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Running title: weir removal effects on smolts

Abstract

Today's river systems have been extensively modified, requiring us to rethink how we approach the management of these important ecosystems. We evaluated the effects of removing six weirs in River Villestrup (Jutland, Denmark) on the smolt run of brown trout (*Salmo trutta*) over the course of 12 years. During five of these years, we evaluated the number, size and timing of smolts during their downstream migration. We found a significant increase in smolt output following the weir removals, along with a decrease in average length and indications of an earlier peak migration. Our results suggest that barrier removal has perhaps led to an increase in spawning success by adults, fry survival, recruitment, and smolt migration success. Weir removal is therefore a viable management approach to restore connectivity in freshwater streams and rivers, which promotes the passage of smolts as they migrate to marine environments.

Keywords: barriers, freshwater ecosystems, migration, removal, river restoration, *Salmo trutta*, smolt

1. Introduction

1.1 River connectivity

The diversity, abundance and sustainability of aquatic species have long been threatened by the human-induced fragmentation of rivers (Saunders et al., 1991; Khan and Colbo, 2008). Barriers in the form of dams, weirs and culverts have become so prominent in today's river systems that the majority of them have lost their original connectivity and natural characteristics (Jungwirth, 1998; Jager et al., 2001). These barriers exacerbate the current poor state of many freshwater ecosystems. Efforts to mitigate the impacts of barriers, such as fishpasses, have seen limited success (Bunt et al., 2012) and are usually costly (Gibson et al., 2005). Furthermore, such approaches do not repair the damage done to the ecosystems as a whole (Birnie-Gauvin et al., 2017); rather, they provide an opportunity for *some* fish to move upstream or downstream past the barrier. This is particularly relevant for migratory fish species like salmonids, which depend on freshwater migrations to complete their lifecycle (Jonsson and Jonsson, 1993; Klemetsen et al., 2003). Better management tools need to be implemented to promote the persistence of these migratory species, such as barrier removal and other types of restoration projects.

1.2 Brown trout

The brown trout (*Salmo trutta*, Salmonidae) is a partially anadromous salmonid species, native to many regions of Europe (Jonsson and Jonsson, 1993). Brown trout spawn in the upper reaches of rivers, where the substrate is typically suitable for spawning and early growth, and predators are typically absent (Shirvell and Dungey, 1983; Armstrong et al., 2003). Juvenile trout generally spend between one to five years in freshwater, after which individuals differentiate phenotypically (Nielsen et al., 2003). Some individuals will assume a resident phenotype and remain in freshwater their entire life, while others will assume the migratory phenotype and migrate to marine environments (Jonsson and Jonsson, 1993; Nielson et al., 2006). This phenomenon is known as partial migration (Chapman et al., 2011).

While the drivers for partial migration remain poorly understood (though many hypotheses exist, Chapman et al., 2011), the benefits of migrating to sea appear to be linked to a larger availability of food items in marine environments, thus allowing migratory individuals to attain larger sizes and a greater reproductive potential (Northcote, 1984; Chapman et al., 2011; Shrimpton, 2013). Juveniles that become migratory individuals are known as smolts, and differ from their resident counterparts both behaviorally and physiologically. For example, smolts appear to be less aggressive (Jonsson and Jonsson, 2011; Thorstad et al., 2012), have greater sodium-potassium ATPase activity in their gills (Aarestrup et al., 2000), and appear to have greater levels of blood-circulating antioxidants (Birnie-Gauvin et al., 2017).

Smolts typically migrate during the months of March to May depending on latitude (peak smolt migration period, e.g., Bohlin et al., 2011), though some migrate during the autumn (Aarestrup et al., 2018). The downstream smolt migration is thought to be triggered by a range of environmental factors, such as photoperiod, temperature and discharge (Hoar, 1988). Furthermore, smolts are thought to migrate downstream during the “smolt window”. This window is thought to be affected by factors such as physiological and ecological readiness to enter marine environments, risk of predation, and growth potential (McCormick et al., 1998). It is thus essential that smolts be able to reach marine waters as quickly and easily as possible, with their passage unhindered.

1.3 The restoration project

Barriers cause the upstream portion of the river to become inundated and thus hinder the passage of smolts heading downstream due to the slowing of water (e.g., Schwinn et al., 2017) and difficulties associated with finding a safe passage route past the structure itself (e.g., Thorstad et al., 2003). Furthermore, barriers hinder the upstream passage of adult trout during their spawning migration. In Denmark, such barriers often occur in the form of weirs in conjunction with fish farms. River Villestrup (northeast Jutland, Denmark) historically had 17 fish farms. In an attempt to restore the river to its original state and reinstate connectivity on the lower two thirds of the river, six weirs (five in the mainstem and one in a tributary) were removed. All associated fish farms were simultaneously closed. The weirs were likely to have been several hundred years old, though precise years of origin are not available. Each weir was originally made of concrete or wood, and removed by digging and removing all parts of the structure completely. Each removal occurred within the course of a few days, though weirs were removed in different years. In 2004, when the restoration project began, seven weirs were left. The lower-most weir was removed in 2005, and five more were subsequently removed between 2010 and 2013 (see Figure 1C for weir locations, and Table 1 for specific details on each weir). Today, only one weir remains in the upstream portion of the river (Figure 1, #6). This study investigated the effectiveness of this restoration approach with regards to the smolt run over the course of 12 years (five study years).

2. Materials and Methods

2.1 Study site and trap set up

River Villestrup is located in northeast Jutland (Denmark), where it runs for 20km before entering the Mariager Fjord (Figure 1). The river is fed by groundwater and rainfall, and has a mean annual discharge of 1.1m^3 s^{-1}. It is home to a wild population of partially anadromous brown trout, with both resident and migratory phenotypes. Before the weir removals, river Villestrup was characterized mostly by sandy and muddy substrates in the close vicinity of the weirs, with little pool/riffle habitat. As in most Danish rivers, river Villestrup had and still has a relatively low gradient (approx. 1.0%), and meandering form. However, following the removals, the river bed is characterized by coarse, gravelly substrates. For every study year (i.e., 2004, 2008, 2009, 2015 and 2016), a full-covering Wolf trap (8mm grid spacing; Wolf 1951) was set up 200m from the mouth of the river (Figure 1C, #1). The trap covered the entire width of the river (approx. 6m), allowing us to capture virtually every fish larger than 10 cm. The trap was in place from April 1st to May 31st every year, and was emptied daily during that period.

Unfortunately, given the expenses and time required to maintain a trap for two months, we could not perform the study continuously between 2004 and 2016. Thus, specific study years were selected to provide the most representative data to evaluate the effects of weir removal through a BACI approach.

2.2 Fish processing

Every day during the study period, the trap was emptied to count and measure (±0.1cm) all smolts. Fish were anesthetized with benzocaine (0.03g l^{-1}) for measurements and fin clipped (adipose fin). Fish were then released just downstream of the trap. While it was unlikely, fish could return upstream after having been measured. In that case, fin-clipping allowed us to detect if a fish had already been measured and counted, and that individual was then removed from the day's count.

2.3 Environmental variables

Water discharge data were obtained from a monitoring station located 750m upstream of the trap. Temperature data were obtained using an underwater temperature data logger (Onset HOBO Tidbit v2 UTBI-001, range: -20°C to 70°C, Massachusetts, USA).

2.4 Data analysis

All trout between 10.0 and 21.0 cm caught in the trap were considered to be smolts (despite coloration) for the purpose of the analysis. This is a fair assumption given the close distance between the trap and the fjord. Furthermore, a follow up electrofishing pass downstream of the trap after the end of the smolt season showed very few trout. Mean length between years was compared using a simple linear regression model:

$$\log(\text{length}_i) = \text{year}_i + \varepsilon_i$$

$$\varepsilon_i \sim N(0, \sigma^2)$$

Lengths were log-transformed to meet assumptions of normality and homoscedacity. All statistical analyses were performed using R version 3.4.1.

3. Results

The size of the smolt run increased significantly following the removal of weirs, with the largest class in 2015, followed by 2016 (Table 2; Fig. 2). Average length of downstream migrating trout was different across study years, decreasing significantly every year (GLM, $p < 0.05$; Fig. 3). We note an indication of earlier peak migration following weir removal (Fig. 2 and 4).

4. Discussion

4.1 Smolt run

The removal of low-head weirs in River Villestrup strongly increased smolt output. The removal of the most downstream weir in 2005 alone led to a large increase in smolts in 2008 and 2009, suggesting that re-establishing the ease of access to the fjord aided a large number of fish in successfully migrating to marine environments. Given that a Danish smolt cohort typically resides in freshwater for one to two years before migrating, the timeline of these observations are in line with the prediction that the effects of weir removal may take 2+ years to appear, though we do not have data for the years of 2006-2007 to demonstrate this. The subsequent removal of five more weirs led to an even greater increase in 2015 and 2016. Our results indicate that weir removal reinstated the natural habitat of the river, with many areas dominated by fast-moving water, riffles, and coarse substrate, where ponded zones previously were. These environmental changes presumably restored or even created new grounds ideal for spawning and early development which adults and fry did not have access to for centuries, when fish farms and mills were first established in the river system. Adult sea trout are also able to spawn farther upstream than when the barriers were present. Preliminary data shows a 9-fold increase in adult spawners between 2004 and 2016 (from an estimated 333 to 3700 individuals, data unpublished). Furthermore, observations also suggest that sedimentation caused by barriers may trap fry upon emergence (Rubin, 1998). The removal of obstacles would then also increase the survival of fry, and thus result in a larger smolt run. Unfortunately, our set up did not allow us to follow sediment displacement post-removal, and we cannot exclude the possibility of sediments being deposited on spawning grounds. However, observations from fisheries technicians and local anglers supported an increase in the number of spawning grounds throughout the river length, with a large increase in sea trout spawners. We therefore suggest that the increase in availability of spawning grounds may have offset the negative impacts of sediment release caused by the removals. Observations of increased spawners suggest that even if sediments ended up on spawning grounds, the effects were non-problematic.

We observed an unexpected significant decrease in the smolt output between 2015 and 2016. Three possible explanations arise. 1. It is possible that the large smolt run from 2015 reduced the smolt output from 2016. Previous research has shown that the density of an age class of brown trout can affect one or more subsequent age classes through intraspecific competition between cohorts (Elliott, 1994; Nordwall et al., 2001). In this case, the 1+ age class which migrated in 2015 may have significantly reduced the abundance of the 0+ age class which would have migrated in 2016, either through predation, density-dependent mortality or intraspecific competition (Elliott, 1994). 2. It is possible that the decrease was due to variation in the annual smolt production, which may vary from year to year due to variation in biotic and abiotic factors (Chadwick, 1982; Warren et al., 2015). In this case, we would expect the number of smolts to increase again in the upcoming years. 3. It is possible that the population suffered high overwinter mortality due to harsh environmental conditions (Elliott, 1993). Other Danish streams were found to have poor overwinter survival (personal observation, K. Birnie-Gauvin, Gudsø stream).

4.2 Smolt size and peak migration

We observed a decrease in the average smolt size through the years. It is possible that following weir removal, smaller fish were also successful in migrating downstream, rather than larger fish only, which are presumably more apt at escaping predators in ponded zones or overcoming weirs (Winstone et al., 1985). In other words, smaller fish no longer get stuck at weirs and/or penetrate the grid used to prevent fish from entering the water intake channel at fish farms, and are capable of descending downstream. Another possibility for progressively smaller fish following weir removal is that a greater number of fish caused higher intraspecific competition for food, and may have resulted in smaller fish (Holm et al., 1990). Additionally, it is likely that spawning success and recruitment increased, which simply increased the number of migrating fish, with a wide range of sizes. Our findings likely reflect a combination of all three possible explanations. Alternatively, it is possible that the removals impacted the invertebrate community, and thus may have reduced food availability. While we cannot rule out this explanation, it is rather unlikely that the post-removal invertebrate community had diminished so much that fish were smaller in size. Because fast-flowing water is typically inhabited by different invertebrate types than slower moving water (Doisy and Rabeni, 2001), we argue that the invertebrate community *changed* rather than *diminished* post-removal.

We expected the peak migration to occur earlier following the removal of the weirs through a reduction in delays at ponded zones, but cannot make that conclusion for certain. While our results indicate a trend for an earlier peak migration, flood events during the study years make it impossible to make a meaningful analysis. Evidence suggests that dams delay the passage of migrating fish greatly (Aarestrup and Koed, 2003; Gauld et al., 2013), and that these effects are worse when multiple dams must be overcome (Caudill et al., 2007). Ponded zones can cause smolts to lose their orientation due to diminished flow, thus delaying them (Schilt, 2007). The removal of five of the six weirs in the main stem of river Villestrup likely prevented such delays in downstream migration, thus enabling fish to reach marine environments faster.

4.3 Implications

Our results suggest that complete barrier removal has several important implications for freshwater fisheries and river management. Weir removal presumably increases the number of adult fish able to successfully migrate upstream and spawn, perhaps due to a reduced incidence of injuries at obstacles, diminished energy expenditure to attain spawning grounds (i.e., adults no longer have to invest energy to surpass barriers), and by making impassable stretches into passable ones (Castro-Santos and Letcher, 2010). Furthermore, weir removal may increase reproductive output through successful egg emergence (i.e., unhindered by sedimentation), which would then lead to an increased recruitment rate and an increased smolt output in the following 2+ years. Weir removal also makes smolts more successful in their downstream migration via reduced mortality at fish farm intake grids (Aarestrup and Koed, 2003), reduced predation at ponded zones (Jepsen et al., 1998), decreased delays (Aarestrup and Koed, 2003; Schilt, 2007) and presumably decreased energy expenditure. In addition, barriers may induce an artificial population structure by favouring larger individuals; removal can reinstate a more natural population structure, with a wider size range.

Many of the fish species that migrate between freshwater and marine waters, including trout, are used as indicator species for good environmental and ecological status, as they experience the many different habitats during their movement from upland streams to lowland rivers and then to the sea (Lasne et al., 2007; Gough et al., 2012). Their importance in the context of management cannot be understated. Fish usually migrate for one of three reasons; migrations are either for spawning, feeding or refuge seeking (Northcote, 1984). Regardless of the causes for migration, barriers diminish the ease of access to spawning and feeding grounds, and hinder passage to refuge areas. These effects are likely exacerbated in rivers with numerous barriers (Lucas and Batley, 1996). Extensive fragmentation of river connectivity limits dispersal of many fish species (McLaughlin et al., 2006). Furthermore, dams impact the hydrogeomorphology of streams in some places. For example, barriers cause a decrease in water velocity, an increase in water temperature, a decrease in oxygen availability, and sedimentation (Baxter, 1977; Petts, 1984). Since most diadromous species exhibit homing behaviour, and because the latter is directly related to predictable environmental conditions such as temperature, water chemistry, and rhythmic patterns of environmental changes, their homing behavior is likely to be greatly impacted by the presence of obstacles (Lucas and Baras, 2008).

In the present study, we demonstrate that weir removal is an appropriate approach to reinstate river connectivity and to increase long-term population sustainability of fish species. We provide some of the first data evaluating the full river system effects of barrier removal, and further emphasize the need to implement this approach in management schemes whenever possible.

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Data

Date will be made available on figshare upon acceptance of the manuscript.

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Table 1. Weirs in River Villestrup. Height (m), width (m), length of ponded zones (m), presence or absence of fishway and date of removal for the weirs found in River Villestrup.

Weir #	Height (m)	Width (m)	Length of ponded zone (m)	Fishway present?	Year of removal
1	1.9	5.9	800	Yes	2005
2	1.8	4.1	180	Yes	2012
3	0.1	5.6	0	Yes	2012
4	1.8	2.7	600	Yes	2012
5	1.5	5.0	600	Yes	2012
6	1.8	4.8	900	No	Not removed
7	1.0	1.7	500	Yes	2012

Table 2. Smolt output. Average length of brown trout (*Salmo trutta*), average daily count, total count and most caught in a single day for each study year.

	2004	2008	2009	2015	2016
Average length (cm)	16.3±3.0	15.5±4.2	14.5±23.6	13.3±2.4	13.2±2.2
Average daily count	27.2	75.4	82.6	312.9	134.2
Total count	1660	4598	5038	19105	8185
Most in a day	92	931	263	5214	1853

Figure Captions

Figure 1. Map of River Villestrup. River Villestrup is situated in northeastern Jutland, Denmark (A). It runs for approximately 20 km before entering the Mariager Fjord (B). A total of 7 weirs were present in the system originally; 6 were removed, with one still remaining (#6, C).

Figure 2. Catch per day. Number of downstream migrating brown trout (*Salmo trutta*) smolts and discharge (m^3 s^{-1}) in River Villestrup between April 1 and May 31, for years 2004 (A), 2008 (B), 2009 (C), 2015 (D) and 2016 (E). Note variable scale on Y-axis.

Figure 3. Length distribution. *Left:* Length distributions of downstream migrating brown trout (*Salmo trutta*). Red dots and intervals indicate mean length ± SD. *Right:* Visualisation of the fitted model. Estimated mean length and associated 95 % confidence intervals (back-transformed to original scale). Mean log (length) were significantly different between all years ($p < 0.05$).

Figure 4. Migration timing. Cumulative migration curve for brown trout (*Salmo trutta*) smolts for each study year.