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1 **River connectivity reestablished: effects and implications of six weir removals on brown trout**
2 **smolt migration**

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21 **Running title: weir removal effects on smolts**

24 **Abstract**

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

35
36 **Keywords:** barriers, freshwater ecosystems, migration, removal, river restoration, *Salmo trutta*, smolt

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47 **1. Introduction**

48

49 *1.1 River connectivity*

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

63

64 *1.2 Brown trout*

65 The brown trout (*Salmo trutta*, Salmonidae) is a partially anadromous salmonid species, native to many
66 regions of Europe (Jonsson and Jonsson, 1993). Brown trout spawn in the upper reaches of rivers,
67 where the substrate is typically suitable for spawning and early growth, and predators are typically
68 absent (Shirvell and Dungey, 1983; Armstrong et al., 2003). Juvenile trout generally spend between
69 one to five years in freshwater, after which individuals differentiate phenotypically (Nielsen et al.,

70 2003). Some individuals will assume a resident phenotype and remain in freshwater their entire life,
71 while others will assume the migratory phenotype and migrate to marine environments (Jonsson and
72 Jonsson, 1993; Nielson et al., 2006). This phenomenon is known as partial migration (Chapman et al.,
73 2011).

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

83 Smolts typically migrate during the months of March to May depending on latitude (peak smolt
84 migration period, e.g., Bohlin et al., 2011), though some migrate during the autumn (Aarestrup et al.,
85 2018). The downstream smolt migration is thought to be triggered by a range of environmental factors,
86 such as photoperiod, temperature and discharge (Hoar, 1988). Furthermore, smolts are thought to
87 migrate downstream during the “smolt window”. This window is thought to be affected by factors such
88 as physiological and ecological readiness to enter marine environments, risk of predation, and growth
89 potential (McCormick et al., 1998). It is thus essential that smolts be able to reach marine waters as
90 quickly and easily as possible, with their passage unhindered.

91

92 *1.3 The restoration project*

93 Barriers cause the upstream portion of the river to become inundated and thus hinder the passage of
94 smolts heading downstream due to the slowing of water (e.g., Schwinn et al., 2017) and difficulties
95 associated with finding a safe passage route past the structure itself (e.g., Thorstad et al., 2003).
96 Furthermore, barriers hinder the upstream passage of adult trout during their spawning migration. In
97 Denmark, such barriers often occur in the form of weirs in conjunction with fish farms. River
98 Villestrup (northeast Jutland, Denmark) historically had 17 fish farms. In an attempt to restore the river
99 to its original state and reinstate connectivity on the lower two thirds of the river, six weirs (five in the
100 mainstem and one in a tributary) were removed. All associated fish farms were simultaneously closed.
101 The weirs were likely to have been several hundred years old, though precise years of origin are not
102 available. Each weir was originally made of concrete or wood, and removed by digging and removing
103 all parts of the structure completely. Each removal occurred within the course of a few days, though
104 weirs were removed in different years. In 2004, when the restoration project began, seven weirs were
105 left. The lower-most weir was removed in 2005, and five more were subsequently removed between
106 2010 and 2013 (see Figure 1C for weir locations, and Table 1 for specific details on each weir). Today,
107 only one weir remains in the upstream portion of the river (Figure 1, #6). This study investigated the
108 effectiveness of this restoration approach with regards to the smolt run over the course of 12 years (five
109 study years).

111 **2. Materials and Methods**

113 *2.1 Study site and trap set up*

114 River Villestrup is located in northeast Jutland (Denmark), where it runs for 20km before entering the
115 Mariager Fjord (Figure 1). The river is fed by groundwater and rainfall, and has a mean annual

116 discharge of $1.1\text{m}^3\text{ s}^{-1}$. It is home to a wild population of partially anadromous brown trout, with both
117 resident and migratory phenotypes. Before the weir removals, river Villestrup was characterized mostly
118 by sandy and muddy substrates in the close vicinity of the weirs, with little pool/riffle habitat. As in
119 most Danish rivers, river Villestrup had and still has a relatively low gradient (approx. 1.0%), and
120 meandering form. However, following the removals, the river bed is characterized by coarse, gravelly
121 substrates. For every study year (i.e., 2004, 2008, 2009, 2015 and 2016), a full-covering Wolf trap
122 (8mm grid spacing; Wolf 1951) was set up 200m from the mouth of the river (Figure 1C, #1). The trap
123 covered the entire width of the river (approx. 6m), allowing us to capture virtually every fish larger
124 than 10 cm. The trap was in place from April 1st to May 31st every year, and was emptied daily during
125 that period.

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

130

131 *2.2 Fish processing*

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

137

138 *2.3 Environmental variables*

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

142

143 *2.4 Data analysis*

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

$$149 \quad \log(\text{length}_i) = \text{year}_i + \varepsilon_i$$

$$150 \quad \varepsilon_i \sim N(0, \sigma^2)$$

151 Lengths were log-transformed to meet assumptions of normality and homoscedacity.

152 All statistical analyses were performed using R version 3.4.1.

153

154 **3. Results**

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

159

160 **4. Discussion**

161

162 *4.1 Smolt run*

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

185 spawners suggest that even if sediments ended up on spawning grounds, the effects were non-
186 problematic.

187 We observed an unexpected significant decrease in the smolt output between 2015 and 2016.
188 Three possible explanations arise. 1. It is possible that the large smolt run from 2015 reduced the smolt
189 output from 2016. Previous research has shown that the density of an age class of brown trout can
190 affect one or more subsequent age classes through intraspecific competition between cohorts (Elliott,
191 1994; Nordwall et al., 2001). In this case, the 1+ age class which migrated in 2015 may have
192 significantly reduced the abundance of the 0+ age class which would have migrated in 2016, either
193 through predation, density-dependent mortality or intraspecific competition (Elliott, 1994). 2. It is
194 possible that the decrease was due to variation in the annual smolt production, which may vary from
195 year to year due to variation in biotic and abiotic factors (Chadwick, 1982; Warren et al., 2015). In this
196 case, we would expect the number of smolts to increase again in the upcoming years. 3. It is possible
197 that the population suffered high overwinter mortality due to harsh environmental conditions (Elliott,
198 1993). Other Danish streams were found to have poor overwinter survival (personal observation, K.
199 Birnie-Gauvin, Gudsø stream).

200

201 *4.2 Smolt size and peak migration*

202 We observed a decrease in the average smolt size through the years. It is possible that following weir
203 removal, smaller fish were also successful in migrating downstream, rather than larger fish only, which
204 are presumably more apt at escaping predators in ponded zones or overcoming weirs (Winstone et al.,
205 1985). In other words, smaller fish no longer get stuck at weirs and/or penetrate the grid used to prevent
206 fish from entering the water intake channel at fish farms, and are capable of descending downstream.
207 Another possibility for progressively smaller fish following weir removal is that a greater number of

208 fish caused higher intraspecific competition for food, and may have resulted in smaller fish (Holm et
209 al., 1990). Additionally, it is likely that spawning success and recruitment increased, which simply
210 increased the number of migrating fish, with a wide range of sizes. Our findings likely reflect a
211 combination of all three possible explanations. Alternatively, it is possible that the removals impacted
212 the invertebrate community, and thus may have reduced food availability. While we cannot rule out
213 this explanation, it is rather unlikely that the post-removal invertebrate community had diminished so
214 much that fish were smaller in size. Because fast-flowing water is typically inhabited by different
215 invertebrate types than slower moving water (Doisy and Rabeni, 2001), we argue that the invertebrate
216 community *changed* rather than *diminished* post-removal.

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

226

227 *4.3 Implications*

228 Our results suggest that complete barrier removal has several important implications for
229 freshwater fisheries and river management. Weir removal presumably increases the number of adult
230 fish able to successfully migrate upstream and spawn, perhaps due to a reduced incidence of injuries at

231 obstacles, diminished energy expenditure to attain spawning grounds (i.e., adults no longer have to
232 invest energy to surpass barriers), and by making impassable stretches into passable ones (Castro-
233 Santos and Letcher, 2010). Furthermore, weir removal may increase reproductive output through
234 successful egg emergence (i.e., unhindered by sedimentation), which would then lead to an increased
235 recruitment rate and an increased smolt output in the following 2+ years. Weir removal also makes
236 smolts more successful in their downstream migration via reduced mortality at fish farm intake grids
237 (Aarestrup and Koed, 2003), reduced predation at ponded zones (Jepsen et al., 1998), decreased delays
238 (Aarestrup and Koed, 2003; Schilt, 2007) and presumably decreased energy expenditure. In addition,
239 barriers may induce an artificial population structure by favouring larger individuals; removal can
240 reinstate a more natural population structure, with a wider size range.

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

254 and rhythmic patterns of environmental changes, their homing behavior is likely to be greatly impacted
255 by the presence of obstacles (Lucas and Baras, 2008).

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

260

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265

266 **Data**

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

268

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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

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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

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540 **Figure Captions**

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

545

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

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

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

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