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North American Journal of Fisheries Management

ISSN: 0275-5947 (Print) 1548-8675 (Online) Journal homepage: http://www.tandfonline.com/loi/ujfm20

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To cite this article: John R. McMillan, George R. Pess, Martin Liermann, Sarah A. Morley, Michael L. McHenry, Lance A. Campbell & Thomas P. Quinn (2015) Using Redd Attributes, Fry Density, and Otolith Microchemistry to Distinguish the Presence of Steelhead and Rainbow Trout in the Elwha River Dam Removal Project, North American Journal of Fisheries Management, 35:5, 1019-1033, DOI: 10.1080/02755947.2015.1074965

To link to this article: http://dx.doi.org/10.1080/02755947.2015.1074965

North American Journal of Fisheries Management 35:1019–1033, 2015
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ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2015.1074965

ARTICLE

Using Redd Attributes, Fry Density, and Otolith Microchemistry to Distinguish the Presence of Steelhead and Rainbow Trout in the Elwha River Dam Removal Project

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Abstract

The removal of impassable dams can affect stream fish communities in many ways, including allowing previously separated anadromous and resident life history types to intermingle. Recolonization of steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) into areas that were previously occupied solely by resident conspecifics presents a challenge for monitoring because (1) staging or spawning adults may be difficult to directly observe; and (2) the offspring of the two life history forms are indistinguishable during early life. We evaluated the utility of using redd attributes, fry (age-0) size, and fry density to distinguish the presence of steelhead and Rainbow Trout in the Elwha River, Washington. Redd area and substrate size differed between forms: steelhead redds were significantly larger and had a greater median substrate particle size than Rainbow Trout redds. Fry density was significantly higher in steelhead spawning reaches than in Rainbow Trout reaches during both survey years (2010 and 2011). Steelhead fry tended to be slightly larger than Rainbow Trout fry but not significantly so in either year. Additionally, otolith microchemical analyses indicated that all fry collected from newly colonized habitat were of steelhead maternal origin, and these fish were intermediate in size to the steelhead and Rainbow Trout fry collected prior to dam removal. Thus, fry size may not effectively differentiate parental origin despite the tendency of anadromous parents to be larger and to spawn earlier than residents. Redd attributes and fry density may be useful for evaluating the spatial distributions and relative abundances of steelhead and Rainbow Trout after dam removal. Our results have implications for other dam removal projects and other monitored species.

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Received April 13, 2015; accepted July 3, 2015

For centuries, river systems throughout the world have been affected by dams. Increasingly, many dams are being removed because they have outlived their economic usefulness or have become unsafe or to facilitate ecological restoration of the river systems (Bednarek 2001; Hart et al. 2002; Pohl 2002). One of the many processes that can occur after dam removal is the resumption of migration (including diadromy) by fish populations into their former habitats (Pess et al. 2014). This is especially important in the case of rivers where dam removal restores diadromous fishes' migration from the sea to previously inaccessible areas, thereby increasing species and life history diversity at upriver locations (Anderson et al. 2008; Weigel et al. 2013a).

In the years after dam removal, landlocked and anadromous components of a species may intersperse and establish new patterns of spatial distribution and relative abundance (Weigel et al. 2013b). Unlike interspecific changes in the fish community, which can be relatively easy to monitor, distinguishing life history variants of the same species can be challenging. For example, many salmonid species in the genera *Oncorhynchus, Salmo*, and *Salvelinus* can exist as anadromous and resident (i.e., nonanadromous) forms (Rounsefell 1958; Quinn and Myers 2004; Pavlov and Savvaitova 2008). After dam removal, a river might support a mix of anadromous and resident breeders. However, observations of staging or spawning adults may be difficult because of the increased sediment loads related to dam removal and because the initial colonizers may be few and widely dispersed (Brenkman et al. 2008; McHenry and Pess 2008). Furthermore, the young offspring of anadromous and resident forms are outwardly difficult or impossible to distinguish, thus hindering efforts to assess the progress of population restoration (Weigel et al. 2013a). Otolith microchemical analysis can distinguish the offspring of anadromous and resident females based on the strontium : calcium (Sr:Ca) ratio (e.g., Rieman et al. 1994; Volk et al. 2000; Zimmerman and Reeves 2000); however, this type of analysis requires specialized equipment and expertise. In addition, the sample sizes must be sufficient to characterize the blend of life history types, and obtaining the required number of samples may be incompatible with conservation goals or regulations. Genetic analyses can distinguish spawners with different life histories and the offspring of those spawners in some cases (e.g., Taylor et al. 1996), but the capacity of each form to produce offspring expressing the alternative life history often reduces the utility of this approach (e.g., Heath et al. 2008; reviewed by Dodson et al. 2013). Lastly, stable isotopes of carbon and nitrogen can also indicate maternal origin (Ciancio et al. 2008; Jardine et al. 2008; Briers et al. 2012), but the signal becomes diluted as the fish grow (Doucett et al. 1999) and as tissues turn over (Heady and Moore 2013); therefore, this technique may be limited to fish of such a small size that sampling is lethal (Thornton et al. 2015).

A species of particular interest with respect to dam removal is *O. mykiss*, which commonly displays anadromous (steelhead) and resident (Rainbow Trout) forms (Kendall et al. 2015). Based on several lines of reasoning, we hypothesized that the characteristics of redds and offspring could provide an additional means of distinguishing between steelhead and Rainbow Trout. First, in salmonids, there is a positive relationship between body size and the size of gravels used for spawning (Kondolf and Wolman 1993; Riebe et al. 2014) or between body size and nest depth (Steen and Quinn 1999). Consequently, steelhead may construct larger redds in larger substrate than the typically smaller-bodied Rainbow Trout (Zimmerman and Reeves 2000). Second, steelhead tend to spawn earlier than Rainbow Trout (Zimmerman and Reeves 2000; McMillan et al. 2007). Earlier spawned offspring from larger mothers may be larger during their first summer of life if they also emerge and commence feeding earlier. Moreover, anadromous females typically produce larger eggs than nonanadromous females—although this is not always the case in *O. mykiss* (Gross 1987)—and larger eggs produce larger emergent fry (Beacham and Murray 1990), potentially magnifying the difference in body size between forms. Finally, female steelhead are typically more fecund and hence capable of producing substantially more fry than the smaller resident females (Gross 1987). This might lead to higher fry densities in areas where anadromous females spawn, as has been reported for other salmonids (Morita et al. 2000; Bohlin et al. 2001).

With the increase in dam removal projects, there is a growing need to test and validate approaches for documenting the extent and rate of recolonization by anadromous salmonids. This need is especially pressing for steelhead, as many populations are listed as threatened or endangered under the U.S. Endangered Species Act (ESA; Busby et al. 1996; Good et al. 2005; NOAA 2007). Sympatric Rainbow Trout are typically managed separately from steelhead and not listed under the ESA. Consequently, there is management and conservation interest in determining the rate of steelhead recolonization in space and time and the eventual relative abundances of anadromous and resident individuals. However, quantifying the rate of recolonization requires biologists to identify the origins of juveniles and to determine the life history type that constructed a given redd in areas where anadromous and resident forms are sympatric.

In the Elwha River on Washington State's Olympic Peninsula, the removal of two large dams began in fall 2011 and was completed in fall 2014; initial stages of colonization by steelhead occurred during 2012, when Elwha Dam was deconstructed. Prior to dam removal, Rainbow Trout were abundant upstream of the dams, whereas steelhead were found only below the dams (Brenkman et al. 2008). The purpose of the present study was to evaluate approaches (involving adults and juveniles) for determining the presence of steelhead in areas that were formerly occupied only by Rainbow Trout. We accomplished this in three ways during two phases of dam removal. First, prior to dam removal, we measured the redds of steelhead and Rainbow Trout to determine whether there were differences in redd size and the size of surrounding substrate that could be used to discriminate redds made by fish of unknown origin; this was based on the hypothesis that larger *O. mykiss* (steelhead) would make larger redds and use larger substrate than smaller *O. mykiss* (Rainbow Trout). Second, the body size and density of fry (i.e., young of the year) in areas where each life history form spawned were measured to test the hypothesis that steelhead would produce larger and more numerous fry than Rainbow Trout. Third, during the initial stages of dam removal in 2012, we used otolith microchemistry to determine the maternal origin of a group of fry that could have been produced by either steelhead or Rainbow Trout. This information allowed us to further test (1) the hypothesis that anadromous females produce larger fry than resident females and (2) the use of fry size to determine the proportion of fry produced by each life history form. Answers to these questions will contribute to the ongoing monitoring of the Elwha River ecosystem and will help in identifying solutions for managers who are tasked with evaluating the extent and rate of steelhead recolonization in other systems with dam removal projects (McHenry and Pess 2008; Pess et al. 2014).

METHODS

Study Area

This study was conducted in the Elwha River watershed (drainage area = 833 km^2), which originates in the mountains of the Olympic Peninsula and flows northward for 72 km into the Strait of Juan de Fuca (Figure 1). Elwha Dam was constructed at river kilometer (rkm) 7.9 in 1912, and Glines Canyon Dam was constructed at rkm 21.6 in 1925; both dams were constructed without fish passage facilities. Dam removal eliminated the impoundments created by Elwha Dam (Lake Aldwell, 108 ha) and Glines Canyon Dam (Lake Mills, 168 ha) and restored riverine processes (Figure 1). Hereafter, we refer to the main-stem river section below the former site of Elwha Dam as the lower Elwha River (7.9 km; elevation = 0–30 m), the section between the two former dam sites as the middle Elwha River (13.7 km; elevation = 30–120 m), and the section from the former site of Glines Canyon Dam to the headwaters as the upper Elwha River (50 km; elevation = 120–1,300 m). The entire upper Elwha River and part of the middle section are within the Olympic National Park, whereas the lower section flows through a mosaic of largely forested private, state, and tribal lands (Duda et al. 2008).

The National Park Service initiated the deconstruction of Elwha and Glines Canyon dams in 2011, dramatically increasing suspended sediment for most of the year. Elwha Dam was fully deconstructed in July 2012, allowing steelhead to access several tributaries that provided clear-water refuges from the sediment in the main-stem Elwha River. Removal of Glines Canyon Dam was completed in September 2014, thus facilitating steelhead access to the remaining upstream habitat. Prior to removal, the barriers provided an opportunity to evaluate characteristics of *O. mykiss* redds and fry in areas where steelhead were present and in areas where they were absent. Initial stages of steelhead recolonization after the removal of Elwha Dam allowed us to test hypotheses about maternal origin and fry size based on analysis of otolith microchemistry.

Salmonid Populations in the Elwha River

We conducted redd surveys and fry sampling in 2010 and 2011 prior to dam removal. During that period, the lower Elwha River supported eight salmonid species, including Chinook Salmon *O. tshawytscha*, Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, resident and anadromous *O. mykiss* (Rainbow Trout and steelhead), Cutthroat Trout *O. clarkii*, and Bull Trout *Salvelinus confluentus* (Pess et al. 2008). The middle and upper sections of the Elwha River supported only Rainbow Trout, Bull Trout, Cutthroat Trout, nonanadromous Sockeye Salmon, and nonnative Brook Trout *Salvelinus fontinalis* (Brenkman et al. 2008; Pess et al. 2008). We also sampled *O. mykiss* fry during the removal of Elwha Dam in 2012, a period when steelhead were relocated to and naturally recolonized the Little River, a tributary of the middle Elwha River (Figure 1).

Prior to and during dam removal, the steelhead population of the Elwha River numbered about 100–300 fish, whereas there were thousands of Rainbow Trout in the upper and middle sections of the river (Brenkman et al. 2008, 2012). Steelhead are typically much larger than Rainbow Trout (Kendall et al. 2015), and this appears to be true of *O. mykiss* in the Elwha River. In 2011 and 2012, we captured and measured the FLs of 134 adult steelhead (76 females; 58 males) during efforts to relocate them to the Little River; FLs were also measured on 288 Rainbow Trout that were captured via angling from 2009 to 2011. Based on these data, adult steelhead (females: mean FL = 700 mm, range = 558–780 mm; males: mean FL = 707 mm, range = 507–936 mm) were much larger than Rainbow Trout (mean FL = 215 mm, range = 101–508 mm) in the Elwha River (J. R. McMillan, unpublished data; Figure 2). The largest Rainbow Trout rarely exceeded 400 mm. These differences in adult size formed the basis for our predictions regarding redd size and fry size differences between life history types.

Survey Reach Selection and Data Collection

Spawn timing, redd size, and redd substrate size.—Survey reaches were selected based on long-term monitoring developed by scientists and managers, and the reaches differed for steelhead and Rainbow Trout (Brenkman et al. 2008; McHenry and Pess 2008; Morley et al. 2008). To locate redds and estimate the spawn timing of steelhead prior to dam removal, we conducted biweekly redd surveys along the

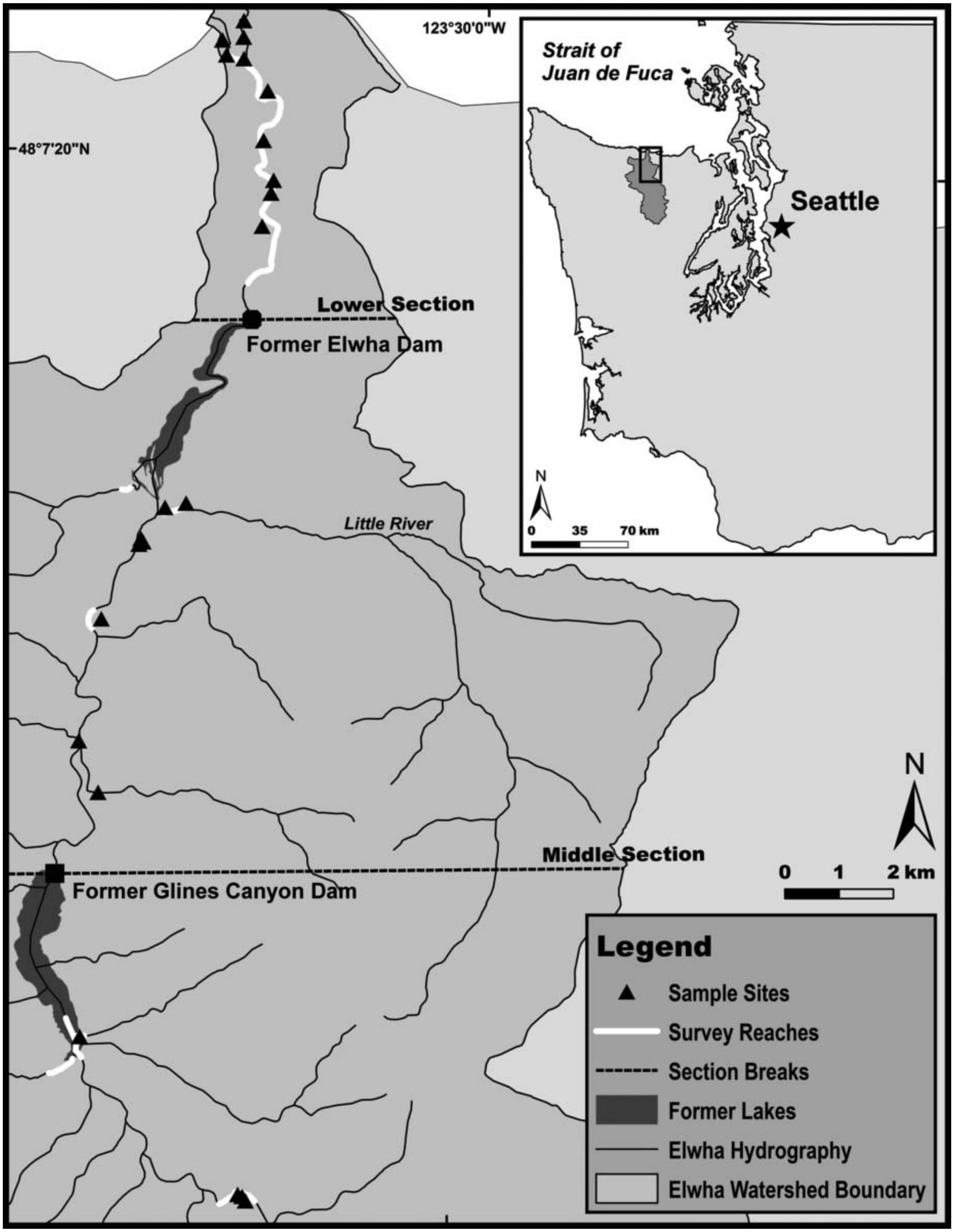

FIGURE 1. Map of the Elwha River basin, Washington, including locations of the two former dam sites (black circle and black square), redd survey reaches (white lines), and fry sampling locations (black triangles) for steelhead and Rainbow Trout. “Lower section” denotes the upper boundary for the lower Elwha River; “middle section” denotes the upper boundary for the middle Elwha River; and the area upstream of the middle section is the upper Elwha River.

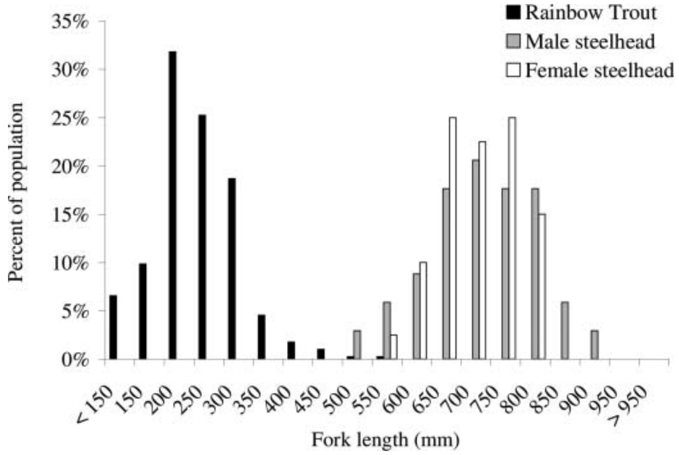

FIGURE 2. Size (FL, mm) of adult steelhead (sex was known based on visual examination of external characters) and Rainbow Trout (sex and state of maturity were not consistently known) in the Elwha River.

downstream-most 6.9 km of the lower Elwha River as well as in several floodplain channels (Figure 1). Rainbow Trout redd surveys were conducted less frequently because several reaches were in remote locations, and the primary goal was not to determine spawn timing but rather to identify areas with redds so that the redds could be measured and the stream reach could be sampled for fry later in the year. We counted Rainbow Trout redds in 1.0–2.5-km-long survey reaches (Table 1) within six tributaries and main-stem floodplain channels in the middle Elwha River; in the upper Elwha River, redds were counted from the head of Lake Mills to 2.0 km upstream and in three floodplain channels located at approximately rkm 30.0 (Figure 1). Overall, we surveyed 23.0 km of stream in the lower section of the river, 25.7 km in the middle section, and 11.3 km in the upper section (Table 1). We conducted eight surveys for steelhead (April 1, 10, and 30; May 13, 21, and 28; June 15; and July 8) and nine surveys for Rainbow Trout (April 25; May 5; June 15 and 17; July 3–9; and August 8) in 2010.

Redds were identified as disturbed areas in the streambed where gravels were overturned to form a depression and tailspill (Zimmerman and Reeves 2000). Gravels in active redds were cleaner and lighter in color than gravels in older redds or areas with no redds. All redds above the dams were presumed to be constructed by Rainbow Trout because Cutthroat Trout are very rare or absent throughout the middle and upper Elwha River (Brenkman et al. 2012) except in Indian Creek, where Cutthroat Trout redds are similar in size to the Rainbow Trout redds we observed (McMillan et al. 2014). We did not survey Indian Creek. Each redd was numbered and flagged to prevent double-counting. Surface area was measured for all counted redds; we also measured the substrate size in the tailspill (e.g., Zimmerman and Reeves 2000) for a subset of redds (n = 30 per life history form) that spanned the range of redd sizes and locations. An electronic rangefinder was used to measure the length (m) and width (m) of each redd at the widest part. We then measured the *b*-axis (Wolman 1954) of 100 randomly selected stones in the tailspill of each redd and also measured 100 stones from the entire stream width where the redd was located. These data allowed us to (1) test the hypothesis that steelhead redds would be characterized by larger substrate than Rainbow Trout redds and (2) determine whether fish of the two life history types excavated redds in substrate that was larger or smaller than the available substrate (i.e., where redds were not constructed). These measurements provided the entire size distribution of the substrate, but median sizes were used in our analyses, consistent with other studies of salmonid redds (e.g., Montgomery et al. 1996).

Fry size and fry density.—During 2010 and 2011, we sampled *O. mykiss* fry size and density (number of fish/100 m^2) in 21 survey reaches, including 10 reaches in the lower Elwha River, 8 reaches in the middle section, and 3 reaches in the upper section (Table 1). Sampling occurred during mid-September, when most age-0 fish had emerged from the gravel based on the presumed spawn timing of steelhead and Rainbow Trout (Brenkman et al. 2008). Many reaches were sampled in both years, so the total number of survey reach data points was 30 (17 in the lower section, 10 in the middle section, and 3 in the upper section; Table 1). The survey reaches

TABLE 1. Description of the three distinct sections (lower, middle, and upper) of the Elwha River, Washington, as delineated by former dam sites (Figure 1), including whether steelhead had access to the habitat prior to dam deconstruction, the number of redd surveys, the length of stream (km) surveyed in 2010 and 2011 (when dams were still in place), the number of reaches that were sampled for *Oncorhynchus mykiss* fry, the total number of surveys in those reaches (shown in parentheses), and the respective habitat types. Survey reach types include main-stem Elwha River (MR), floodplain channel (FPC), and tributary (TRB). The upper Elwha River sites were only sampled in 2010.

		Redd surveys		Fry surveys	
Elwha River section	Steelhead access?	Number of surveys	Length surveyed (km)	Number of reaches (total surveys, 2010–2011)	Reach types
Lower	Yes	8	23.0	10 (17)	3 MR reaches, 7 FPC reaches
Middle	No	6	25.7	8 (10)	5 TRB reaches, 3 FPC reaches
Upper	No	3	11.3	3 (3)	3 FPC reaches

were 100 m long, and with the exception of the main-stem Elwha River above Lake Mills, all fry survey reaches were located within the longer reaches visited during spawning counts (Figure 1); this was done to ensure that sampling locations of *O. mykiss* fry were near areas where redds were measured.

Data collection focused on parameters that can be used as indicators of female anadromy after dam removal. A backpack electrofisher (Model LR-24 or 12B; Smith-Root, Inc., Vancouver, Washington) was used to capture as many *O. mykiss* fry as possible during a single pass. Fish were lightly anesthetized with tricaine methanesulfonate (MS-222), and FLs were measured for 30 individuals (or all individuals if fewer than 30 were captured). After recovery from the anesthetic, all fish were released near their point of capture. The next day, *O. mykiss* fry were enumerated via three successive passes by a snorkeler working in an upstream direction (McMillan et al. 2012). The snorkeler only enumerated *O. mykiss* that were estimated to be smaller than 80 mm long (i.e., age 0). To eliminate inconsistencies among divers, the same person conducted all snorkeling surveys (Thurow 1994; McMillan et al. 2013). The average of the three counts was used as the estimated number of fry; this estimate was divided by the surface area surveyed, and the resulting value was multiplied by 100 to yield the number of fry per 100 m^2.

Otolith Collection and Examination

During the dam removal process—and after the removal of Elwha Dam—we retained 28 *O. mykiss* fry that were accidentally killed during mid-September sampling in the lower 3.0 km of the Little River (2012: $n = 16$ fry; 2013: $n = 12$ fry; Figure 1). The fry could have been produced by naturally occurring Rainbow Trout or by steelhead, as some steelhead were relocated to the Little River via trapping and hauling, and others naturally recolonized the stream after passing the former site of Elwha Dam (McMillan et al. 2012). Externally, the life history forms are indistinguishable during early ontogeny (McMillan 2009), but the potentially mixed population at the Little River location in those years allowed us to test (1) whether we could use otolith microchemistry to determine maternal origin as anadromous or resident (e.g., Zimmerman and Reeves 2000) and (2) whether there were differences in length between fry with different maternal life histories, as might be indicated by the fry sampling described above.

Both sagittal otoliths were extracted from each of the 28 fry (with unknown maternal life histories) collected during the initial stages of steelhead recolonization and from each of 12 known Rainbow Trout offspring collected in the Little River and Boulder Creek (both upstream of dams) prior to dam removal. To serve as a baseline for anadromous Sr:Ca ratios, the otoliths of 30 steelhead offspring from the nearby Dungeness Fish Hatchery (Sequim, Washington) were collected; all of the fish should have had anadromous origins because they were selectively bred using only adult steelhead. We used the sagittal otoliths to examine microchemistry and identify maternal origin as anadromous or resident (e.g., Mills et al. 2012). Otoliths were prepared via the methods described by Berejikian et al. (2013). Briefly, sagittal otoliths were mounted in thermoplastic resin (Crystalbond 509) and were ground in both the proximal and distal planes until exposed primordia were visible. All microchemical analyses were performed at the Keck Collaboratory for Mass Spectrometry at Oregon State University, Corvallis. A Photon Machines G2 193-nm excimer laser coupled with a Thermo X Series II inductively coupled mass spectrometer was used for all analyses of otolith microchemistry.

Data Analysis

Spawn timing and redd attributes.—We summarized and analyzed the data in four steps. First, to account for strong skew and unequal variances, we used a nonparametric Wilcoxon rank-sum test to compare the timing of redd construction by Rainbow Trout and steelhead. Second, we calculated geometric means of redd length, width, and surface area (length × width) for steelhead and Rainbow Trout redds. We also calculated the 25% and 75% quartiles to more fully characterize the data. Third, we calculated the median substrate particle size (*D*50) and associated 25% and 75% quartiles for steelhead and Rainbow Trout redd tailspills and for proximate non-redd areas. Lastly, to account for unequal variances, we conducted Welch's two-sample *t*-tests to compare (1) redd length, width, and surface area (geometric means for each metric) between steelhead and Rainbow Trout; (2) redd tailspill *D*50 between the life history forms; and (3) redd tailspill *D*50 versus non-redd substrate *D*50 for each life history form.

Fry size, fry density, and otolith microchemistry.—We analyzed data on fry size, fry density, and otolith microchemistry in three steps. First, Welch's two-sample *t*-test (one-sided; accounting for unequal variances) was used to test the hypotheses that fry FLs and densities would be higher in steelhead spawning areas than in Rainbow Trout spawning areas. Second, Sr:Ca ratios in the otolith primordial region (core) were calculated for individuals in the three groups of fry: hatchery steelhead (sampled from Dungeness Fish Hatchery), Rainbow Trout (sampled above the dams), and the 28 fry of unknown origin (collected from the Little River during the initial stages of recolonization). Maternal origin for the unknown-origin fry was determined by comparing Sr:Ca ratios in the otolith core with Sr:Ca ratios from the fry of known origin. A fish was classified as being of anadromous maternal origin if the Sr:Ca ratio in the otolith core was significantly higher than that for the known Rainbow Trout fry and was not significantly different from that for known steelhead based on unpaired one-tailed *t*-tests ($\alpha = 0.05$; Zimmerman and Reeves 2000).

Likewise, a fish was identified as being of resident maternal origin if the Sr:Ca ratio in the otolith core was significantly higher than that for the known steelhead fry and did not significantly differ from that for the known Rainbow Trout fry. Finally, body sizes were compared between the fry of steelhead maternal origin and the fry of Rainbow Trout origin. All analyses were performed in R software (R Development Core Team 2011).

RESULTS

Redd Attributes

Steelhead redds were constructed earlier (mean = May 14; $P < 0.001$) than Rainbow Trout redds (mean = July 15; Table 2), and redd construction by steelhead occurred during a narrower window of time than Rainbow Trout redd construction (Figure 3). However, we likely missed some earlier spawning by steelhead due to poor visibility in the main-stem Elwha River.

We counted and measured the dimensions of 119 Rainbow Trout redds; 114 steelhead redds were counted, but only 77 were measured (Table 2) because the remaining redds were so closely clustered that it was impossible to distinguish one redd from another. Steelhead redds were significantly longer (geometric mean = 1.2 m; $P < 0\ 0.001$) and significantly wider (geometric mean = 0.7 m; $P < 0.001$) than Rainbow Trout redds (geometric mean length = 0.2 m; geometric mean width = 0.2 m); the differences were so great that there was no overlap in either metric (Figure 4). The smallest measured Rainbow Trout redd was 0.01 m^2 and the largest was 0.25 m^2, whereas the smallest measured steelhead redd was 0.3 m^2 and the largest was 2.5 m^2. The mean surface area of steelhead redds (geometric mean = 0.9 m^2) was significantly greater ($P < 0.001$) than that of Rainbow Trout redds (mean = 0.03 m^2; Table 2). Based on the nonoverlapping ranges in our population of interest, we inferred that redds larger than 0.3 m^2 were constructed by steelhead and that redds smaller than 0.2 m^2 were constructed by Rainbow Trout.

Redd Substrate Sizes

The tailspill *D*50 values for steelhead redds were significantly larger ($P < 0.001$) than those for Rainbow Trout redds (Table 3; Figure 5). The maximum *D*50 for a Rainbow Trout redd (29 mm) was significantly smaller than ($P < 0.001$) and did not overlap with the smallest *D*50 for a steelhead redd (33 mm; Figure 5). The maximum substrate size in steelhead redds was more than triple that in Rainbow Trout redds ($P < 0.001$), while the minimum substrate sizes were not significantly different ($P = 0.20$; Table 3). Hence, we infer that in the Elwha River, redds with a tailspill *D*50 greater than 33 mm were constructed by steelhead, and redds with a tailspill *D*50 less than 30 mm were constructed by Rainbow Trout.

For Rainbow Trout, the *D*50 in redd tailspills was significantly smaller ($P = 0.003$) than the *D*50 in the entire riffle crest, indicating that Rainbow Trout selected smaller gravel than was generally available (Table 3; Figure 5). Steelhead also spawned in significantly smaller substrate ($P < 0.001$) than was found in the adjacent streambed, as the *D*50 in the redd tailspills was about half the *D*50 of the adjacent non-redd substrate (Table 3; Figure 5). The difference between redd and non-redd substrates was greater for steelhead than for Rainbow Trout (Figure 5).

Fry Size and Fry Density prior to Dam Removal

We measured FLs for 882 *O. mykiss* fry collected on 30 occasions in 15 stream reaches where we observed redds during 2010 surveys (Table 4). We collected 30 fry in all but two reaches (both in the upper Elwha River), where densities were so low that only 18 and 23 fry were captured. Shallow water and poor visibility prohibited the use of snorkeling surveys in three reaches of the lower Elwha River, but fry length and density data were collected from 18 reaches. Sampling dates were similar between years except in 2011 (Table 4), when we sampled three steelhead reaches during the first week of August;

TABLE 2. Attributes of Rainbow Trout and steelhead spawning in the Elwha River, including the date of spawning (with number of days in parentheses), the number of redds counted (with number sampled for attributes in parentheses), and the total number of redds per kilometer surveyed. Metrics include geometric mean redd length, width, and surface area (with 25% and 75% quartiles in parentheses). Welch's two-sample *t*-test (one-sided) was used to evaluate differences between Rainbow Trout and steelhead attributes. An asterisk indicates a statistically significant difference (α = 0.05).

Attribute	Rainbow Trout	Steelhead
Spawning date in 2010 (number of days)	Jul 15 (22.0)*	May 14 (15.2)
Number of redds counted (number sampled for attributes)	114 (114)	119 (77)
Total redds per kilometer	3.1	5.2
Geometric means of redd metrics (with 25%, 75% quartiles)		
Redd length (m)*	0.2 (0.1, 0.3)	1.2 (1.0, 1.7)
Redd width (m)*	0.2 (0.1, 0.2)	0.7 (0.6, 0.9)
Redd surface area (m^2)*	0.03 (0.02, 0.1)	0.9 (0.7, 1.2)

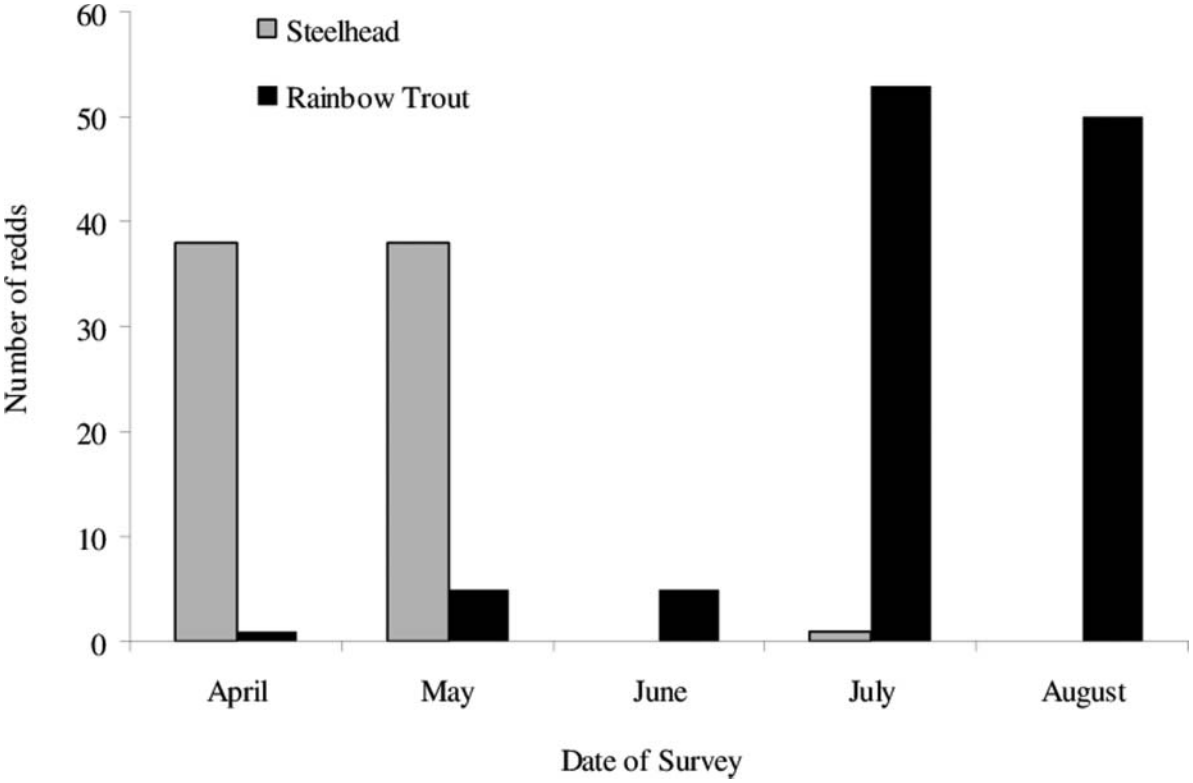

FIGURE 3. Monthly total counts of steelhead and Rainbow Trout redds in the Elwha River, April–August.

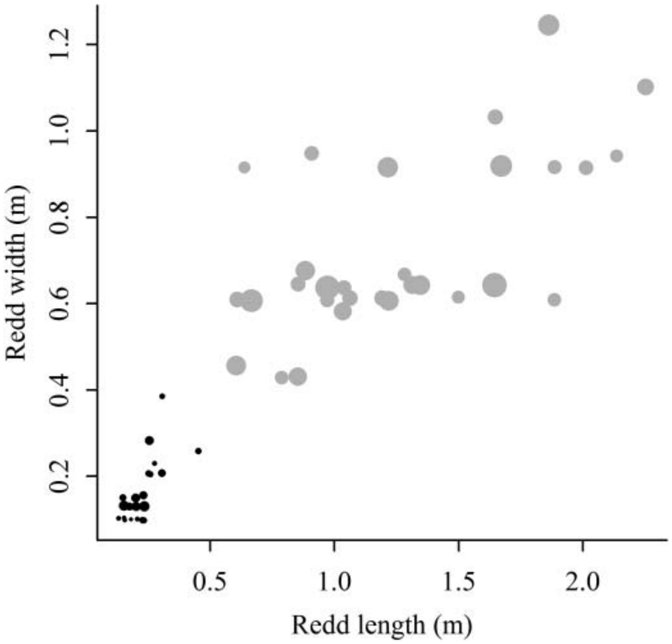

FIGURE 4. Width (m) and length (m) for the subset of Elwha River steelhead redds (gray circles) and Rainbow Trout redds (black circles) that were measured for redd size and substrate size. Symbol size reflects the relative substrate size in the redd tailspills (i.e., larger circles represent larger substrate sizes).

therefore, those fry had less time to grow than the fry in reaches that were sampled during September.

In both years, the mean FL of fry was slightly greater in the steelhead spawning areas than in the Rainbow Trout spawning areas, but the difference was not significant in either year (2010: $P = 0.61$; 2011: $P = 0.42$; Table 4; Figure 6). In contrast to fry FL, mean densities of fry were significantly higher in steelhead reaches than in Rainbow Trout reaches during both years (2010: $P = 0.04$; 2011: $P = 0.002$; Table 4; Figure 6). Densities ranged from 13.3 to 62.1 fry/100 m^2 in steelhead reaches and from 0.2 to 28.4 fry/100 m^2 in Rainbow Trout reaches. Overall, the mean density of fry in the steelhead reaches during 2010 and 2011 was more than twice that in the Rainbow Trout reaches (Table 4).

Fry Maternal Origin after Dam Removal

The mean Sr:Ca ratio in the otolith cores was 1.90 mmol/mol (SD = 0.15) for the 14 fry with known-anadromous mothers (hatchery steelhead), 0.52 mmol/mol (SD = 0.11) for the 12 fry with known-resident mothers (Rainbow Trout), and 1.55 mmol/mol (SD = 0.19) for the 28 fry of unknown maternal origin (Figure 7). The highest observed Sr:Ca values for individual fish were the otolith core values for fry of known-anadromous maternal origin, whereas the lowest

TABLE 3. Redd substrate attributes for steelhead and Rainbow Trout in the Elwha River, including the median substrate particle size (*D*50; with 25% and 75% quartiles in parentheses) in the redd tailspill; the *D*50 in the entire stream transect where the redd was located (non-redd substrate); and the minimum and maximum substrate particle sizes in the tailspill. Welch's two-sample *t*-test (one-sided) was used to evaluate differences between Rainbow Trout and steelhead attributes. An asterisk indicates a statistically significant difference ($\alpha = 0.05$).

Attribute	Rainbow Trout	Steelhead
Tailspill substrate *D*50 (mm)*	17.2 (14.0, 20.9)	45.2 (39.1, 52.5)
Non-redd substrate *D*50 (mm)*	28.3 (14.6, 53.5)	86.2 (78.8, 100.5)
Tailspill substrate minimum particle size (mm)	3.1 (2.1, 4.0)	3.7 (3.1, 5.8)
Tailspill substrate maximum particle size (mm)*	31.4 (26.2, 40.3)	95.1 (82.5, 105.5)

observed Sr:Ca values were the otolith core and edge values for fry of known-resident maternal origin and the otolith edge values for unknown-origin fry. Otolith core Sr:Ca values for the unknown-origin fry only overlapped with those for fry of known-anadromous origin (Figure 7). Interestingly, all 28 fry of unknown origin had otolith core Sr:Ca ratios that were significantly greater than those for fry of known-resident maternal origin (all $P < 0.0001$).

The Sr:Ca values indicated that all of the unknown-origin fry had anadromous mothers; thus, it was not possible to determine whether body size differed between fry with steelhead mothers and fry with Rainbow Trout mothers. However, the mean FL of unknown-origin fry was 45.4 mm (SD = 9.6), which was intermediate to the mean FLs observed for Rainbow Trout fry and steelhead fry prior to dam removal. The minimum FL (32 mm) and maximum FL (61 mm) of unknown-origin fry were well within the ranges observed for both life history forms prior to dam removal.

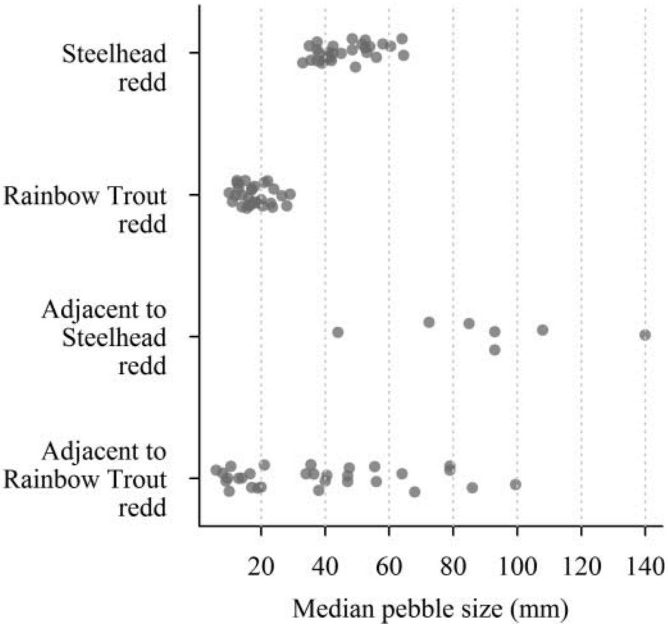

FIGURE 5. Median substrate particle size (*D*50) in steelhead and Rainbow Trout redds and in the adjacent streambed (non-redd areas) within the Elwha River.

DISCUSSION

Redd Size and Substrate Size as Indicators of Life History

We successfully used metrics based on redd size and redd substrate size to distinguish between steelhead redds and Rainbow Trout redds. The differences were so great that the redd sizes and tailspill *D*50 values did not overlap between the two life history forms. However, comparisons with other research revealed a number of interesting points that are relevant to the use of redd metrics for estimating the rate and distribution of steelhead recolonization in other populations. For example, the steelhead redds we measured were at the smaller end of sizes previously reported for steelhead (Zimmerman and Reeves 2000; Gallagher and Gallagher 2005) and were actually more similar to prior observations of Rainbow Trout redd size (Zimmerman and Reeves 2000), which were much larger than the Rainbow Trout redds we measured. The steelhead and Rainbow Trout redds examined by Zimmerman and Reeves (2000) were also more similar in size than the redds in our study. The difference between our study and theirs is likely attributable to differences in body size. Steelhead FLs in our study were similar to those in the Zimmerman and Reeves (2000) study; however, Rainbow Trout in their study ranged from 16 to 50 cm and 70% of the population was 20–35 cm (Schroeder and Smith 1989), whereas 74% of the Elwha River Rainbow Trout were no larger than 25 cm FL. Accordingly, although Elwha River *O. mykiss* redds larger than 0.30 m^2 can be confidently categorized as steelhead redds, this cutoff size may not be appropriate in all cases.

We also found that steelhead created redds in significantly larger gravel than Rainbow Trout and that life history could be inferred based on the redd tailspill *D*50. Unlike redd sizes, however, the mean *D*50 (45.2 mm) in redd tailspills from Elwha River steelhead was larger than the typically reported *D*50 values (range = 13.5–23.0 mm, Cederholm and Salo 1979; range = 26.5–36.7 mm, Shirazi and Seim 1981; mean = 32.5 mm, Zimmerman and Reeves 2000; range = 13.0–37.0 mm, Gallagher and Gallagher 2005), despite no obvious differences in fish size between our study and the previous studies. Orcutt et al. (1968) were the only authors to report similar *D*50 values (range = 42.0–46.0 mm) for redds from larger steelhead (mean FL = 76 mm).

TABLE 4. Attributes of fry sampled from Rainbow Trout and steelhead spawning areas in the Elwha River, including the mean date of capture in 2010 and 2011 (SD in parentheses), total number of fry measured during each sample year, fry FL, and fry density. Welch's two-sample *t*-test (one-sided) was used to evaluate differences between Rainbow Trout and steelhead attributes. An asterisk indicates a statistically significant difference ($\alpha = 0.05$).

Attribute	Year	Rainbow Trout spawning areas	Steelhead spawning areas
Date of capture (SD)	2010	Sep 13 (2.6)	Sep 14 (3.6)
	2011	Sep 17 (8.1)	Sep 2 (25.0)
Total number of fry measured	2010	129	213
	2011	240	300
Geometric means of fry attributes (with 25%, 75% quartiles)			
Fry FL (mm)	2010	48.5 (41.8, 54.2)	50.4 (49.1, 52.1)
	2011	41.6 (41.5, 42.5)	43.7 (41.4, 43.7)
Fry density (fish/100 m^2)	2010*	11.6 (8.3, 23.9)	31.0 (24.5, 40.8)
	2011*	12.6 (10.8, 14.4)	25.8 (18.8, 30.8)

Steelhead in the Elwha River may have constructed smaller redds in larger gravel relative to steelhead in other studies because the dams had disrupted sediment transport, thereby reducing the supply of gravel to the lower Elwha River (Duda et al. 2008). As a result, substrate was generally larger in the lower Elwha River than in the undammed upper section (Kloehn et al. 2008). Therefore, the available habitat in our study area likely constrained steelhead to construct smaller redds in larger substrate than would otherwise typically be used. For instance, the mean *D*50 for Rainbow Trout redds (17.2 mm) in our study fell within previously reported ranges for steelhead (Cederholm and Salo 1979; Gallagher and Gallagher 2005), and our mean *D*50 value for steelhead redds overlapped the Rainbow Trout redd *D*50 values from other studies (range = 13.0–25.1 mm; Hartman and Galbraith 1970; Platts et al. 1979; Spoon 1985; Maddux et al. 1987; Zimmerman and Reeves 2000). This information suggests that redd substrate size is not always a reliable metric. Additionally, although Elwha River steelhead currently spawn in relatively large substrate, they may begin to excavate redds in smaller substrate as they colonize areas with a greater supply of

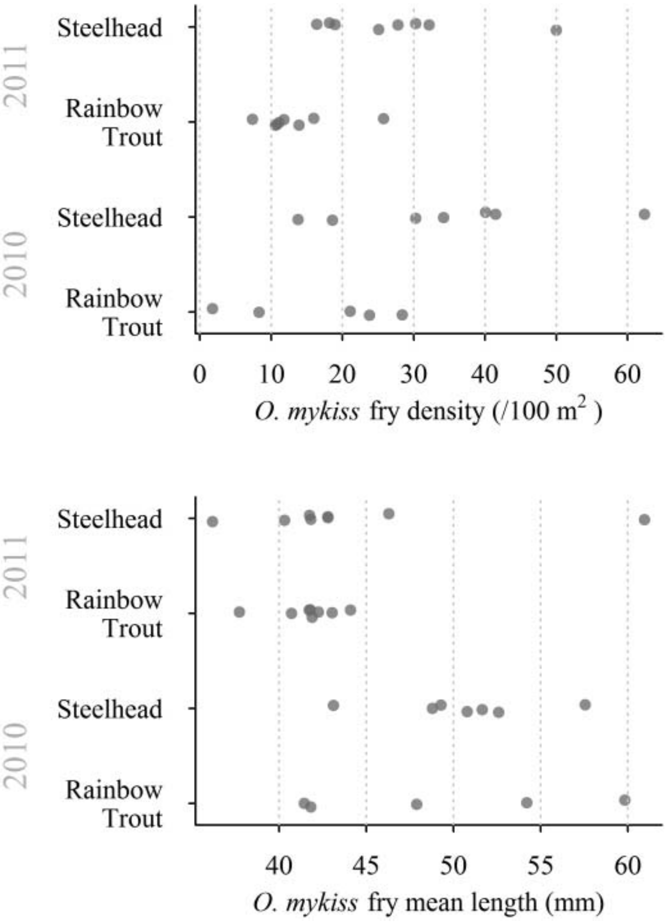

FIGURE 6. Density (number of fish/100 m^2) and mean FL (mm) of fry sampled from Rainbow Trout and steelhead spawning areas within the Elwha River during 2010 and 2011.

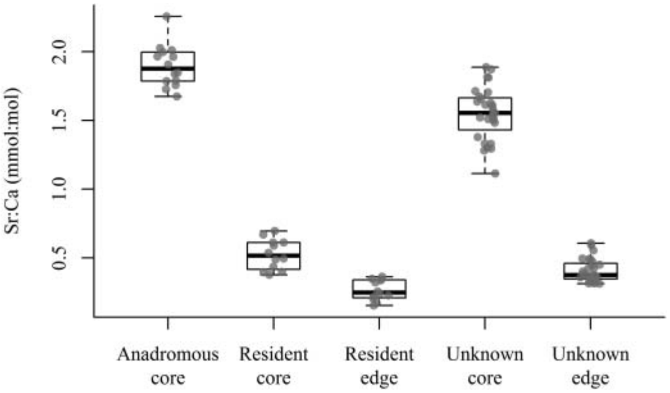

FIGURE 7. Box plot displaying Sr:Ca ratios in the otolith core and otolith edge for *Oncorhynchus mykiss* fry with known-anadromous (hatchery steelhead) mothers (Dungeness Fish Hatchery; anadromous core); fry with known-resident (Rainbow Trout) mothers (resident core and resident edge); and fry of unknown maternal origin ($n = 28$ fry; unknown core and unknown edge) collected from the Little River, Washington, during September 2012 and 2013 (i.e., the initial stages of steelhead recolonization).

spawnable substrate and as the sediment supply is restored to the lower section of the river. Such changes could lead to greater overlap in redd *D*50 values between life history forms. Indeed, since dam removal in the Elwha River, there has been substantial bed aggradation and the substrate size has decreased markedly in the middle and lower sections (East et al. 2015). As a result, the redd metrics we generated will require further testing to determine whether there are still differences in redd size and substrate size between steelhead and Rainbow Trout. We hypothesize that the same could be true for other dam removal projects.

Based on the aforementioned comparisons, we proffer three considerations for managers and scientists preparing to monitor postdam recolonization by steelhead and other anadromous salmonids. First, redd counts require good visibility within a stream (McMillan et al. 2012), so a reliance on counts may underestimate the extent of recolonization when visibility is reduced or poor. Second, redd size is likely a better indicator of life history than substrate size, as large fish can and do spawn in smaller substrate and likewise small fish can spawn in larger substrate. Third, the FLs of steelhead in our study were on average almost triple the FLs of Rainbow Trout, which is not necessarily representative of the two forms when sympatric. Among salmonids, differences in mean length between anadromous and resident forms seem to be greatest for Cutthroat Trout, Arctic Char *Salvelinus alpinus*, and Dolly Varden *Salvelinus malma*, followed by Brown Trout *Salmo trutta* (Gross 1987). On the other hand, differences in body size are less in (1) Brook Trout *Salvelinus fontinalis* because even anadromous individuals may be relatively small and (2) *O. mykiss* because steelhead and Rainbow Trout may mature at similar sizes depending on the population (Gross 1987). Consequently, the distinction in redd metrics for other *O. mykiss* populations or for other salmonid species may be greater or lesser than we observed based on body size, and applications to other dam removal projects should be formulated with local data.

Fry Size and Fry Density as Indicators of Life History

Steelhead tend to spawn earlier than Rainbow Trout within a given watershed (Zimmerman and Reeves 2000; McMillan et al. 2007), and larger anadromous salmonid females tend to produce larger and more numerous eggs (Beacham and Murray 1990; Wood and Foote 1996) than smaller resident females. Although we observed that fry in steelhead spawning areas were longer than fry in Rainbow Trout spawning areas, the difference was slight and nonsignificant. On the other hand, fry densities were significantly higher in steelhead spawning reaches than in Rainbow Trout spawning reaches. The range of fry densities we observed for both life history forms (0.2–62.1 fry/100 m^2) fell within the lower end of ranges previously reported for *O. mykiss* (10–300 fry/100 m^2; Bjornn and Reiser 1991; Roper et al. 1994; McMillan et al. 2013), and the lowest fry densities occurred in the Rainbow Trout spawning reaches.

We are unaware of other studies that have used fry densities to distinguish steelhead and Rainbow Trout as part of a dam removal project. However, in a study of Whitespotted Char *Salvelinus leucomaenis*, Morita et al. (2000) documented greater fry densities below a dam, where anadromous fish were present, than above the dam, where only resident fish existed. Higher fry densities have also been found in reaches where anadromous Brown Trout were present compared to reaches that contained only resident Brown Trout (Elliot 1994; Bohlin et al. 2001).

Fry densities likely reflect egg densities (Morita et al. 2000). Given the positive relationship between female FL and fecundity, individual steelhead can produce far more eggs than Rainbow Trout (Gross 1987). However, our study raised several concerns regarding the use of fry density to indicate steelhead presence. First, low densities of anadromous spawners during the initial stages of colonization may make differences harder to detect if fry density is a function of egg density (Morita et al. 2000). It may also be too time consuming and expensive for managers to sample enough reaches and enough fry to detect steelhead. Second, differences in body size and fecundity between life history forms vary among species (Gross 1987), making it more or less difficult to use fry density as a general indicator of life history type. Third, we sampled fry in mid-September because we wanted to allow time for all of the Rainbow Trout to emerge, but earlier sampling could have revealed much higher densities of steelhead fry (Lau 1994)—and presumably much lower densities of Rainbow Trout fry due to the later spawning by this life history form. Hence, the timing of sampling may influence both the size and density of fry and the difference between anadromous and resident forms. Lastly, sample timing can be a conservation concern if one form spawns considerably earlier than the other but the two forms spawn in similar locations (Zimmerman and Reeves 2000). If we had attempted to collect fry from earlier spawning individuals in the resident reaches, we would have encountered numerous spawning adults. Electrofishing can harm breeding individuals and their embryos (Cho et al. 2002), which is an important consideration when monitoring at-risk populations (Nielsen 1998).

The observed differences in density could help to explain the extensive overlap in fry FL despite the earlier spawning and presumably larger eggs of steelhead. Connolly and Brenkman (2008) sampled *O. mykiss* fry over two summers in similar habitats and found that fry grew faster in the upper Elwha River than in the middle section, which they interpreted as being related to higher densities in the middle section. Indeed, the growth of salmonids in streams can be density dependent (e.g., Keeley 2001; reviewed by Grant and Imre 2005). We did not find a correlation between fry density and fry FL, but sampling earlier in the summer, when fry can be more abundant, might have yielded such a correlation (Lau 1994).

Alternatively, the density effects on fry growth may have operated at more restricted spatial scales (e.g., 1 m to tens of meters) than we accounted for (Einum et al. 2011).

Other factors, such as water temperature (Railsback and Rose 1999), food supply (Benjamin et al. 2013), streamflow (Harvey et al. 2006), and depth (Harvey and Nakamoto 1997), may have influenced the growth of fry above the dams, at least in the habitats where we collected fish. These factors could have reduced any differences in fry FL between the life history forms. For example, we sampled several groundwater-fed floodplain channels and small tributaries (<15 m wide) above both dams. Those streams are generally narrower, shallower, warmer, and clearer than the glacially turbid main-stem Elwha River and the floodplain channels it directly sources, which are the dominant stream habitats below the dams (Pess et al. 2008). Salmonid fry can grow faster in small floodplain streams than in main-stem rivers (Jeffres et al. 2008), perhaps because warmer waters are more productive (Jeffres et al. 2008). The shallower habitats can also reduce competition with older age-classes (Harvey and Nakamoto 1997) and limit access by larger salmonid predators, thereby increasing the amount of time and energy available for foraging (Harvey 1991). Better habitat conditions for growth of Rainbow Trout fry above the dams combined with a negative influence of competitor density on the fry in the steelhead spawning areas may have thus outweighed the maternal benefits of egg size and earlier emergence. Whatever the reasons, fry FL could not be used to reliably distinguish between steelhead spawning areas and Rainbow Trout spawning areas.

Otolith Microchemistry and Maternal Origin of Fry

Consistent with prior research, we used Sr:Ca ratios in the otolith core to distinguish between fry of anadromous (steelhead) versus resident (Rainbow Trout) maternal origin (Volk et al. 2000; Zimmerman and Reeves 2000; Mills et al. 2012). Interestingly, all of the unknown-origin fry we collected from the Little River in 2012 and 2013 (i.e., during the initial stages of recolonization) were estimated to be the offspring of steelhead mothers. The absence of resident fry in the unknown-origin sample prevented us from testing whether fry size differed between life history types during the initial stages of recolonization, but the findings raised two issues. First, the size of unknown-origin fry was similar to that of both Rainbow Trout and steelhead prior to dam removal, providing further evidence that fry size is not a reliable indicator of steelhead spawning. Second, the result suggests that soon after recolonizing one stream, steelhead females were potentially producing the numerically dominant form of fry. If this pace of recolonization continues, the proportion of Rainbow Trout in the system may decline markedly, underscoring the importance of monitoring the transitional periods during and soon after dam removal.

Conclusions

The removal of large dams is very costly, and managers are tasked with monitoring the response of species that may display anadromous and resident forms (e.g., *O. mykiss*). Estimating the return on investment in large-scale habitat projects is challenging in such situations because (1) river conditions that occur after dam removal may hinder monitoring efforts and (2) reduced numbers of fish may make them difficult to directly observe, particularly for fish like steelhead, which are less commonly found on their redds during daytime (McMillan et al. 2007). Our results indicate that measurements of redd size and redd substrate could be important tools for distinguishing the presence of steelhead from that of Rainbow Trout in newly accessible habitats above dams. Fry density was also higher in steelhead spawning areas than in Rainbow Trout spawning areas, but it seems less likely that density alone could be used by managers to determine the extent of steelhead recolonization and distribution. For situations in which redds cannot be observed and fry densities are low, otolith microchemistry may be necessary to detect the presence of steelhead. Perhaps the best approach is thus to use the metrics as complementary tools: potential steelhead spawning reaches are initially identified by using redd surveys and measurements, and those areas are re-evaluated later based on fry sampling and otolith collection to test assumptions about the presence of spawning steelhead.

Although the metrics we examined were useful for application to *O. mykiss* in the Elwha River, managers should remember that the efficacy with which redd and fry density metrics can distinguish steelhead presence will depend on the size differences between the life history forms and on habitat-specific features. Furthermore, metrics and assumptions that are valid prior to dam removal may change in the postremoval period as steelhead access a greater range of substrate sizes and have increased interactions with Rainbow Trout. Consequently, the future use of redd attributes and fry density to predict the presence of steelhead is more likely to succeed if the data are tailored to populations before and after dam removal.

ACKNOWLEDGMENTS

We thank Keith Denton (National Oceanic and Atmospheric Administration [NOAA], Northwest Fisheries Science Center [NWFSC]), Todd Bennett (NOAA, NWFSC), and Raymond Moses (Lower Elwha Klallam Tribe) for help in collecting and measuring fish; Matt Sloat for discussions, reviews, and suggestions during the early stages of the research; Alex Stefankiv (NOAA, NWFSC) for creating Figure 1; and Sam Brenkman and Pat Crain (Olympic National Park) for sharing their data and observations on Rainbow Trout and steelhead in the Elwha River. We especially thank Andrew Claiborne and Anna Hildebrandt (Washington Department of Fish and Wildlife, Fish Aging Laboratory) for otolith sample preparation and chemical analysis. We are grateful to Polly Hicks

(NOAA, NWFSC) for funding support for J.R.M. Funding was partly provided through a grant to T.P.Q. from Washington Sea Grant, University of Washington (NOAA Award Number NA10OAR4170075, Project R/LME-7). We also thank Jim Myers, Krista Nichols, Phil Roni (NOAA, NWFSC), and anonymous reviewers for suggestions that improved the manuscript. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

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