the year from the Elwha River below, between, and above the dam sites, in the Elwha River estuary before and after dam removal, and at multiple locations in the nearby Dungeness River (Fig. 1). Sampling of bull trout fin tissues prior to dam removal was conducted for a population genetics study (DeHaan et al. 2011), which demonstrated that the Elwha and Dungeness river populations were distinct. Most were measured for fork length, some for fork and total length, and some for only total length, which were converted to fork length using a relationship derived from the fish for which both measurements were taken ($\text{fork length} = (\text{total length} * 0.955) - 3.095$, $r^2 = 0.998$). In the Elwha River, 28 non-anadromous bull trout (i.e., above dams) were sampled prior to dam removal, 14 of which were collected in September 2009 from the Elwha River between Elwha and Glines Canyon dams. The two distinct size modes (fork length = 78–95 mm and 150–163 mm) suggested that they were at the end of their first and second summers in the river but this was not validated, and there was also a single larger fish 257 mm long. Another 14 fish were sampled in June 2011 from the river upstream of Glines Canyon Dam, ranging from 164 to 225 mm in length.

Sixty-one bull trout were sampled in the estuary on the east side of the Elwha River in 2014 and 2015 combined: one each in January and February, four in March, 21 in April, 15 in May, three each in June and July, and 13 in November. These fish ranged from 132 to 450 mm in length but most overlapped in size with those sampled in the river prior to dam removal (41 were < 250 mm; Fig. 2). In addition, 102 fish from 290 to 640 mm long (Fig. 2) were sampled from the middle and lower Elwha River after dam removal in 2014 and 2015:

one in February, four in April, 11 in May, 60 in June, 13 in July, seven in August, and six in October. The three main collections from the Elwha River will be referred to as juveniles prior to dam removal, juveniles in the estuary (after dam removal), and adults in the river (after dam removal) based on the size distributions. No information on sexual maturity or spawning history was obtained or inferred, and in only some cases was sex noted so there were no analyses of life history other than size, location, and date of capture. These collections were complemented by three collections from the Dungeness River, whose mouth enters the Strait of Juan de Fuca about 30 km east of the Elwha River (Fig. 1), each roughly comparable to one of the Elwha River collections. First, five fish were sampled in a screw trap deployed in the lower Dungeness River just above tidal influence to catch seaward migrants in late June and early July 2007. These fish had presumably been feeding in the river, and their sizes (125–216 mm) overlapped broadly with those of the juveniles sampled in the Elwha River prior to dam removal. Second, nine fish (one in May, six in June, and two in July) were sampled in the Dungeness River estuary in 2006 and 2007 to assess salmonid early life history in the estuary (Sather 2008). These fish were similar in size (141–215 mm) to those sampled in the screw trap, and in the Elwha River estuary. Third, 18 fish were caught in the Dungeness River in 2002, 2005 and 2006, most near the salmon hatchery at river km 17 but some farther downriver (one each in April, May, and August, six in November and nine in December). These fish ranged widely in length, from 198 to 581 mm.

Tissue processing and data analysis

Samples of fin tissue were removed and preserved in ethanol, both because lethal samples of muscle were not an option and because the primary purpose was DNA analysis for population structure. Isotopic signatures of fin and muscle samples are strongly correlated in salmonids (Hanisch et al. 2010; Curry et al. 2014), though Sanderson et al. (2009) reported that $\delta^{15}\text{N}$ tended to be lower in fin than muscle tissue, and $\delta^{13}\text{C}$ tended to be higher in fin than muscle. Storage in ethanol can also affect isotope values (Vizza et al. 2013) but all samples were stored for at least two months, after which time changes seem to be minimal so the samples were comparable to each other. The values reported here should be taken in the context of these methodological issues

but the goal of the study was to detect the large-scale shifts in isotopic signature typically associated with freshwater vs. marine systems (Kline et al. 1993; Dixon et al. 2012).

To perform stable isotope analyses, fin tissue samples were freeze-dried in a lyophilizer for 24 h, then ground to a fine homogeneous powder and loaded (60 μg) into tin capsules. Stable isotope analyses were conducted at the University of Washington Isolab with a Costech elemental analyzer (Analytical Technologies Inc., Valencia, CA) coupled to a Finnigan MAT-253 stable isotope-ratio mass spectrometer (Thermal Electron Corporation, Bremen, Germany). The isotopic ratios of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) were expressed in standard notation of per mil differences from the standard atmospheric nitrogen gas and Vienna Pee Dee Belemnite, respectively (Fry 2006). In-house calibrated standards were included in each run to insure a precision of $\pm 0.3\%$. In some instances, high lipid concentrations can create an unexpectedly depleted $\delta^{13}\text{C}$ value relative to sources, and $\delta^{13}\text{C}$ is routinely corrected for C:N ratio values in excess of 3.5, a proxy for lipid concentration (Post et al. 2007). The average C:N ratio of fin clips was 3.44 so $\delta^{13}\text{C}$ was not adjusted for lipid concentration.

Data analysis was designed to determine whether the Elwha River juveniles collected in the estuary and adults in the river had made substantial use of marine food resources. To do so, we compared them to bull trout sampled prior to dam removal, and to the samples from the Dungeness River. We therefore first tested to see whether the data differed between the Elwha and Dungeness rivers for any of three collections (juveniles in the river, juveniles in the estuary, and adults in the river). They did not (details below) so the data from the two rivers were pooled for subsequent analyses but the three types of collections were kept separate. We needed to account for two other potential sources of variation: fish size and sampling date. The $\delta^{15}\text{N}$ is strongly related to trophic position and so was expected to increase with body size. $\delta^{13}\text{C}$ tends to be less affected by trophic position but if fish of different sizes fed in different places or on different prey there might be a relationship between size and $\delta^{13}\text{C}$ as well as $\delta^{15}\text{N}$. Therefore, rather than evaluate differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ simultaneously, we tested each isotope separately. Specifically, we performed two ANCOVAs to evaluate the effects of collection site (upstream juvenile, estuary, upstream adult) and fish length, and the interaction between length and collection site. To account for possible

seasonal variation for estuary fish we regressed $\delta^{13}\text{C}$ on the day of year of capture to determine if fish collected in the estuary became more enriched with seasonal progression. To account for possible consumption of salmon eggs by adults, we performed an ANOVA on $\delta^{13}\text{C}$ and collection season (spring: April – May, summer: June – August, autumn: October – December) for adult fish collected in-river.

Results

Isotope samples were obtained from a total of 223 bull trout, including 32 from the Dungeness River and 191 from the Elwha River over a wide range of body lengths (Table 1) that overlapped broadly between the two rivers (Fig. 2). To meet assumptions of the ANOVA test for differences in length between rivers and sites, we power transformed length ($x^{0.6}$) to ensure normality (Shapiro-Wilk, $w = 0.99$, $p = 0.18$) and homogeneity of variances (Levene's test, $F(5215) = 1.45$, $p = 0.21$) among groups. The resulting ANOVA indicated that there was no significant effect of river ($F(1215) = 2.27$, $p = 0.13$), or a river \times site interaction ($F(2215) = 2.60$, $p = 0.07$). Thus values for fish did not differ between the Elwha and Dungeness rivers, for a given collection site. For example, the adult Dungeness River bull trout $\delta^{15}\text{N}$ averaged 14.9 (range: 9.6 to 17.1, $SD = 2.1$) compared to 15.3 (range: 12.8 to 18.3, $SD = 1.2$) for the Elwha River adults, and $\delta^{13}\text{C}$ values averaged -18.8 (range: -16.5 to -22.3 , $SD = 1.6$) in Dungeness River adults compared to an average of -18.0 (range: -15.3 to -22.6 , $SD = 1.4$) in the Elwha River adults. However, there was significant variation among sites ($F(2215) = 433.40$, $p < 0.001$). A Tukey post-hoc test indicated that the

length of fish collected at each site differed significantly ($p < 0.001$), confirming our expectation that length and site were confounded. Because trophic level strongly affects $\delta^{15}\text{N}$ (fractionation of 3.4 per mil per trophic level), we tested for the effects of river, site, and length on each isotope separately. The ANCOVA for $\delta^{15}\text{N}$ on site and length showed a significant length by site interaction ($F(2215) = 7.25$, $p < 0.001$), indicating that $\delta^{15}\text{N}$ varied by fish length within each site (Fig. 3, upper panel). In contrast, the ANCOVA for $\delta^{13}\text{C}$ on site and length showed no significant interaction ($F(2215) = 0.044$, $p = 0.96$), and an intercept only model was the best fit for $\delta^{13}\text{C}$ on length regressions for each collection location (Fig. 3, lower panel). Specifically, $\delta^{13}\text{C}$ values of juveniles in the Elwha River estuary differed significantly from those of juveniles above the dam (-23.8 vs. -26.5 , $t = 7.63$, $df = 87$, $p < 0.001$). However, we detected no effect of collection date on $\delta^{13}\text{C}$ for juveniles in the estuary (adj. $r^2 = -0.015$, $F(1,66) < 0.001$, $p = 0.99$) or for adults collected in-river ($F(2117) = 1.49$, $p = 0.23$).

The isotope values for the adult bull trout in the Elwha River differed markedly from those of the juveniles in the river and the estuary (Table 1) but the adults were not all captured in the same location. Records were sufficiently detailed for us to divide 38 of them into two groups: 20 were caught near marine waters (river km 1.3 to 2.6) and 18 were caught in the upper river, where Glines Canyon Dam had been located (rkm 21.2 to 21.4). The $\delta^{15}\text{N}$ values were higher in the fish caught in the upper part of the river (15.7 vs. 14.4, $t = 4.75$, $df = 36$, two-tailed $p < 0.001$) but both groups differed from the juveniles (mean = 6.2, Table 1). The $\delta^{13}\text{C}$ values did not differ significantly between adults in the upper and

Fig. 2 Length frequency histogram of bull trout sampled from the Elwha River system in white bars above the line ($n = 189$) and the Dungeness River ($n = 32$) in dark bars below, expressed as a percent of the sample at each site

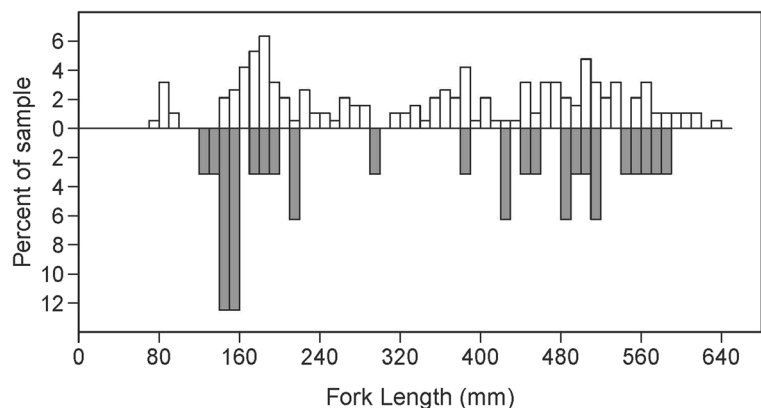


Table 1 Mean values for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, fork length (mm), and sample size (N) of fishes from the Elwha River and nearby Dungeness River

River, species, stage, and habitat	Isotopic exposure	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Length	N
Elwha River brook trout	fresh water	-28.7	7.6	114.7	9
Elwha River (upper) rainbow trout	fresh water	-27.5	5.6	Ca. 200	
Elwha River juvenile bull trout*	fresh water	-26.5	6.2	154.4	28
Dungeness River juvenile bull trout*	fresh water	-25.8	7.9	156.2	5
Elwha River (middle) rainbow trout	fresh water	-25.4	5.4	Ca. 200	
Elwha estuary juvenile bull trout*	intermediate	-23.8	11.5	227.3	61
Dungeness estuary juvenile bull trout*	intermediate	-23.0	9.7	163.2	9
Elwha River (lower) rainbow trout	intermediate	-22.5	7.6	Ca. 200	12
Elwha River adult pink salmon	marine	-20.9	11.7	No data	10
Dungeness River adult bull trout*	marine	-18.8	14.9	469	18
Elwha River adult coho salmon	marine	-18.2	14.2	No data	10
Elwha River adult bull trout*	marine	-18.0	15.3	478.2	102
Elwha River adult Chinook salmon	marine	-16.9	15.9	No data	10

Data are sorted by increasing $\delta^{13}\text{C}$ enrichment and the column isotopic exposure refers to the observed or likely environment. Samples categorized as “fresh water” were either collected above dams, during seaward migration, or non-anadromous fish (brook trout). Fish with “intermediate” exposure were sampled in the estuaries or the lower river where they could have accessed the estuary, and fish categorized as “marine” were anadromous Pacific salmon, or adult bull trout whose $\delta^{13}\text{C}$ signatures strongly indicated marine feeding. Data sources are as follows: bull trout from this study marked with asterisks, brook trout from Thornton (2015), adult Chinook, coho and pink salmon from Tonra et al. (2015), rainbow trout from Duda et al. (2011), collected prior to dam removal from the lower river (below Elwha Dam), middle river (between Elwha and Glines Canyon dams) and upper river (above Glines Canyon Dam). The rainbow trout length estimate was provided by Jeffrey Duda (USGS), with a range of about 150–300 mm

lower sections (-18.3 vs. -17.7, $t = 1.84$, $df = 36$, two-tailed $p = 0.07$), but both differed from the value for juveniles in the river prior to dam removal (-26.5; Table 1).

The length frequency distributions of juvenile bull trout in the Elwha River prior to dam removal revealed distinct size modes (Fig. 2), indicative of age groups (Table 2). In the middle Elwha River (between the two dams) the samples in September included modes with a means of 86 and 156 mm, and a single 257 mm fish, likely corresponding to fish at the end of their first, second and third summers of life (i.e., aged 0+, 1+ and 2+). The samples in the upper Elwha River were collected in June and the modes had means of 181 and 224 mm, likely at the beginning of their third and fourth summers of life. The $\delta^{15}\text{N}$ values showed the expected increase with body size. The $\delta^{13}\text{C}$ values were lower (i.e., more negative) in the upper compared to the middle reach of the river. Only five samples of downstream migrants in the Dungeness River were obtained but they ranged from 125 to 216 mm in June and July. The Elwha River estuary samples ranged from 150 to 450 mm but > 50% were 175 to 225 mm.

Discussion

Our overall objective was to determine whether stable isotopes provide evidence that the Elwha River bull trout are using marine food resources as juveniles and adults, indicating expanded anadromy in this population after dam removal. The isotope values of juveniles in the estuary indicated that they had fed on marine prey, and the values of adults caught in the river at different locations and times of the year strongly indicated marine foraging by many though perhaps not all individuals. These results are encouraging for the restoration of this population because they indicate expanded foraging opportunities and resumption of anadromy after being almost entirely land-locked for over a century. Such spatial expansion and increased life history diversity is consistent with increased probability of persistence under the Viable Salmonid Population concept (McElhany et al. 2000) for this component of a threatened species. In addition, it builds on growing evidence of the flexibility of anadromy in salmonids in general (Quinn and Myers 2004; Spares et al. 2015), and char in particular (Dunham et al. 2008; Bond et al. 2015).

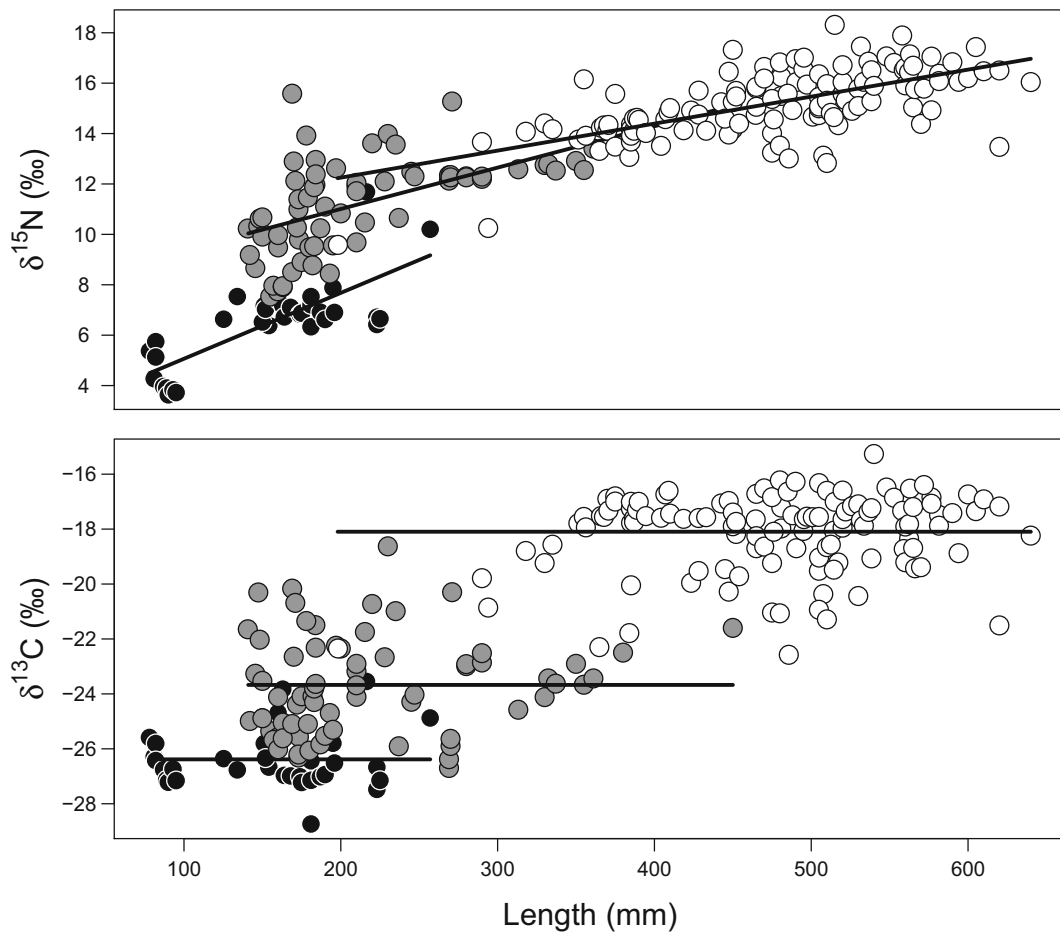


Fig. 3 Isotope values of nitrogen ($\delta^{15}\text{N}$, top) and carbon ($\delta^{13}\text{C}$, bottom) from bull trout as a function of fork length, separated by collection location (Elwha and Dungeness rivers combined). For each collection location, filled black = in-river pre-smolt,

gray = estuary, open white = in-river adult. Lines are best-fit regressions of isotope value on length for each collection location. All regressions for $\delta^{15}\text{N}$ have significant slopes ($p < 0.001$), while all regressions for $\delta^{13}\text{C}$ are intercept only models

The adult bull trout (mean lengths > 450 mm; Table 1, Fig. 2) sampled in the Elwha River in mid-summer after dam removal had similar isotope values to those in the Dungeness River sampled in the late fall, when they would have had access to eggs and tissue from adult

Pacific salmon (Lowery and Beauchamp 2015). However, most of the Elwha River adults were sampled too early in the season to have had access to eggs from fall-spawning Pacific salmon, and we detected no difference in isotope values with collection date so this does not

Table 2 Means (SD) for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and fork length (mm) of juvenile bull trout sampled from the Elwha River's middle reach (in September) and upper reach (in June) prior to dam removal.

Age groups were estimated based on the length frequency modes and month of sampling

Reach	Age group	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Length	Sample
Middle	0+	4.40 (0.80)	-25.56 (0.59)	86.3 (5.9)	9
Middle	1+	7.04 (0.37)	-24.91 (1.04)	156.3 (6.2)	4
Middle	2+	10.21	-23.87	257	1
Upper	2+	7.00 (0.43)	-26.97 (0.71)	181.1 (10.4)	11
Upper	3+	6.60 (0.15)	-27.09 (0.41)	223.7 (1.2)	3

explain the marine signal in our data. Moreover, diet analysis indicated that very few eggs had been eaten by these fish (Roger Peters and Roger Tabor, USFWS, unpublished data). The availability of eggs as food depends on salmon populations at such high densities that eggs buried by one female are dislodged by females spawning later (Moore et al. 2008). The Elwha River salmon populations are still small but perhaps in the future salmon eggs may become an important food source for this population.

The isotopic signatures of adult bull trout sampled near the mouth of the river might have been influenced in part by consumption of euryhaline fishes, and sampling in the estuary (Shaffer et al. 2017) revealed that three such species were common: staghorn sculpin (*Leptocottus armatus*), starry flounder (*Platichthys stellatus*), and threespine stickleback (*Gasterosteus aculeatus*), and others such as eulachon (*Thaleichthys pacificus*) were also present. However, the signatures of the adults sampled at rkm 21.2 to 21.4 are best explained by foraging in marine waters, followed by migration upriver. Given the absence of spawning habitat near the river's mouth and the timing of capture (summer), the most plausible explanation is that the adults sampled between rkm 1.3 and 2.6 had been in marine waters and were migrating upriver to spawn. However, isotope values in soft tissues change over time with diet, and so the data were consistent with variable foraging in fresh water prior to sampling, or non-anadromy in some individuals. Indeed, the nature of the sampling for adults may have been biased towards migratory rather than more sedentary fluvial fish, so the proportion of the adults that migrates cannot be estimated from our data.

Adult Elwha River bull trout after dam removal were isotopically similar to those from the Dungeness River population and their values were similar to those of adult coho, pink, and Chinook salmon that returned to the Elwha River (Tonra et al. 2015), as summarized in Table 1. The bull trout had $\delta^{15}\text{N}$ values between those of coho and Chinook salmon, two species that tend to be most piscivorous (Quinn 2005), indicating that they fed at a high trophic level. The $\delta^{13}\text{C}$ values in the adult bull trout were similar to those of adult Elwha River coho salmon, and intermediate between those of adult Chinook and pink salmon (Table 1). This indicated reliance by the bull trout on marine prey for a substantial period of time, as these Pacific salmon are at sea for a year and a half (coho and pink) or more (Chinook). However, the specific duration of marine residence by bull trout from

the Elwha and Dungeness rivers is not known. In Puget Sound they seem to migrate downstream primarily in spring and return in early summer (Hayes et al. 2011; Goetz 2016), well in advance of their typical spawning period in October, though some moved in late fall as well. In contrast to this pattern of primarily overwintering in fresh water, radio-tracking indicated that bull trout from the coast of Washington commonly entered marine waters in late fall and winter, and spent the winter at sea or moved into other rivers (Brenkman and Corbett 2005; Brenkman et al. 2007). The Elwha and Dungeness rivers are geographically intermediate between the coast of Washington and Puget Sound and represent physically intermediate conditions between the very exposed coast and much more protected, estuarine waters at the mouths of large Puget Sound rivers such as the Skagit, Snohomish and Stillaguamish. It is therefore not clear, a priori, which type of migration pattern the Elwha and Dungeness river bull trout might display. Our results, however, indicated substantial reliance on marine prey at a high trophic level. The Dungeness River population contains anadromous bull trout but not all individuals seem to migrate to sea as adults (Ogg et al. 2008). The $\delta^{13}\text{C}$ values from our adult Dungeness River samples averaged -18.81 but the range was consistent with some variation in use of marine resources by this population.

The isotopic signals of juvenile bull trout in the two estuaries were similar to each other and distinctly different from juveniles sampled between the Elwha River dams, and Dungeness River juveniles trapped migrating to sea. Such similarity of fish in the estuaries might be observed if all the fish in the Elwha River had moved there from the Dungeness River. However, genetic analysis indicated that they were distinct (DeHaan et al. 2011), so this is not the explanation. $\delta^{15}\text{N}$ values increased with fish size but for fish of similar length the values of fish in the estuary differed from those in the rivers, and in $\delta^{13}\text{C}$ there was no effect of fish length (Fig. 3). These results seem to indicate some estuarine feeding by these fish but there are two caveats. First, there was no relationship between isotope values and collection date, in contrast to the expectation that fish sampled later in the summer would have increasingly marine signatures. The estuary of the Elwha River at the time of dam removal had been reduced by a century of sediment deposition behind the dams (Warrick et al. 2012). The estuary is growing (Shaffer et al. 2017) but will probably remain small so anadromous bull trout

may move along the nearshore or make frequent short forays between the lower river and nearshore area. Some juvenile bull trout have been caught in the estuary in all months of the year (Rebecca Paradis and J. Anne Shaffer, unpublished data) but each individual does not necessarily stay there for a long time.

The second caveat is that the Elwha River is not a homogeneous place (nor, presumably, is the Dungeness River). Rainbow trout were sampled in the upper Elwha River (above Glines Canyon Dam), middle river (between Glines Canyon and Elwha dams) and the lower river, below Elwha Dam as part of a study of spatial patterns of stable isotopes prior to dam removal (Duda et al. 2011). The $\delta^{13}\text{C}$ values of rainbow trout differed between the three collections. The fish in the lower river were assumed to have not been to sea but they had values similar to those of the bull trout in the estuary (Table 1). Therefore, the comparison between bull trout above Elwha Dam with ones in the estuary later is complicated by differences in isotopic signals within the river. The bull trout samples that were obtained (Table 2) revealed the same pattern seen in the rainbow trout; lower $\delta^{13}\text{C}$ values in the upper compared to the middle section, making it unclear how much foraging the juveniles had done in the estuary to generate the observed values. On the other hand, not only juvenile bull trout but also juvenile rainbow/steelhead trout have been sampled in the Elwha River estuary in many months of the year (Rebecca Paradis, unpublished data, see also Hall et al. 2016). The isotopic signatures of any salmonids in the lower reach of the river might be influenced by riverine differences compared to the upper river, and by possible foraging in the estuary. The variation in use of the estuary and nearshore waters by juveniles of these facultatively anadromous fishes may play an important role in their ecology in general, and also predispose them to take advantage of reconnected migration corridors.

Overall, our results revealed that the adult Elwha River bull trout sampled in the river after dam removal had made substantial use of marine resources, to the same extent as the nearby Dungeness River population which was never dammed and where bull trout are at least partially anadromous (Ogg et al. 2008). The extent to which juveniles relied on marine prey resources was somewhat less clear because of variation in isotope values within the river. Nevertheless, the juveniles sampled in the Elwha River estuary were as large or larger than those leaving the Dungeness River and in its

estuary, and also those migrating down the Skagit River in Puget Sound (Zimmerman and Kinsel 2010). This information is consistent with volitional use of the Elwha River estuary rather than displacement from high flows. Taken together, these data indicate rapid resumption of anadromy by a population that was almost entirely land-locked, contributing to our understanding of the flexibility of anadromy in this species. In general, the marine migrations of Pacific char species are less well-studied than those of Pacific salmon and steelhead. The northern form of Dolly Varden makes distant migrations to open waters (Morita et al. 2009) and relies heavily on marine prey, even in populations that are only partially anadromous (Hart et al. 2015). In most cases Dolly Varden and Arctic char only spend the summer in marine waters (Armstrong 1974; Bond and Quinn 2013; Quinn et al. 2016) but the bull trout of the Washington coast seem to contradict this pattern (Brenkman and Corbett 2005; Brenkman et al. 2007). Comparisons to other populations in the region would help determine the ways in which variation in river and nearshore conditions modify the patterns of migration.

More broadly, anadromy in bull trout seems generally analogous to that seen in the congeneric brook trout, *S. fontinalis*. As in bull trout, brook trout often occur as non-anadromous populations (Curry et al. 2010), migrations to marine waters seem facultative and not distant but as the fish become large they prey heavily on fishes (Morinville and Rasmussen 2006). In addition, the native distribution of each species is limited to one coast of North America (Atlantic for brook trout and Pacific for bull trout), also consistent with limited marine migration. These species both enter marine waters at a comparatively large size, and if the flexible osmoregulatory physiology described for brook trout (McCormick 1994) characterizes bull trout as well, it might explain how they can enter and leave marine waters throughout the year. Such flexibility contrasts with the narrower period of “parr-smolt transformation” that is typical of Atlantic salmon and coho salmon. Such flexibility might contribute to their rapid ability to resume anadromy in this case.

In addition to the implications for bull trout, our results contribute to a growing body of evidence that land-locked populations can resume anadromy once the barrier has been removed. For example, dams precluded anadromy in the Coquiltam and Alouette rivers in British Columbia for nearly a century (about 25 generations) but experimental water releases from the reservoirs

allowed juveniles to migrate and then return from the ocean (Godbout et al. 2011). Indeed, the separation between anadromy and non-anadromy is less distinct in salmonids than was once believed (Pavlov and Savvaitova 2008; Sloat et al. 2014). Combined with the tendency of salmonids and other diadromous fishes to colonize upriver after dam removal (Pess et al. 2014), including shortnose sturgeon (Wippelhauser et al. 2015), sea lamprey (Hogg et al. 2013), and American eels (Hitt et al. 2012), this flexibility in migratory life histories makes it likely that projects reconnecting rivers with marine habitats will benefit the fishes and their ecosystems.

Acknowledgements Many individuals assisted with the sampling but we especially thank Matt Beirne for help in the Elwha River estuary, and Randy Cooper, Larry Ogg, and Nikki Sather for sampling in the Dungeness River. For the Elwha River sampling, we especially thank Patrick Connolly, Anna Geffre, Josh Geffre, Heidi Hugunin, Phil Kennedy, Michaela Lowe, Kaylee Moser, Raymond Moses, Michelle Pena-Ortiz, James Starr, Todd Bennett, Keith Denton, Steve Corbett, Brieuc Couillerot, Kinsey Frick, Mike McHenry, and Dan Spencer. Austin Anderson prepared the samples for processing, which was conducted at the University of Washington's IsoLab. Sampling in the Elwha River estuary was supported by the U.S. Environmental Protection Agency–Puget Sound Partnership Puget Sound Protection and Restoration Tribal Assistance Program (CFDA#66.121), and by the Olympic National Park, U.S. Fish and Wildlife Service, and Lower Elwha Klallam Tribe. Sample processing and analysis was supported by the Washington Sea Grant program, University of Washington, pursuant to NOAA Award No. NA10OAR4170075, Project R/LME-7, and the H. Mason Keeler and the Richard and Lois Worthington endowments at the University of Washington. Helpful comments on a draft were provided by George Pess, Jeffrey Duda, Patrick Crain, and four anonymous reviewers. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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