



30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam

Birnie-Gauvin, Kim; Larsen, Martin Hage; Nielsen, Jan; Aarestrup, Kim

Published in:
Journal of Environmental Management

Link to article, DOI:
[10.1016/j.jenvman.2017.09.022](https://doi.org/10.1016/j.jenvman.2017.09.022)

Publication date:
2017

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
Birnie-Gauvin, K., Larsen, M. H., Nielsen, J., & Aarestrup, K. (2017). 30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam. *Journal of Environmental Management*, 204, 467-471. <https://doi.org/10.1016/j.jenvman.2017.09.022>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

**30 years of data reveal dramatic increase in abundance of brown trout following the removal of a
small hydrodam**

Accepted in Journal of Environmental Management

Kim Birnie-Gauvin¹, Martin H. Larsen^{1,2}, Jan Nielsen¹, Kim Aarestrup¹

¹ DTU Aqua, Section for Freshwater Fisheries and Ecology, Vejlsovej 39, 8600 Silkeborg

² Danish Centre for Wild Salmon, Brusgårdsvej 15, 8960 Randers, Denmark

Author for correspondence: K. Birnie-Gauvin, kbir@aqua.dtu.dk

Running head: Dam removal increases trout density

24 **Abstract**

25 Humans and freshwater ecosystems have a long history of cohabitation. Today, nearly all major rivers
26 of the world have an in-stream structure which changes water flow, substrate composition, vegetation,
27 and fish assemblage composition. The realization of these effects and their subsequent impacts on
28 population sustainability and conservation has led to a collective effort aimed to find ways to mitigate
29 these impacts. Barrier removal has recently received greater interest as a potential solution to restore
30 river connectivity, and reestablish high quality habitats, suitable for feeding, refuge and spawning of
31 fish. In the present study, we present thirty years of data from electrofishing surveys obtained at two
32 sites, both prior to and following the removal of a small-scale hydropower dam in Central Jutland,
33 Denmark. We demonstrate that the dam removal has led to a dramatic increase in trout density,
34 especially in young of the year. Surprisingly, we found that this increase was not just upstream of the
35 barrier, where the ponded zone previously was, but also downstream of the barrier, despite little
36 changes in habitat in that area. These findings suggest that barrier removal may be the soundest
37 conservation option to reinstate fish population productivity.

38
39 **Keywords:** conservation, dams, fish passage, migration, population, Salmonidae

40
41 **Abbreviations:** YOY – young of the year

42 OLD – older fish

43

44

45

46

47 **Introduction**

48 Obstacles within watercourses, such as dams and weirs, have become pervasive in today's freshwater
49 ecosystems. Beginning in the tenth century, humans have modified rivers to operate mills, net fish as a
50 food source, navigate to trade with foreign countries, generate energy and regulate water (Baxter 1977;
51 Dudgeon 1992; Northcote 1998; Downward and Skinner 2005; Nützmann et al. 2011). Today, scarcely
52 any river systems remain unaltered by anthropogenic structures (Morita and Yamamoto 2001; Hall et
53 al. 2011).

54 The impacts that dams have had on freshwater ecosystems are considerable; alterations to the
55 physical and chemical characteristics of the water and surrounding landscapes has resulted in the
56 increase of homogeneity and a decrease in suitable habitat for many species, including the loss of low-
57 water spawning and nursery habitats for salmonids and lampreys in ponded zones (Baxter 1977;
58 Jungwirth et al. 2000; Birnie-Gauvin et al. in press); and interference with one or more stage in the life
59 cycle of many fish species has led to changes in fish assemblages (Lucas and Baras 2001). For
60 example, brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) smolts showed significant delays
61 and increased mortality when released upstream of a small weir in comparison to individuals released
62 downstream of the barrier (Aarestrup and Koed 2003). Furthermore, the natural flow patterns of
63 regulated rivers, which provide important cues for fish migrations, have been altered extensively,
64 thereby also reducing biodiversity (Bunn and Arthington 2002). This reduction in biodiversity and
65 population numbers is further exacerbated by an increased mortality of migratory fish in reservoirs (or
66 ponded zones) formed by dams (Jepsen et al. 1998). Fish will often accumulate in these ponded zones,
67 as well as just downstream of a dam (Koed et al. 2002), making them more susceptible to predation by
68 other fish and to exploitation by fisheries (Poe et al. 1991; Lucas and Baras 2001). Taken together, the
69 construction of dams and weirs is estimated to account for 55 to 60% of the known causes leading to

70 freshwater fish endangerment (Northcote 1998). To aggravate their status, freshwater species are
71 already considered more imperiled than terrestrial species (McAllister et al. 1997; Ricciardi and
72 Rasmussen 1999), requiring us to take action.

73 The recognition of the negative impacts of barriers in the last few decades has led to the quest
74 for solutions that would enable safe passage. For example, many hydrodams in the United States have
75 adopted the policy of manually trapping and moving fish passed dams (Cada 1998). In other cases, fish
76 passes, such as fish ladders, fish elevators or nature-like fish passes, have been implemented (see
77 Jungwirth et al. 1998 for review). Despite these efforts however, the efficiency of fish passage facilities
78 remains underwhelming in many cases. In the River Gudena, Denmark, the Tangeværket Dam has
79 resulted in the extinction of Atlantic salmon and the near-elimination of upstream migrating sea trout
80 (*S. trutta*), despite the presence of a fish ladder (Aarestrup and Jepsen 1998).

81 Though larger obstacles are viewed as having more significant consequences, smaller barriers
82 such as weirs are more common (estimated two- to four-fold; Lucas et al. 2009). On a large scale, their
83 cumulative effects are likely to be significant (Cooke et al. 2005), though these low-head barriers
84 continue to be less studied (Lucas and Baras 2001). No matter the barrier size however, barrier removal
85 is presumably the most appropriate solution (Cowx and Welcomme 1998). It (1) restores longitudinal
86 connectivity, (2) restores the natural habitat (including physical and chemical properties), and (3)
87 enables safe fish passage. Despite the recognition that removal is likely the soundest of all conservation
88 options since 1998 (by Cowx and Welcomme), relatively few studies have examined the consequences
89 of barrier removal (but see Bednarek 2001 for review on ecological effects), especially in the context of
90 smaller obstacles and over long timescales. The recovery response of fish populations and communities
91 to removal remains largely undocumented (Doyle et al. 2005) making it difficult to make predictions
92 and influence decisions made at the management level. Existing recommendations include viewing

93 small barrier removals as opportunities to educate ourselves on the impacts before contemplating large
94 barrier removals, which are likely accompanied by greater consequences (Doyle et al. 2003). The few
95 studies that have examined the effects of barrier removal on fish assemblage and distributions have
96 been carried over relatively short periods of time, but all indicated or predicted positive impacts of
97 removal on native species (e.g., Catalano et al. 2007; Pess et al. 2008; Burroughs et al. 2010; Hitt et al.
98 2012). Here, we present 30 years of data on brown trout numbers both before and after the removal of a
99 small hydropower dam (Vilholt, Central Jutland, Denmark). Such temporal data on the subject has
100 never been available prior to this study (that we know of), making it the first of its kind.

101 **Methods**

102

103 *Study site*

104 River Gudenaå is one of the largest rivers in Jutland, Denmark, running for approximately 149 km
105 before entering the Randers Fjord. In 1866, the Vilholt hydropower dam (Vilholt Mølle) was
106 established in River Gudenaå (Figure 1). Since 1987, the local authorities (Vejle County and Horsens
107 Municipality), along with the National Forest and Nature Agency, had debated with stakeholders for
108 the removal of the Vilholt dam to restore natural conditions and faunapassage in the river. The dam was
109 finally removed in 2008 after nearly two decades of debate. Lake Mossø is located approximately
110 6.5km downstream of where the dam used to be. The river system is now home to a large population of
111 brown trout (*S. trutta*), with Lake Mossø serving as highly productive feeding grounds for lake-
112 dwelling brown trout (herein referred to as lake trout). These lake trout originate from the spawning
113 and nursery areas of River Gudenaå, migrate down to the lake to feed, and return to the river to spawn.

114

115 *Electrofishing surveys*

116 Starting in 1997 through 2016, electrofishing surveys were conducted (end of August to beginning of
117 October) 1.5km upstream of the dam within the ponded zone (Figure 1, A). Prior to removal, the
118 decreased velocity and increased water depth in this area led to the accumulation of sand and silt on the
119 bottom, with a minimum water depth of approximately 0.7m. Following the removal of the dam, the
120 ponded zone disappeared and the natural shallow water habitat was restored to its original state, with
121 faster-flowing water, a water depth of 10-30cm, a natural substrate dominated by stones and cobbles,
122 the original gradient (approx. 0.3%) and the presence of water riffles, thus highly suitable brown trout
123 (*S. trutta*) spawning and nursing grounds. It is worth noting that this type of habitat is scarce in larger
124 Danish streams due to years of human alterations, making this location of particularly high interest.

125 A second location was surveyed from 1987 through to 2016, 1.5km downstream of the dam
126 (Figure 1, B). This stretch was recognized as excellent for spawning, even before the dam was
127 removed. The lake trout from Lake Mossø gained easier access to this area after 1992, when a fish
128 ladder was built at a weir near the lake. Before 1992, the brown trout population was almost entirely
129 dependent on the spawning of resident brown trout.

130

131 *Fish density: mark-and-recapture*

132 In the fall, the upstream (from 1997 to 2016) and the downstream (from 1987 to 2016) locations were
133 surveyed for lengths of 160m and 600m, respectively. The width of the river at these locations was
134 approximately 20m. Each location was electrofished once using two electrodes, with all captured
135 brown trout marked (fin-clipped in this case). The following day, the same locations were electrofished
136 a second time. All previously marked fish (i.e., recaptures) and unmarked fish (i.e., new captures) were
137 counted. The numbers were then used to calculate fish density estimates. Fish below 14cm were
138 considered young of the year (YOY) while larger fish (above 14cm) were pooled together and

139 considered older fish (OLD). The two groups were distinguishable due to a bimodal length distribution.

140 The following formula was applied to calculate density estimates of brown trout:

141
$$N = \frac{(M + 1)(C + 1)}{R + 1}$$

142 Where, N is the density estimate, M is the number of fish caught and marked during the first sampling,
143 C is the total number of captured fish during the second sampling (including recaptures), and R is the
144 number of recaptures during the second sampling (Lockwood and Schneider 2000). Results are
145 presented as number of fish per meter (length) of river, in accordance to the national Danish Brown
146 Trout Index (Kristensen et. al 2014), which states that population estimates of YOY in Danish streams
147 wider than 2m should not be calculated as number per m² as YOY mainly inhabit the river banks.

148

149 *Statistical analyses*

150 Mann-Whitney U-tests were used to compare trout density before and following removal of the Vilholt
151 dam. The density (fish per m) of yearling (YOY) and older (OLD) fish were analyzed separately in
152 both the upstream (A) and downstream (B) zones. The analyses were done using R 3.1.2 (R Core
153 Team, 2014). Variation in association with recorded mean values is given as standard deviation (\pm SD)
154 throughout.

155

156 **Results**

157 An immediate increase of YOY brown trout was observed at the upstream stretch after removal of the
158 dam, followed by a downstream increase in YOY after three years. In the upstream zone, mean YOY
159 density was 0.03 ± 0.04 fish per m before removal of the dam and 6.21 ± 2.77 fish per m following dam
160 removal. The mean upstream OLD density before removal was 0.16 ± 0.08 fish per m, and 0.30 ± 0.07

161 fish per m following removal. The mean downstream YOY density before and following the dam
162 removal was 1.2 ± 0.99 and 6.2 ± 2.8 fish per m, respectively. For OLD fish, the mean downstream
163 density was 0.31 ± 0.16 fish per m before dam removal and 0.43 ± 0.21 fish per m following dam
164 removal.

165 In the upstream zone, both YOY ($U = 24.0$, $p = 0.019$) and OLD fish ($U = 22.5$, $p = 0.041$)
166 densities increased significantly following dam removal (Figure 2A, 3A). In the downstream zone,
167 YOY density increased significantly following dam removal ($U = 62$, $p < 0.001$, Figure 2B, 3A), but no
168 significant change in OLD density was found ($U = 46$, $p = 0.14$; Figure 2B, 3B).

169

170 Discussion

171 The EU Water Framework Directive states that a watershed with a “good” ecological status should
172 have biological elements that show little distortion as a result of anthropogenic activities, though the
173 quality of these elements may deviate slightly from those observed in undisturbed conditions. A “high”
174 ecological status requires that a system suffer no or very minor anthropogenic disturbances, with
175 biological elements completely unaffected (Directive 2000/60/EC of the European Parliament and of
176 the Council, 2000). Simultaneously, the European Renewable Electricity Directive (2001/77/EC)
177 encourages the use of small-scale hydropower facilities to generate renewable energy. The presence of
178 dams (both small and large), and their associated environmental and biological impacts to freshwater
179 ecosystems, precludes an ecologically good status, as defined by the framework. The difficulty of
180 achieving this status is further exacerbated by the encouragement of the directive to establish small
181 hydrodams, making management and recovery plans contradictory and almost unachievable. Similar
182 contradictory directives exist at the international level (e.g., Sustainable Development Goals by United
183 Nations).

184 The availability and access to suitable habitats is of crucial importance for a wide range of
185 freshwater species, whether during spawning migration, feeding or refuge seeking (Northcote 1984;
186 Taylor et al. 1993; Lucas and Baras 2001). The observed increase in YOY density both upstream and
187 downstream of where the Vilholt dam was located, along with the upstream increase in OLD fish,
188 suggests that (1) the natural habitat quality was restored in the ponded zone as a highly suitable
189 spawning and nursing habitats, (2) safe passage and access to highly suitable spawning habitat
190 upstream was reestablished, and (3) movement between the two spawning grounds increased
191 recruitment. Here, we demonstrate that restoring river connectivity has allowed for a huge number of
192 fish to be born and thrive in an area previously devoid of YOY fish, presumably due to restored
193 spawning habitat and the ease of access to these high quality spawning grounds. The recorded density
194 of YOY trout in the present study (mean=6.2 YOY/m on both stretches) place the river in “good
195 ecological status” according to the EU Water Framework Directives (the Danish threshold is 2.5
196 YOY/m) and is in fact greater than normally observed in large Danish rivers, suggesting that barrier
197 removal may be the best mitigation approach in the context of river restoration in fragmented rivers.

198 The removal of the Vilholt dam restored the naturally adequate trout habitat in the former
199 ponded zone, resulting in an immediate increase in both YOY and OLD fish upstream in 2009. This is
200 likely because the removal allowed for the upstream passage of spawners from the lake, along with
201 providing highly suitable habitat for young fish to thrive, thus increasing survival. The removal had
202 little physical effect on the downstream habitat, which was already suitable for spawning. We note that
203 beginning in 1992, an increase in OLD fish was observed downstream. This is due to the establishment
204 of a fish ladder at a dam located between Vilholt and Lake Mossø. This fishpass led to a larger YOY
205 density in 1993. We also note that a sudden decrease in fish was observed in 1994; a large storm caused
206 the dam to break down, letting large amounts of mud and silt to be flushed downstream, practically

207 eliminating the year class. The year following removal (2009), neither YOY nor OLD fish densities
208 increased downstream of the dam. In 2011, a large increase in YOY individuals downstream was
209 observed. The large increase in YOY upstream in 2009 would have yielded a large smolt cohort (length
210 12-15cm) which likely migrated down to Lake Mossø. These individuals would then be returning to
211 spawn in both stretches in winter 2010-2011, likely contributing to the large YOY density observed in
212 2011 both upstream and downstream of the former dam. Furthermore, it is also possible that YOY from
213 upstream moved downstream to find suitable habitat if the density of fish is too high upstream.

214 We have shown that barrier removal can be beneficial for fish density especially upstream, but
215 also downstream. Since the removal, local anglers have also noticed an increase in the size and number
216 of lake trout caught in Lake Mossø. While these observations suggest that the removal of an artificial
217 obstacle may be beneficial at a whole-system level, we cannot make that conclusion for certain as our
218 study did not specifically evaluate this. While the Gudena river system supports a sustainable
219 population of older fish, including returning lake trout spawners from Lake Mossø as well as resident
220 trout, a wide spatial distribution of spawning and recruitment is needed to maintain population levels
221 over time (Berkeley et al. 2011). Before the Vilholt dam was removed, the rate of spawning was low,
222 with few YOY surviving in the ponded zone. YOY are an important component for maintaining
223 population sustainability, and barriers may truncate the age-structure and the range of distribution of
224 fish species, with potentially devastating effects on population sustainability.

225 This study demonstrates the extent to which small-scale obstacles (a 2.4m high dam in this
226 case) can affect the density and distribution of river spawning fish. Low-head barriers of this type,
227 which can obviously lead to the deterioration of natural spawning and nursery areas in ponded zones,
228 are rarely considered in management plans. It is our hope that these results will reinforce the need to
229 firstly, include smaller weirs and dams in management plans, and secondly, considered removal as an

230 option rather than immediately attempt to establish artificial fish passage. Our findings have important
231 implications for the management of barriers across the world. Environmental directives from many
232 agencies (e.g., EU Waterframe Directive, UN Sustainable Development Goals) have made
233 contradicting requests, with emphasis on reducing pollution, but little to no demands made to improve
234 ecosystems impacted by barriers. Given the immediate positive effects of the removal of small barriers,
235 this approach should be viewed as an economically and ecologically profitable option.

236

237 **Authors' Contributions**

238 KBG participated in the data analysis, data interpretation, manuscript conception and revision. JN
239 participated in the data acquisition and interpretation, as well as manuscript revision. KA and MHL
240 participated in data interpretation and manuscript revision.

241

242 **Acknowledgments**

243 We are thankful to all the volunteers (including community members and anglers) who helped with the
244 electrofishing surveys through the years. Funding for this research was provided by the Danish Rod and
245 Net Fish License and the European Union AMBER (Adaptive Management of Barriers in European
246 Rivers) project.

247

248 **Data Accessibility**

249 Data will be deposited on figshare upon acceptance of the manuscript.

250

251 **Literature Cited**

- 252 Aarestrup, K., & Jepsen, N. (1998). Spawning migration of sea trout (*Salmo trutta* (L)) in a Danish
253 river. *Hydrobiologia*, 371, 275-281.
- 254 Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon
255 (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater*
256 *Fish*, 12(3), 169-176.
- 257 Baxter, R.M. (1977). Environmental effects of dams and impoundments. *Annual Review of Ecology*
258 *and Systematics*, 8(1), 255-283.
- 259 Bednarek, A. T. (2001). Undamming rivers: a review of the ecological impacts of dam
260 removal. *Environmental management*, 27(6), 803-814.
- 261 Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via
262 protection of age structure and spatial distribution of fish populations. *Fisheries*, 29(8), 23-32.
- 263 Birnie-Gauvin, K., Aarestrup, K., Riis, T.M.O., Jepsen, N., Koed, A. (in press). Shining the light on the
264 loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers and its
265 implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*. doi:
266 10.1002/aqc.2795
- 267 Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow
268 regimes for aquatic biodiversity. *Environmental management*, 30(4), 492-507.
- 269 Burroughs, B. A., Hayes, D. B., Klomp, K. D., Hansen, J. F., & Mistak, J. (2010). The effects of the
270 Stronach Dam removal on fish in the Pine River, Manistee County, Michigan. *Transactions of*
271 *the American Fisheries Society*, 139, 1595-1613.
- 272 Catalano, M. J., Bozek, M. A., & Pellett, T. D. (2007). Effects of dam removal on fish assemblage
273 structure and spatial distributions in the Baraboo River, Wisconsin. *North American Journal of*
274 *Fisheries Management*, 27, 519-530.

275 Cooke, S. J., Bunt, C. M., Hamilton, S. J., Jennings, C. A., Pearson, M. P., Cooperman, M. S., &
276 Markle, D. F. (2005). Threats, conservation strategies, and prognosis for suckers
277 (Catostomidae) in North America: insights from regional case studies of a diverse family of
278 non-game fishes. *Biological Conservation*, 121(3), 317-331

279 Cowx, I. G., & Welcomme, R. L. (1998). *Rehabilitation of rivers for fish*. Food & Agriculture
280 Organization of the United Nations. Oxford: Fishing News Books.

281 Downward, S., & Skinner, K. (2005). Working rivers: the geomorphological legacy of English
282 freshwater mills. *Area*, 37, 138-147.

283 Doyle, M. W., Stanley, E. H., Harbor, J. M., & Grant, G. S. (2003). Dam removal in the United States:
284 emerging needs for science and policy. *Eos, Transactions American Geophysical Union*, 84, 29-
285 33.

286 Doyle, M. W., Stanley, E. H., Orr, C. H., Selle, A. R., Sethi, S. A., & Harbor, J. M. (2005). Stream
287 ecosystem response to small dam removal: lessons from the Heartland. *Geomorphology*, 71,
288 227-244.

289 Dudgeon, D. (1992). Endangered ecosystems: a review of the conservation status of tropical Asian
290 rivers. *Hydrobiologia*, 248(3), 167-191.

291 Hall, J. W., Smith, T. I., & Lamprecht, S. D. (1991). Movements and habitats of shortnose sturgeon,
292 *Acipenser brevirostrum* in the Savannah River. *Copeia*, 695-702

293 Hitt, N. P., Eyler, S., & Wofford, J. E. (2012). Dam removal increases American eel abundance in
294 distant headwater streams. *Transactions of the American Fisheries Society*, 141, 1171-1179.

295 Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radio-tagged Atlantic
296 salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward

297 migration. In *Advances in Invertebrates and Fish Telemetry* (pp. 347-353). Springer
298 Netherlands.

299 Jungwirth, M., Schmutz, S., & Weiss, S. (Eds.). (1998). *Fish migration and fish bypasses* (Vol. 4).
300 Oxford: Fishing News Books.

301 Jungwirth, M., Muhar, S., & Schmutz, S. (2000). Fundamentals of fish ecological integrity and their
302 relation to the extended serial discontinuity concept. In *Assessing the Ecological Integrity of*
303 *Running Waters* (pp. 85-97). Springer Netherlands.

304 Koed, A., Jepsen, N., Aarestrup, K., & Nielsen, C. (2002). Initial mortality of radio-tagged Atlantic
305 salmon (*Salmo salar* L.) smolts following release downstream of a hydropower station.
306 In: *Aquatic Telemetry* (pp. 31-37). Netherlands: Springer.

307 Kristensen, E.A., Jepsen, N., Nielsen, J., Pedersen, S., & Koed A. (2014). Dansk Fiskeindeks For
308 Vandløb (DFFV). Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, 58 s. -
309 Videnskabelig rapport fra DCE - Nationalt Center for Miljø og Energi nr. 95.

310 Lockwood, R.N. & Schneider, J.C. (2000). Chapter 7: Stream fish population estimates by mark-and-
311 recapture and depletion methods. In: *Manual of Fisheries Survey Methods II: with periodic*
312 *updates*. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.

313 Lucas, M.C., & Baras, E. (2001). *Migration of freshwater fishes*. John Wiley & Sons.

314 Lucas, M.C., Bubb, D.H., Jang, M.H., Ha, K., & Masters, J. E. (2009). Availability of and access to
315 critical habitats in regulated rivers: effects of low-head barriers on threatened
316 lampreys. *Freshwater Biology*, 54(3), 621-634.

317 McAllister, D.E., Hamilton, A.L., & Harvey, B. (1997). Global freshwater biodiversity: striving for the
318 integrity of freshwater systems. *Sea Wind*, 11, 1-40.

319 Morita, K., & Yamamoto, S. (2001). Contrasts in movement behavior of juvenile white-spotted charr
320 between stocks above and below a dam. *Fisheries science*, 67(1), 179-181.

321 Northcote, T.G. (1984). Mechanisms of Fish Migration in Rivers. In: Mechanisms of Migration in
322 Fishes (McCleave, J.D., Dodson, J.J., Neill, W.H. eds.). Plenum, NY, USA, pp 317-355.

323 Northcote, T.G. (1998). Migratory behaviour of fish and its significance to movement through riverine
324 fish passage facilities. In: *Fish migration and fish bypasses*, Jungwirth, M., Schmutz, S. &
325 Weiss, S. (eds). Fishing News Books: Cambridge, 3-18.

326 Nützmann, G., Wolter, C., Venohr, M., & Pusch, P. (2011). Historical patterns of anthropogenic
327 impacts on freshwaters in the Berlin-Brandenburg region. *Die Erde*, 142, 41-64.

328 Pess, G. R., McHenry, M. L., Beechie, T. J., & Davies, J. (2008). Biological impacts of the Elwha
329 River dams and potential salmonid responses to dam removal. *Northwest Science*, 82, 72-90.

330 Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E., & Prendergast, L.A. (1991). Feeding of predaceous
331 fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia
332 River. *Transactions of the American Fisheries Society*, 120, 405-420.

333 R Core Team. (2014). R: a language and environment for statistical computing. R Foundation for
334 Statistical Computing, Vienna, Austria.

335 Ricciardi, A., & Rasmussen, J.B. (1999). Extinction rates of North American freshwater fauna.
336 *Conservation Biology*, 13, 1220-1222.

337 Taylor, P.D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of
338 landscape structure. *Oikos*, 68, 571-573.

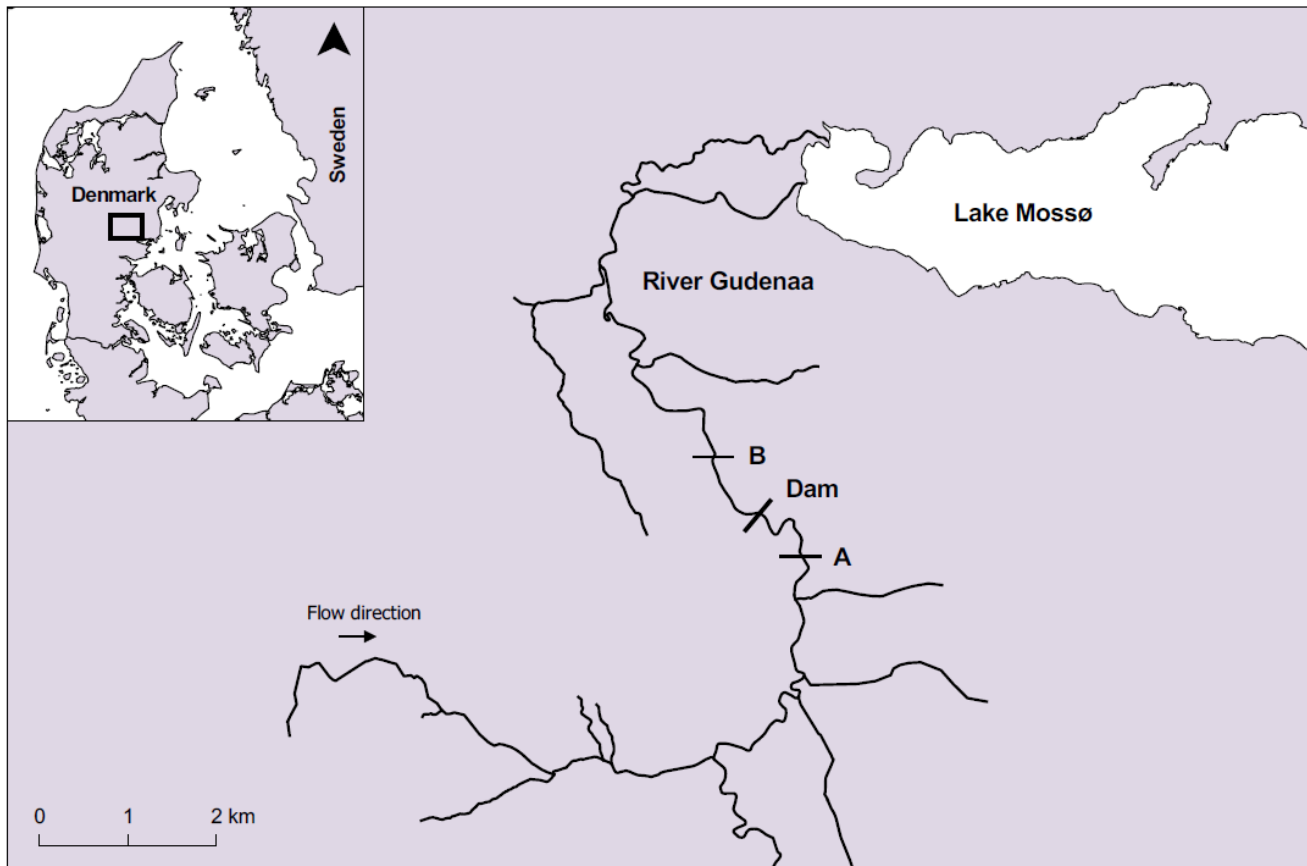
339

340

341

342 **Figures**

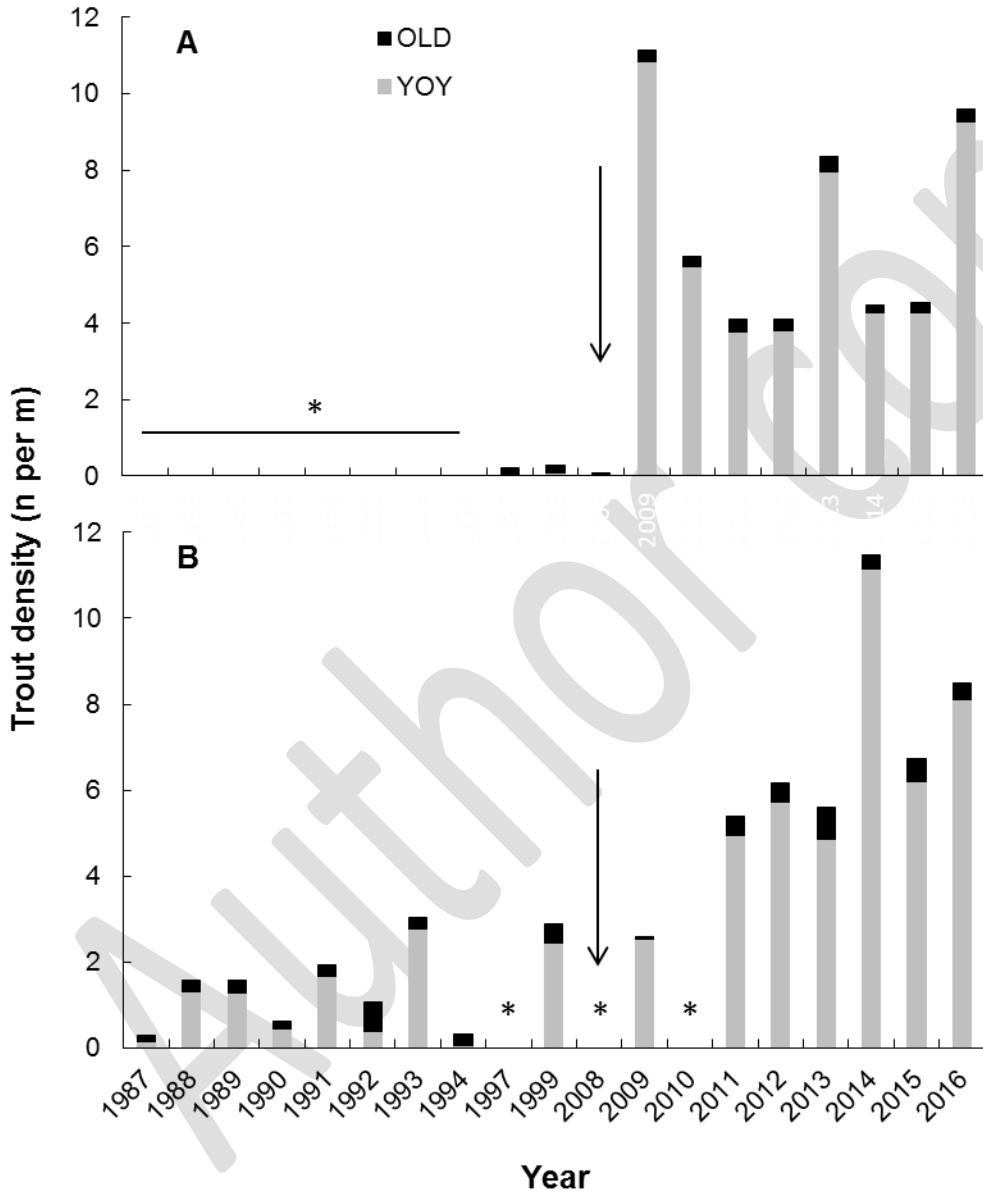
343 **Figure 1.** The Vilholt dam was located in the Gudena river system, in central Jutland, Denmark, until
344 2008. The upstream and downstream sampling locations are represented by letters A and B,
345 respectively.



346

347

348 **Figure 2.** Brown trout (*Salmo trutta*) density number of individuals per m of river) upstream (A) and
 349 downstream (B) of the Vilholt dam. Downward pointing arrow shows dam removal. Asterisks
 350 represent years when no surveys were carried out.



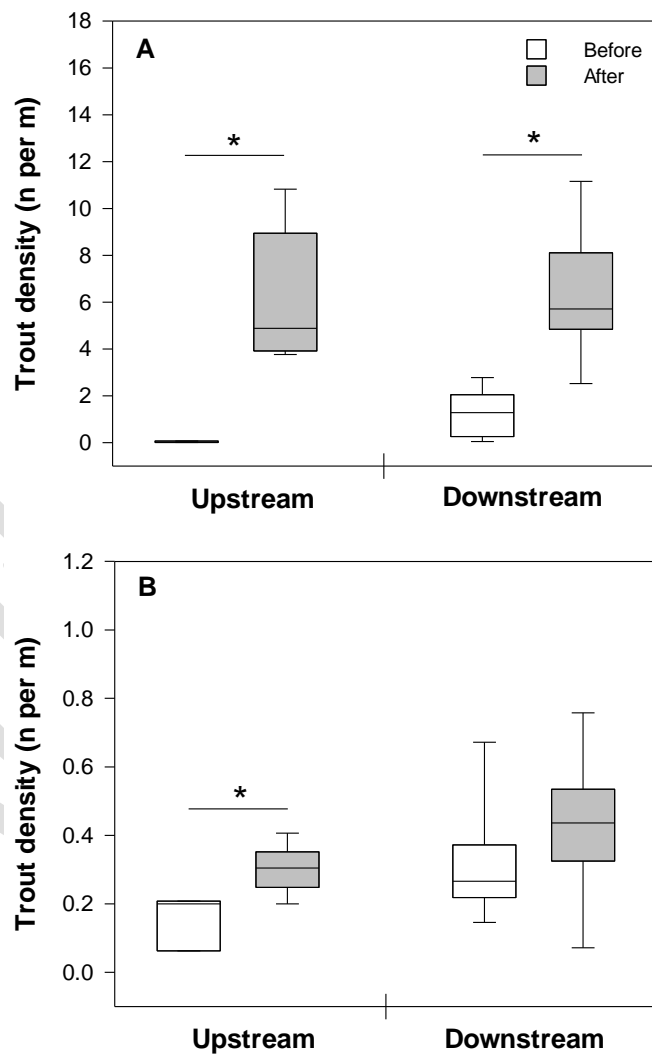
351

352

353

354 **Figure 3.** Boxplots showing the density of YOY (A) and OLD (B) trout (*Salmo trutta*) in the upstream
355 and downstream zones of the Vilholt dam before and after it was removed. The line within each box
356 represents median fish density, ends of boxes represent the 25th and 75th percentiles, and whiskers
357 represent the 10th and 90th percentiles. Asterisks indicate significant difference at $p < 0.05$. Note the
358 different scales on y-axes.

359



360
361