

FEATURE

Does River Restoration Increase Fish Abundance and Survival or Concentrate Fish? The Effects of Project Scale, Location, and Fish Life History



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Despite billions of dollars spent on various river restoration techniques, we still find ourselves debating whether habitat restoration increases fish abundance or concentrates fish. Based on the available literature, I discuss three important questions related specifically to the restoration of salmonid habitat: (1) “Does river restoration increase fish abundance or concentrate fish?”; (2) “Does river restoration increase fish survival or increase abundance?”; and (3) “Does the size or amount of river restoration influence fish response?” First, there is scant evidence to support the contention that river restoration leads to the concentration of fish at restoration projects. Second, the literature suggests that river restoration may lead to increased survival, increased abundance, or both. Third, recent studies have found little relationship between restoration project length and physical or biological response. The scientific literature does suggest that fish response to restoration varies greatly depending on the watershed template, location, and characteristics of the habitat restoration, and the life history of and limiting factors for a species. Thus, adequately determining whether changes in fish abundance observed in a restored area are due to increased movement, survival, or the amount of restoration will require detailed monitoring of these factors simultaneously.

River restoration is one of the oldest forms of modern ecological restoration, with early efforts dating back at least 100 years or more (Thompson and Stull 2002; White 2002; Roni and Beechie 2013). Modern river restoration comprises a suite of different types of habitat improvement activities, including placement of instream structures; re-meandering of straightened channels; removal of levees or bank armoring; re-connecting or creation of side channels, ponds, and other off-channel habitats; and riparian replanting. Most early river restoration efforts focused on increasing instream structure through placement of log and boulder structures (Figure 1), bank stabilization, and replanting of riparian vegetation. Despite the economic investment, long history, and volumes of literature on river restoration, there remains considerable uncertainty about its biological effectiveness (Roni et al. 2015). Historically, this has been attributed to poor or limited effectiveness monitoring for many restoration techniques (Bernhardt et al. 2005). Even for techniques like instream restoration (e.g., placement of logs, boulders, and gravel) that have been well studied, there is continued discussion about their effectiveness at increasing fish numbers (Roni et al. 2015). Most studies on instream or floodplain habitat restoration have shown increases in juvenile salmonids at the reach scale (Whiteway et al. 2010; see Roni et al. 2008a, 2014 for a detailed review); however, questions about fish movement, survival, and the appropriate scale of restoration are commonly debated. In particular, three key questions continue to be discussed regarding fish response to river restoration: (1) “Does restoration increase fish abundance or concentrate fish?”; (2) “Does

restoration increase fish abundance, survival, or both?”; and (3) “Does the size or amount of river restoration influence fish response?” These questions are related, as increased fish numbers within a restored reach could be the result of immigration, increased survival, or increased capacity of a reach to support fish (Figure 2). Thus, restoration changes the habitat carrying capacity through modification in the quantity or quality of habitat that, in turn, influences fish movement and survival and ultimately determines fish abundance. Moreover, the size (scale) and amount of a restoration project play a role not only in the physical response but also more importantly in fish population processes, such as movement, recruitment, and survival.

The question of whether restoration actions attract and concentrate fish or lead to increased fish numbers is likely as old as river restoration itself, with early studies noting this and attempting to tag fish to answer this question (e.g., Shetter et al. 1949; Jester and McKirdy 1966). Although this question has been debated for many years, the listing of several species of salmon and trout as threatened or endangered under the Endangered Species Act, coupled with efforts to recover these species, has recently put a strong emphasis on improving survival (UCSRB 2007; NMFS 2008, 2009; U.S. Office of the Federal Register 2016). Finally, the size of restoration projects has become increasingly important, as the total amount (number of projects and their length and area) and scale (size of individual projects) of restoration have accelerated in recent years (Roni et al. 2010; Schmutz et al. 2016).

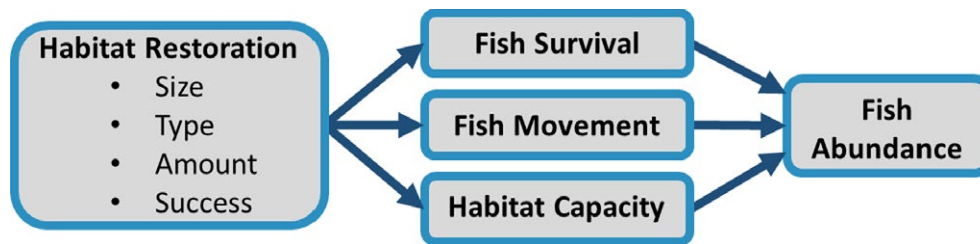
To address the three questions posed in this paper, the literature and the evidence are reviewed to provide guidance for future river restoration efforts and studies on restoration effectiveness for salmonids and other fishes. Literature from previous systematic reviews of restoration effectiveness (Roni et al. 2002, 2008a, 2014) is used to examine the relevant evidence and shed light on these questions. The resulting information is placed in the context of other studies on movement, survival, and restoration size to provide recommendations for future research. Much of this literature is on instream habitat improvement (e.g., large wood, boulder, and gravel placement), as it is arguably the oldest, most widespread, and most evaluated river habitat restoration technique (Roni and Beechie 2013), but other restoration techniques (e.g., channel re-meandering, levee setback, and side channel connection and creation) elicit similar physical and biological responses.

DOES RIVER RESTORATION INCREASE FISH ABUNDANCE OR CONCENTRATE FISH?

While many studies on instream and other river restoration techniques have shown localized (reach-scale) increases in salmonid abundance, the question of whether river restoration



Figure 1. Biologists snorkeling nearby placed large wood for the purposes of examining fish use and estimating fish abundance.



Survival	Movement (Immigration)	Habitat Carrying Capacity	Change in Fish Abundance
Increase	Increase	Increase	Increase
Increase	Increase	No Change	Increase
Increase	No Change	Increase	Increase
Increase	No Change	No Change	Increase
No Change	Increase	Increase	Increase
No Change	Increase	No Change	Increase
No Change	No Change	Increase	Increase
No Change	No Change	No Change	No Change

Figure 2. Relationships between the characteristics of a habitat restoration project and its influence on habitat carrying capacity, fish movement and survival, and, ultimately, fish abundance in the restored area (flow chart). The lower panel shows potential combinations of increases in survival, movement (immigration), and habitat carrying capacity that can lead to an increase in fish abundance in the restored reach (or section).

leads to increased abundance or concentrates fish has been debated for decades (Shetter et al. 1949; Latta 1972; Reeves and Roelofs 1982; Naslund 1989; Gowan et al. 1994; Roni et al. 2008a). This is also a topic of considerable debate with regard to the lacustrine and marine environment, where artificial reefs are rapidly colonized by fish (Bassett 1994; Bohnsack et al. 1997; Lindberg 1997) and fish aggregation structures are well-known fish attraction devices (Higashi 1994). In the riverine environment, it is a less-obvious question, as most river restoration in North America is focused on coldwater streams inhabited by salmonids that are often relatively short-lived (i.e., 3–5 years) compared to some marine fishes, which may be more than 20 years old. Thus, in the freshwater environment, attracting short-lived fish from other areas would presumably lead to short-term vacancy of habitat rather than long-term vacancy, such as in the marine environment. To answer the question of whether restoration concentrates fish or leads to increased abundance, I first examined the literature on fish movement and then examined the studies that specifically attempted to determine whether river restoration increased fish abundance or concentrated the fish.

The literature on movement of stream fishes—and resident salmonids in particular—is extensive, dating back decades (Gowan et al. 1994; Kahler and Quinn 1998; Rodriguez 2002). Most of the literature on the movement of stream fishes prior to 1990 indicated that resident trout and juvenile salmon moved only short distances during low-flow periods (Gowan et al. 1994; Rodriguez 2002). Gowan et al. (1994) demonstrated that many of these earlier studies on fish movement were flawed, as they focused only on fish that were recaptured in a short stream reach (i.e., a few hundred meters) and ignored fish that were not recaptured. Moreover, studies on a handful of small streams in Colorado indicated that increased adult trout numbers were the result of fish movement into restored areas rather than improved growth or survival (Riley et al. 1992; Gowan et al. 1994; Riley and Fausch 1995). This suggests that smaller, younger, or less-dominant fish moved

into vacated habitats; however, it still strongly suggested that short-term increases in trout numbers were due to movement. Thompson (2006) also demonstrated that early studies showing positive trout response to restoration had overlooked fish movement into the study area and increased fishing pressure. These studies renewed questions about whether river restoration increases fish numbers or concentrates fish. Despite this, many subsequent studies indicated that most juvenile anadromous fish and juvenile and resident trout moved short distances (<100 m)—at least during low-flow periods (Kahler et al. 2001; Rodriguez 2002). In an in-depth review of literature on the movement of resident trout and in an analysis and model that included not only movement but also replacement and turnover, Rodriguez (2002) reported that restricted movement is the norm in populations of stream salmonids during nonmigratory periods. Rodriguez (2002) did not, however, specifically examine fish movement and concentration related to habitat restoration.

Several authors have contended that the increased abundance versus concentration debate is a non-issue for most salmonids because they are short-lived, and concentration or immigration would only occur in the first few years of the project as vacated habitats are colonized by younger fish (Reeves and Roelofs 1982; Naslund 1989; Reeves et al. 1991). This assumes that fry or recruits exceed habitat carrying capacity, which is often the case (Naslund 1989; Lehane et al. 2002). This is particularly relevant for anadromous or adfluvial salmon and trout, which have a high fecundity and produce a new cohort each year that would rapidly colonize vacated habitats, with juveniles typically spending 2 years or less in freshwater prior to seaward migration (Reeves and Roelofs 1982; Reeves et al. 1991; Roni et al. 2008a, 2015).

Previous comprehensive literature reviews located more than 400 papers pertaining to the effectiveness of various river restoration techniques (Roni et al. 2008a, 2014, 2015). I updated these reviews by using a systematic search of Google Scholar, Web of Science, and other databases and more than

40 combinations of keywords related to river restoration, resulting in more than 600 papers on river restoration effectiveness. These papers were reviewed to find studies that specifically examined fish movement in relation to river or floodplain habitat restoration or improvement. Removal of barriers and restoration of streamflow, which are typically designed to reconnect isolated habitats and encourage movement of fishes, were not examined.

In my review of studies that attempted to determine whether river restoration increases fish abundance or concentrates fish, 20 papers reported on movement of fish, and only 10 papers from 9 different studies reported on whether increased fish numbers were due to attracting the fish (Table 1). For example, Slaney et al. (1994), Riley and Fausch (1995), Gowan and Fausch (1996a), and Quinn and Kwak (2000) examined fish response anywhere from 1 to 6 years postrestoration and reported that increased numbers were due to the immigration of fish into restored areas. In contrast, Shetter et al. (1949), Naslund (1989), Roni and Quinn (2001b), and Lehane et al. (2002) examined fish response 1–5 years postrestoration and found little evidence that increased salmonid numbers were due to the movement of fish into restored reaches from other nearby areas. Those authors suggested that the increased fish numbers were due to increased habitat capacity to support fish (increase in area or quality) or increased survival at younger life stages. Another study examined the effects of livestock exclusion (riparian fencing) on trout numbers and found that increases in adult Brown Trout *Salmo trutta* were

due to both increased production (survival) and immigration from unfenced areas (Summers et al. 2008). Latta (1972) similarly indicated that increased numbers of trout in reaches with instream structures were due to both immigration and increased habitat carrying capacity, suggesting increased survival. It should be noted that these studies examined different species and, although they all used marked fish, they varied in study design, sample size, and scientific rigor. One of the more thorough evaluations of log structures and fish movement in six Colorado alpine streams found that in the first 5–6 years after restoration, increases in adult trout abundance were in part due to immigration into the restored reaches (Gowan and Fausch 1996a). However, a follow-up study at the same sites 20 years later found that the restored reaches had higher numbers of adult trout and suggested that this long-term response of adult trout demonstrated increased production rather than immigration (White et al. 2011).

All of the examined studies except Slaney et al. (1994) focused on marking fish, although there are other ways of determining whether increased abundance is simply due to movement. For example, Frissell and Ralph (1998) proposed an approach that coupled collecting data on restored and adjacent unrestored areas and the age structure of salmonids to help determine whether increases in fish numbers in the restored area were simply due to movement from unrestored areas: if similar age structures of fish are found in treatment and control reaches before and after restoration, then this demonstrates increased abundance. Frissell and Ralph (1998)

Table 1. Summary of results from papers on river restoration effectiveness that examined both fish movement and abundance.

Reference	Summary of findings
Shetter et al. 1949	Reported increased Brook Trout <i>Salvelinus fontinalis</i> abundance after placement of log deflectors in a Michigan stream. Marked fish, both in the treatment and adjacent control sections, exhibited little movement between reaches. Concluded that the increase in fish numbers was because of increased survival.
Saunders and Smith 1962	Increased numbers of Brook Trout after restoration (log weirs and deflectors) in a Prince Edward Island stream. Before restoration, 57–66% of Brook Trout in the reach were immigrants from upstream reaches; after restoration, 45% were immigrants from other reaches. Suggested that the increases were not due to immigration but to increased survival or abundance.
Latta 1972	Examined Brook Trout and Brown Trout <i>Salmo trutta</i> response to placement of log structures and found considerable movement among five study reaches. Reported increased fish numbers in the one treatment reach and attributed the increase to both migration and increased survival.
Naslund 1989	Examined Brown Trout response to boulder dams, log deflectors, and other structures in a Swedish stream. Reported increased fish numbers in the treatment reach; 80% of tagged fish were recovered in the same reach, and most (92%) moved less than 100 m. Suggested that increased numbers were due to increased survival rather than to immigration.
Slaney et al. 1994	Monthly examination of Chinook Salmon <i>Oncorhynchus tshawytscha</i> fry colonization of large woody debris (LWD) structures found higher colonization and densities of fry at structures than in other areas.
Riley and Fausch 1995; Gowan and Fausch 1996a, 1996b	Examined trout response to placement of artificial log structures in six Colorado streams and reported that increased abundance of adult trout in restored reaches was due to immigration.
Quinn and Kwak 2000	Examined Rainbow Trout <i>O. mykiss</i> and Brown Trout response to log and rock structures in an Arkansas river. Reported that increased trout numbers in the restored area was mainly due to immigration, although restoration increased habitat carrying capacity.
Roni and Quinn 2001b	Examined movement of juvenile steelhead, Coho Salmon <i>O. kisutch</i> , and Cutthroat Trout <i>O. clarkii</i> between treatment (restored) and control reaches in a Washington stream. Reported little movement of fish between treatment and control reaches, but a rapid decline in marked fish within both the treatment and control reaches during late fall suggested that movement occurred at a much broader scale than study reaches.
Lehane et al. 2002	Reported increased Brown Trout density and biomass in areas with LWD structures within an Irish stream. The proportion of marked fish that were recaptured did not differ between sections with and without LWD structures in spring or fall, suggesting that increased abundance was not due to immigration.
Summers et al. 2008	Reported Brown Trout response to riparian fencing and some pool excavation in England. Control reach densities stayed low and consistent throughout the study, while treatment reaches saw large increases. Ninety percent of recaptures in the treatment reaches were in the same location (90/102), while only 1 of 15 recaptures in control reaches was in the same location. Authors concluded that increased abundance in treatment reaches was due to both increased production and immigration.

provided a hypothetical graphical example, but they did not have data to demonstrate their approach. Polivka et al. (2015) used a similar approach, comparing densities of fish in restored and unrestored pools at multiple times throughout summer to demonstrate that increased juvenile steelhead (anadromous Rainbow Trout *Oncorhynchus mykiss*) abundance was likely the result of increased habitat carrying capacity rather than concentration of fish. While not specifically measured, Polivka et al. (2015) suggested that the lack of movement from non-restored pools implied that increased recruitment and survival accounted for the observed increase in abundance.

Successful restoration is often dependent upon restoring habitats needed for the entire life history of single or multiple species, and studies focusing on movement within a reach may overlook seasonal migrations. For example, salmonid spawning areas often are not located near rearing habitats, and seeding of rearing areas in both restored and unrestored reaches is dependent on redistribution of fry and parr to suitable habitats and the connectivity of those habitats (Kennedy et al. 2014). Of course, if restoration improves spawning habitat, then the colonization of restored habitat by fry from distant spawning areas may only happen in the first few years after restoration, assuming that adequate fry are produced within the newly restored area. However, it is important to consider the life history of the fish in question when examining movements to or from restored areas in a watershed.

Some restoration efforts, such as removal of barriers and increasing instream flows, are designed to increase fish movement, redistribution, and colonization of restored habitat (Zitek and Schmutz 2004; Pierce et al. 2013, 2014). Studies of fish movements after barrier removal or increases in instream flows show rapid fish colonization of newly accessible habitats and the success of these projects (Roni et al. 2008a). Although such studies do not typically address whether increased fish numbers are a result of fish movement and colonization or increased abundance, they do emphasize the role habitat connectivity can play in the response of fish to restoration actions and movement among restored and unrestored habitats.

There is evidence that placement of large woody debris (LWD) may reduce the distances typically moved by juvenile anadromous salmonids (Jester and McKirdy 1966; Roni and Quinn 2001b) and may reduce the number of fish that emigrate from a site over time (summer to fall, or fall to spring) in search of suitable fall or winter rearing habitat (Lehane et al. 2002). For example, a study in constructed side channels found that the addition of LWD led to lower Coho Salmon *O. kisutch* emigration and higher overwinter survival than in sections of channel without LWD (Giannico and Hinch 2003). This is supported by work in unaltered streams, which found that fish moved shorter distances in habitats with abundant wood cover than in habitats with little wood cover (e.g., Bjornn 1971; Wilzbach 1985; Heggenes et al. 1991; Harvey et al. 1999). In addition, instream structures, such as log weirs, can inhibit the natural movement of fishes, but this appears to be limited to instances in which artificial weirs create potential migration barriers that exceed the height that juvenile or adult trout can ascend (Rinne 1982). Obviously, many natural wood accumulations, such as logjams or beaver dams, can influence fish movements, but artificial habitat structures that potentially limit fish movement and migration should not be part of stream habitat restoration projects.

When discussing whether river restoration concentrates fish or increases their abundance, it is important to consider

the type of movement or migration and the temporal frequency of those movements (Figure 3). The scale of localized movements, home ranges, larger seasonal migrations to rearing habitat, spring smolt out-migration (for anadromous fishes), and adult spawning migrations differs from tens of meters to hundreds of kilometers (Northcote 1992; Quinn 2005; Jonsson and Jonsson 2011). Moreover, some movements occur daily or over the course of weeks, whereas others are one-time seasonal migrations. Obviously, adult salmonids migrate long distances to upstream spawning areas, and their progeny migrate long distances downstream to rear and mature in riverine, marine, or lacustrine environments (Groot and Margolis 1991; Quinn 2005). Juvenile salmonids often move only short distances during low-flow periods, but they may migrate long distances to reach overwinter habitats (Northcote 1992; Quinn 2005), and large-scale movements (i.e., reach or watershed scale) of juvenile salmonids in streams to overwintering habitats have been well documented (Cederholm and Scarlett 1982; Peterson 1982; Bendock 1989). Naslund (1989) examined the response of native Brown Trout to restored and unrestored reaches throughout a watershed and indicated that all study reaches were dependent on fry colonization from upstream spawning areas. More recent evidence from PIT tagging studies shows that juvenile salmonids move long distances or emigrate out of watersheds or subwatersheds in fall or winter (Achord et al. 2012; Roni et al. 2012; Ibbotson et al. 2013). Conversely, Roni and Quinn (2001b) found little exchange of fish between restored and unrestored reaches, although a large portion of fish moved out of the study area altogether, likely as part of larger seasonal migrations. Migrations to seasonal rearing habitat or spawning habitat are at a scale (i.e., several kilometers) that is broader than the scale of most restoration projects (hundreds to thousands of meters) and thus are unlikely to lead to a concentration of fish in restored reaches at the expense of unrestored reaches (Figure 3). Presumably, habitat restoration that specifically targets improving some of these seasonal habitats would lead to some fish migrating shorter distances. However, little evidence is currently available to support this presumption. The question of concentration versus increased abundance is therefore most appropriate

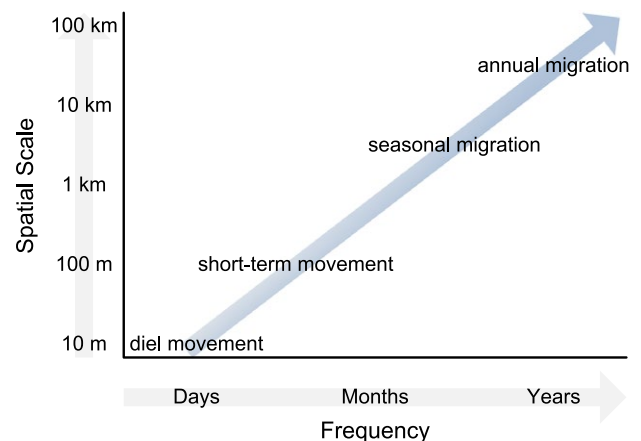


Figure 3. Approximate spatial scale and temporal frequency of movement by salmonid fishes based on the available literature on salmonid movements. Because restoration typically occurs at a reach scale, it is likely that only movements at that scale could lead to a concentration of fish in those areas at the expense of nearby unrestored areas.

at the reach scale over a period of days to weeks. As previously noted, most of the literature on the movement of salmonids—particularly at low flows during summer and winter—has indicated that most fish move less than 50 or 100 m (Rodriguez 2002; Schmetterling and Adams 2004). The frequency and duration of local movements have not been well studied, but they are believed to range from days to weeks, with diel movements within an individual habitat unit or reach being common for many salmonids and other species, particularly during winter months (Shuler et al. 1994; Jakober et al. 2000; Roni and Fayram 2000). This would suggest that if any concentration of fish occurs, it is generally limited to fish emigrating from areas that are immediately adjacent to restored areas. Moreover, it suggests that fish demonstrate a preference for the restored habitat, likely due to improved cover, favorable velocities, food, or other factors.

DOES RIVER RESTORATION INCREASE FISH SURVIVAL OR INCREASE ABUNDANCE?

River restoration can increase fish numbers by increasing habitat carrying capacity (number of fish that the habitat can support), survival, or some combination of habitat carrying capacity and survival. For example, if juvenile steelhead numbers do not increase after restoration, fish in the restored reach may receive some benefit in fitness from the improved habitat and therefore have increased overwinter or smolt-to-adult survival once they emigrate from the restored reach. Although there is increased emphasis on measuring and increasing fish survival through river restoration and although new tagging and monitoring techniques make it easier to measure survival now than a decade ago, survival has not been frequently measured or used to assess restoration effectiveness. There are many reasons for this, including the cost associated with tagging and recapturing large numbers of fish or, in the case of spawning adults, the difficulty in measuring egg-to-fry survival (Johnson et al. 2012). However, the question remains: does river restoration increase juvenile salmonid survival?

I examined a total of 21 papers that specifically investigated whether instream or floodplain restoration affected salmonid survival (Table 2). Five studies looked at egg-to-fry survival for various species (Chinook Salmon *O. tshawytscha*, Pink Salmon *O. gorbuscha*, and Brown Trout) and showed improved survival after gravel addition, gravel cleaning, or LWD or boulder addition (Table 2). Of the remaining studies, 11 reported increases in survival, while the others reported no change or only reported what survival was after restoration (Table 2). To answer the question of whether restoration increases survival or abundance requires measuring both; only seven studies reported changes in both survival and abundance. Riley and Fausch (1995) and Gowan and Fausch (1996a), two papers based on the same data, found limited changes in resident trout survival after restoration and attributed the increases in abundance to immigration rather than increased survival. Pulg et al. (2013) reported short-term increases in Brown Trout embryo and fry densities after gravel cleaning to restore spawning habitat. Both Solazzi et al. (2000) and Giannico and Hinch (2003) reported increased abundance and survival of juvenile Coho Salmon after LWD addition and off-channel habitat construction. In contrast, Johnson et al. (2005) did see some changes in survival and abundance for steelhead and Coho Salmon, but due to study design limitations, these changes could not be attributed to restoration (LWD placement). In probably the most rigorous

of the studies examined, Bouwes et al. (2016) showed that addition of artificial beaver dams increased both the survival and density of juvenile steelhead.

Although it is hard to draw firm conclusions from existing studies because so few have examined both survival and abundance, it appears that river restoration can lead to increases in both. In some cases, an increase in total fish numbers may be the result of simply adding habitat capacity by increasing either the area (quantity) or quality of habitat (Lepori et al. 2005). In fact, a common error in examining monitoring data from restoration projects that increase the area of habitat (e.g., pool area) is to look at fish densities per meter squared before and after restoration. Fish densities might remain the same, but because the total area has increased, there are now more fish in the restored reach. Similarly, if the quality of habitat is improved by increasing the proportion of a reach or stream that is in pools, increasing cover or food resources, or reducing predation, one might see an increase in the overall density of fish (fish/m²). If there are more fish using restored habitat and little change in the number of fish using unrestored habitat, it suggests that even if some of these fish moved into the restored area, there must be increased survival at some point in the life cycle. This is most easily seen with increased egg-to-fry survival leading to increased fry densities (Pulg et al. 2013). Increased survival at other life stages would require confirmation by intensive tracking of survival and movement at each life stage across a broad area. However, it is unclear whether restoration leads to increased abundance through (1) immigration or production within a reach, (2) increased survival, or (3) a combination of these factors; all are plausible based on the available literature. Because most of the literature is based on placement of LWD or instream structure, it is also unclear whether certain restoration techniques increase survival more than others (Table 2).

DOES THE SIZE OR AMOUNT OF RIVER RESTORATION INFLUENCE FISH RESPONSE?

The optimal size or footprint of river restoration is a subject that has been receiving increased attention (e.g., Hering et al. 2015; Schmutz et al. 2016). Do the size and amount of habitat restoration matter? This question can be divided into three related issues: the size or area restored in a given reach, the amount by which the quality (e.g., cover and complexity) of the habitat is increased, and the total amount of habitat that is restored in a watershed. All of these issues are related to fish movement and survival, as the size, quality, and amount of restoration presumably will influence fish movement and survival.

The first issue is whether larger projects produce proportionally larger increases in fish numbers per unit area or length than smaller projects. This is an important aspect, as there is concern that the length of a restoration project is not adequate to allow full geomorphic processes to occur or that biota may not respond fully until enough high-quality habitat is created (Pope et al. 2016; Schmutz et al. 2016). One would assume that larger projects would produce more fish by simply creating or improving more habitat. However, rather than a simple linear response, fish numbers may not increase until a certain length of stream is restored, or instead they may increase exponentially with the length of stream restored. Because geomorphic processes, water quality, and viable population size for biota are all related to stream area or length, it is assumed that there is a positive relationship between river restoration

Table 2. Summary of results from papers on river restoration effectiveness that examined fish survival, and a description of whether each paper reported increases in both survival and abundance (density).

Reference	Treatment and location	Key survival results
Gard 1961	Large woody debris (LWD) and boulder structures in California	During the three summers after dam installation, the numbers of introduced Brook Trout were counted. Forty-nine trout were collected during the second summer, yielding a 1-year survival rate of 38%. Seventy-three percent of the fish surviving to the second summer were collected during the third summer, and 39% of those surviving to the third summer lived to the fourth summer. No data on density were reported.
Saunders and Smith 1962	Log weirs and deflectors on Prince Edward Island	Increased numbers of Brook Trout after restoration (log weirs and deflectors). Significant increase in fingerling survival to age 1 (from 27% to 77%) was observed after placement of instream structures.
Jester and McKirdy 1966	LWD and boulder structures in New Mexico	Trout overwinter survival was enhanced by the presence of structures. No data on density were reported.
Cederholm et al. 1988; Cederholm and Peterson 1989	Constructed floodplain habitat in Washington	Overwinter survival and growth of Coho Salmon increased significantly after construction (survival increased from 11% to 56%; mean change in length from 13 to 41 mm; mean change in weight from 3 to 13 g). Limited information was given on fish numbers and no indication of whether they increased.
Klassen and Northcote 1988	Rock structures (gabions) in British Columbia	Pink Salmon <i>Oncorhynchus gorbuscha</i> egg survival at one site in its first year did not differ significantly from survival at two nearby reference sites. No data on density were provided.
Raastad et al. 1993	Constructed side channel in Norway	Survival of age-1 and older (age-1 +) Atlantic Salmon <i>Salmo salar</i> was 30%. No data on density or capacity were reported.
Lonzarich and Quinn 1995	LWD additions in Washington	Coho Salmon survival was greatest in the deep, structured treatment (89%), nearly twice that in the shallow, nonstructured treatment (47%). Both age-0 and age-1 + steelhead showed higher survival in the deep, structured treatment (71% and 89%, respectively) than in the shallow, nonstructured treatment (29% and 33%, respectively). Authors did not examine density.
Riley and Fausch 1995	LWD structures in Colorado	Recaptures of tagged trout in two streams showed that the logs did not result in increased growth or survival of resident trout, although recaptures of fin-clipped trout in other streams suggested that apparent survival may have increased temporarily in treatment sections. Number of age-2 + trout did increase after treatment.
Gowan and Fausch 1996a	LWD additions in Colorado	Recaptures of tagged trout and batch-marked trout revealed that immigration was primarily responsible for increased adult abundance and biomass, whereas no biologically significant differences occurred for recruitment, survival, or growth.
Solazzi et al. 2000	LWD additions in Oregon	Overwinter survival of Coho Salmon increased from a mean of 13% to 38% in one treatment stream (survival in the control was 0.17–0.20%). In another treatment stream, mean overwinter survival increased by 250% (i.e., from 11% to 39%), whereas survival in the control stream fell from 19% to 10%. Densities of Coho Salmon parr increased in treatment streams.
Sommer et al. 2001	Levee removal in California	Survival indices for coded-wire-tagged Chinook Salmon were somewhat higher for those released in the floodplain than for those released in the river, but the differences were not statistically significant. No data on density were provided.
Giannico and Hinch 2003	LWD additions in British Columbia	Although the values of the relative index of survival for juvenile Coho Salmon varied widely between both side channels and from year to year, they were consistently higher in the LWD-treated side. Capacity (Coho Salmon numbers) also increased with the addition of LWD.
Merz et al. 2004	Gravel additions in California	Chinook Salmon embryos that were planted in enhanced gravels had higher rates of survival to the swim-up stage than embryos planted in unenhanced spawning gravels.
Johnson et al. 2005	LWD additions in Oregon	Steelhead smolt abundance, steelhead freshwater survival, and Coho Salmon freshwater survival increased in one creek after the input of LWD, but similar results were found in the reference stream.
Paulsen and Fisher 2005	Various restoration measures in Idaho	There was a significant positive correlation between the number of habitat actions in a basin and Chinook Salmon parr-to-smolt survival. No data on density were reported.
Henning et al. 2006	Reconnection and enhancement of wetlands in Washington	Specific growth rate and minimum estimates of survival for yearling Coho Salmon in enhanced wetlands (1.43%/d by weight and 30%; 1.37%/d and 57%) were comparable to those in other side channel rearing studies (survival was not estimated in unenhanced wetlands). Enhanced wetlands had significantly higher juvenile Coho Salmon abundance than unenhanced wetlands.
Palm et al. 2007	Boulder and gravel addition in northern Sweden	Brown Trout egg-to-fry survival was significantly higher in the boulder-plus-gravel section ($10.3 \pm 2.6\%$; mean \pm SE) compared to the boulder-only section ($1.7 \pm 1.1\%$; mean \pm SE).
Pulg et al. 2013	Gravel cleaning in Germany	In the first 2 years of the study, highly suitable conditions were maintained, with a potential Brown Trout egg survival rate of more than 50%. Increased egg-to-fry survival resulted in increased densities of fry. In the last 2 years of the study, egg survival decreased to less than 50%.
Michel et al. 2014	Log weirs in Switzerland	Brown Trout embryo survival to emergence was negatively correlated with distance from log weirs, with redds closer to weirs having higher survival (no control sites were sampled). No data on density were reported.
Bouwes et al. 2016	Beaver dam analogs (artificial beaver dams) in Oregon	Juvenile steelhead survival (overwinter) increased by 52% relative to that in the control stream. Density also increased in the treatment stream relative to the control stream.

project size and physical, chemical, and biological responses (Kail and Hering 2009; Hering et al. 2015). However, only a few studies have directly examined this subject. Most of these were recent European studies that specifically compared short and long river restoration (instream and floodplain restoration) projects and examined a variety of fish species, including salmonids (Table 3). Hering et al. (2015) investigated a suite of physical and biological metrics for two paired short and long reaches and found a difference in fish response (abundance) between short and long river restoration projects. Schmutz et al. (2016) looked at 15 paired short and long reaches; they found a larger response by small rheophilic fishes in longer compared to shorter reaches, but they observed no difference for other fishes or in fish species diversity. However, because restoration of short reaches (<1 km) is often not sufficient to allow for dynamic rejuvenation of a variety of habitat types or to provide habitat for all life stages, Schmutz et al. (2016) recommended that restoration should focus on dynamic, self-sustaining habitat improvement over several kilometers. In studies examining 24 and 62 European river restoration projects, respectively, Haase et al. (2013) and Thomas et al. (2015) found no correlation between a project's linear length and fish response or fish community composition. Muhar et al. (2016) synthesized the results of these and other European studies and concluded that restoration response did not increase with project size. Similarly, in a meta-analysis of river restoration on the Danube River, Austria, Schmutz et al. (2014) found that the number and density of rheophilic fishes were positively correlated with linear restoration length, but they observed no such relationship for eurytopic fish species. Their

analysis also looked at a variety of restoration measures and concluded that regardless of the type of restoration measure implemented (e.g., gravel bars, instream structures, or reconnected side channels), length was not an important factor in project success until a project was longer than 4 km. Sweka et al. (2010) found no effect of the length of restoration (LWD placement) on Brook Trout *Salvelinus fontinalis* response to restoration.

Although this literature review focuses on fish response, no relationship between the level of biotic response and restoration project size has been reported for macroinvertebrates, aquatic macrophytes, or riparian vegetation (Miller et al. 2010; Haase et al. 2013; Göthe et al. 2015; Hering et al. 2015; Kail et al. 2015). Similarly, Poppe et al. (2016) reported that the hydrogeomorphic response (meso- and microhabitats and morphology) for a variety of river restoration measures (e.g., widening, restoring meanders, and instream structures) was not influenced by project length.

In contrast to riverine habitats, where length appears to be important, the relationship between fish production and project size or area for floodplain habitat restoration (off-channel ponds and constructed side channels) appears to be positive, but it plateaus after a certain size in some cases. For example, Roni et al. (2006b) found a positive but asymptotic relationship between the size of off-channel habitats that were created or reconnected and Coho Salmon smolt production, with maximum production appearing to plateau at about 2 ha. Similarly, Rosenfeld et al. (2008) observed that Coho Salmon smolt density was a decreasing function of side channel area and that the optimal area of constructed side channels or

Table 3. Summary of results from papers that examined size (length or area) of restoration (number of structures per meter) and biological or physical response. Five of the studies reported an effect of project length or area on biota.

Reference	Summary of findings
Roni et al. 2006b	Examined Coho Salmon smolt production from 30 off-channel restoration sites in Washington State and found a positive correlation between smolt production and project area, with smolt production appearing to plateau at a project size of approximately 20,000 m ² .
Muhar et al. 2008	Examined six river-widening projects in the River Drau, Austria, and found a positive correlation between fish ecological status and area restored.
Rosenfeld et al. 2008	Examined effects of constructed floodplain ponds and channels on Coho Salmon and steelhead parr and smolt density and production in British Columbia. Total Coho Salmon and steelhead smolt production was positively correlated with total project area. However, Coho Salmon smolt density and parr density were negatively correlated with project area, indicating that smolt production plateaued at a pond size of about 5,000–10,000 m ² .
Haase et al. 2013	Examined the responses of macroinvertebrates, fish, and aquatic macrophytes to 24 German hydromorphological restoration projects. Detected no correlation between the length of river restored and the fish or benthic macroinvertebrate response to restoration.
Schmutz et al. 2014	Examined fish response at 19 sites in the Danube River, Austria, and found that rehabilitation success was dependent mainly on spatial extent based on the positive correlation between rheophilic fish response and river restoration length. Suggested that the strongest response occurred when restoration length exceeded 3.9 km.
Göthe et al. 2015	Looked at the response of riparian habitats to small and large restoration projects across 20 European catchments. Project type had the greatest effect on plant community, whereas little to no effect of project size was detected.
Hering et al. 2015	Compared biological response in 10 pairs of long and short (<2 km) northern European river restoration projects. They found no effect of project size on the response of fish, benthic invertebrates, or aquatic macrophytes.
Thomas et al. 2015	Examined fish community response at 62 reach-scale restoration projects throughout Europe. The authors found no relationship between the length of the restoration project and fish community response.
Muhar et al. 2016	Summarized the findings of several studies under the REFORM (Restoring Rivers for Effective Catchment Management) project across Europe and concluded that there was not a positive relationship between project size and the physical and biological response. (However, they did acknowledge the response for rheophilic fishes as reported by Schmutz et al. 2014, 2016).
Poppe et al. 2016	Examined the hydrogeomorphic response (habitat) associated with 10 pairs of small and large European river restoration projects and found no difference between small and large projects.
Schmutz et al. 2016	Investigated 15 paired short and long river restoration projects in Europe and found no response for diversity or species density, but they did detect a larger response for small rheophilic fishes in longer compared to shorter reaches.

ponds was between 5,000 and 10,000 m². Muhar et al. (2008) found a strong positive correlation between fish diversity and total area restored at river widening sites in the Drau River, Austria. Studies on natural beaver ponds have similarly suggested that Coho Salmon smolt production was highest when pond area was less than 10,000 m², presumably because larger ponds have less suitable littoral habitat (Zarnowitz and Raedeke 1984; Reeves et al. 1989). Thus, there is evidence that the effect of restoration project size may depend upon the type of restoration and habitat created as well as the species of interest.

The roles of connectivity and a species' ability to disperse and colonize new areas are sometimes overlooked in understanding fish response to restoration and project size. For example, Zitek and Schmutz (2004) did not directly examine the length of a restoration project, but they reported that many rheophilic species only responded to river restoration when connectivity and habitat improvement occurred over several kilometers or the subcatchment scale. Their study and other studies demonstrate that removal of a barrier and other measures of restoring habitat connectivity can be critical to the success of riverine habitat restoration projects (Pierce et al. 2013, 2014). Species with high dispersal and colonization abilities have been reported to respond most positively to river restoration techniques (Thomas et al. 2015). Moreover, there is evidence that the ability of many non-salmonids to colonize habitat is dependent on their presence in nearby pools and on within-reach movement (Sundermann et al. 2011). Although the relationship between restoration project length and fish abundance appears weak, restoration of larger and longer river reaches allows for natural creation and regeneration of habitat needed for various life stages, and larger projects and reaches may allow for colonization by more species.

It is well known that the type and quality of restoration can have a key impact on the physical and biological response (Roni et al. 2008a, 2010). Rather than the size of the project or the type of restoration, the amount by which the habitat quality is increased (e.g., is pool area increased by 5% or 50%?) can be a key driver of fish response. For example, a positive correlation between the amount of pool-forming LWD or the number of boulder weir structures per 100 m and fish response has been reported (Roni and Quinn 2001a; Roni 2003; Roni et al. 2006a). These studies indicated a positive relationship between the amount of LWD placed and the response of juvenile Coho Salmon, steelhead, Reticulate Sculpins *Cottus perplexus*, larval Pacific Lampreys *Entosphenus tridentatus*, and larval lampreys *Lampetra* spp. to restoration. However, the response of age-0 resident and anadromous trout (steelhead/Rainbow Trout, Cutthroat Trout *O. clarkii*, and Brown Trout) has been found to be negatively correlated with LWD addition (Roni and Quinn 2001a) and naturally occurring LWD (Langford et al. 2012). These negative relationships are thought to be attributable to the elimination of shallow-water habitat preferred by young-of-the-year trout or increased predation due to increased numbers of older, larger trout after LWD placement.

While not related directly to the amount of improvement, the distance between instream structures (log or boulder weirs) has been shown to be strongly correlated with Coho Salmon redd density and Brown Trout egg-to-fry survival (Roni et al. 2008b; Michel et al. 2014). The distance of a redd from an instream structure is not directly equivalent to the density of instream structures in the reach, but these results do suggest

that the spacing and number of structures may be important factors in spawning use and success. Pess et al. (2012) hypothesized that the density of juvenile salmonids in habitat units with engineered logjams decreased as the number of logjams in their study reach increased from 8 to 19 during 2000–2003. This suggests either that juvenile abundance was at carrying capacity before the placement of additional logjams or that fish had not yet fully responded to the placement of logjams that were added during the study period. Unfortunately, Pess et al. (2012) did not monitor beyond 2003 and did not have long-term data to examine whether the fish response would increase with increasing numbers of logjams.

Studies examining restoration length, restoration type, and the amount by which habitat quality is increased often overlook the total amount of restoration that may occur in a watershed. Typically, a small fraction (i.e., <10%) of any one watershed has been restored (Roni et al. 2010). Modeling for Pacific Salmon *Oncorhynchus* spp. and steelhead has indicated that restoring a minimum of 20% or more of the available habitat in a watershed is necessary to detect a population- or watershed-level response (Roni et al. 2010). Only a few studies have examined watershed- and population-level responses to restoration, and the most successful have included restoration of large amounts of habitat (e.g., Solazzi et al. 2000; Pierce et al. 2013; Ogston et al. 2015). For example, Solazzi et al. (2000) reported nearly eightfold increases in smolt production after improving most of the anadromous habitat in their two treatment watersheds. In addition, there is evidence that little biological response may occur at a watershed scale until enough habitat restoration occurs (Wu et al. 2003). The total amount of habitat that needs to be restored is obviously unique to a watershed, its disturbance history, and the populations of interest and is an area of study that merits further examination.

The location of the restored habitat within a watershed and how that location might influence the fish response to restoration and fish movement have been largely overlooked in the existing literature. For example, a small project located immediately adjacent to high-quality habitat might see an immediate response to restoration as fish quickly move into the restored area. In contrast, a large project located tens of kilometers from other spawning or rearing habitat might see slower fish responses and colonization rates. Moreover, understanding the life history of the species of interest, the habitats that limit their production, the location of these habitats, and the areas in a watershed used for different life stages (e.g., spawning, holding, summer rearing, and winter rearing) is critical for measuring fish response to restoration (Beechie and Bolton 1999; Pierce et al. 2007, 2013, 2014).

FACTORS INFLUENCING FISH RESPONSE TO RIVER RESTORATION

Several factors influence fish response to restoration projects. These factors have often been overlooked in published studies to examine whether river restoration concentrates fish, increases fish abundance, or increases survival. Ultimately, the watershed template (location, quality, and quantity of habitats), the life history of the species of interest, food resources and predation, and the river restoration type, size, location, and amount will influence the movement, survival, and growth of individual fish. It is important to understand that fish movement, growth, and survival are all inextricably linked and will ultimately influence fish abundance at the habitat unit,

reach, and watershed scales. To untangle the influences of size, location, and amount of river restoration on fish movement, survival, and abundance, it is important to understand these linkages (Figure 4). For example, to determine whether increases in abundance at a restoration project were simply due to fish movement from other areas in the watershed requires understanding the underlying life history and seasonal movement patterns of the species in question. Data on when and how far fish move in a watershed and where the restoration will occur provide important information on whether restoration will lead to movement and potential short-term concentrations of fish. It should also be noted that the possible movement and short-term concentration of fish into restored habitats are not an issue if overall long-term abundance and survival increase in restored habitats.

SUMMARY AND CONCLUSIONS

Clearly, additional research is needed on all three of the major questions related to fish response to river restoration. The intent of this review was not to suggest that these questions have been answered definitively but rather to shed light on the current information to support or refute some of the commonly held beliefs about fish response to restoration. The available literature that specifically examines whether instream structures concentrate fish is equivocal. Based on this literature—and information on the scale, duration, and frequency of salmonid movements, which suggests that salmonids generally move less than 100 m during low-flow periods—there is little evidence to support the contention that instream restoration or river restoration techniques concentrate fish. Moreover, if fish do vacate habitats to colonize newly restored habitat, it is more than likely that the vacated habitat would eventually be colonized by subdominant fish or a new cohort in subsequent years. There may, however, be a concentration of adult resident trout that have vacated less-favorable habitat in the years immediately after river restoration—most likely equal to one or two generations for a species (i.e., 5–10 years).

The limited information on whether river restoration leads to increased fish abundance or increased survival suggests that it may be either or both. Moreover, while many studies (particularly for instream structure placement) have reported increased abundance, this suggests that habitat carrying capacity increased through increases in either the quantity or quality of habitat, and presumably more fish are surviving at

that life stage or at some point in the life cycle. The widespread use of PIT tagging and other fish marking technologies (e.g., telemetry and genetic fingerprinting) has made monitoring fish movement and survival much easier and has helped facilitate research and monitoring on survival and concentration questions. In addition, almost all of the literature on fish movements and river restoration is focused on salmonid fishes, providing little information for non-salmonids. Although the results may be similar for other riverine species and other areas, there are few data to support this, and additional information is needed for other species, particularly warmwater fishes.

Several recent European studies have examined project length, but there is limited evidence that length is an important factor in determining the response of fish or other biota to restoration. In contrast, for constructed or reconnected floodplain habitats (ponds and channels), the area of the project appears to be strongly correlated with fish response, particularly for Coho Salmon. There appears to be an optimal size at which fish density is maximized, likely due to decreasing amounts of littoral habitat in large, pond-like habitats. The amount of increase in habitat quality is correlated with fish response; therefore, the number of structures or pieces of wood, boulder, or gravel placed in a reach is an important determinant of fish response. Moreover, the total amount of restoration and the connectivity of those habitats are important drivers of population- or watershed-level response to restoration but have received little attention in the literature. This further suggests that rather than focusing on the concentration of or movement of fish into a restored section, the focus should be on the amount and quality of the restoration effort.

To disentangle the complex relationships between river restoration and fish movement, abundance, and survival, future studies should consider the life history of the fish in question, the habitats limiting their production, the current distribution of habitats in the watershed, and how restoration will modify the distribution and connectivity of those habitats (Figure 4). This will require comprehensive studies that measure seasonal fish movement, abundance, and survival at both the reach scale and the watershed scale. It will also require watershed assessments that document the quantity and quality of different habitats within a watershed and when they are used by different species and life stages. In the absence of these types of studies and assessments, given that fish abundance at a given

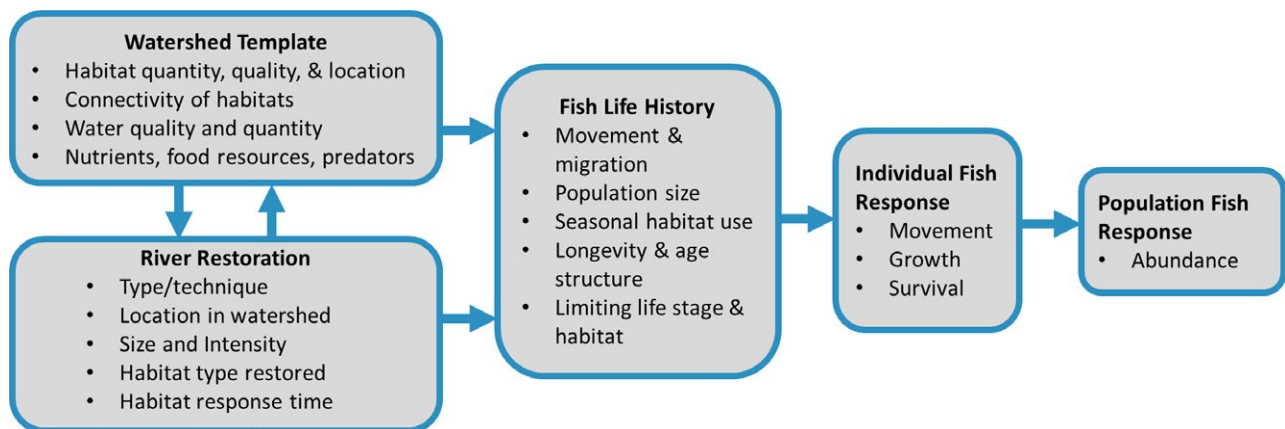


Figure 4. Conceptual diagram of linkages between the watershed template, fish life history, river restoration characteristics, and fish response to restoration. Adequately addressing questions about the effects of river restoration on fish movement and survival requires an understanding of these relationships.

location and time is the great integrator of all these factors, it likely remains the simplest way to quickly evaluate fish response to river restoration.

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