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**Shining a light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers and its implications for management**

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**Running title:** Habitat loss as a forgotten consequence of barriers

47 **Abstract**

48 1. The majority of rivers around Europe have been modified in one way or another, and no  
49 longer have an original, continuous flow from source to outlet. The presence of weirs and dams  
50 has altered habitats, thus affecting the wildlife that lives within them. This is especially true for  
51 migrating rheophilic fish species, which in addition to safe passage depend on gradient and fast  
52 flowing waters for reproductive success and early development.

53 2. Thus far, research has focused on investigating the impacts of weirs and dams on fish passage,  
54 with less attention paid to the loss of habitat entrained by such infrastructures. The loss of  
55 rheophilic habitat is particularly important in lowland streams, where gradient is limited, and  
56 dams and weirs can be constructed with less effort.

57 3. Denmark is considered a typical lowland country, where the landscape around streams and  
58 rivers has been modified by agriculture and other human activities for centuries, leaving  
59 management practitioners wondering how much change is acceptable to maintain sustainable  
60 fish populations and fisheries practices.

61 4. With examples from Denmark, we attempt to conceptualize the loss in habitat as a result of  
62 barriers in lowland streams and rivers, and the repercussions that such alterations may have on  
63 rheophilic fish populations. Furthermore, we emphasize the need for management to address  
64 habitat loss and its related consequences concurrently with the improvement of fish passage.

65

66 **Keywords:** river, stream, fish, river management, catchment management, indicator species,  
67 hydropower, impoundment

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69

70 **Introduction**

71 The presence of barriers (such as weirs, dams and culverts) in rivers has grown immensely in the  
72 last centuries. These barriers are most often put in place to serve human needs, such as to  
73 generate electricity (Welcomme, 1995), though fish farming, irrigation and flood control are also  
74 common (Jungwirth, 1998; Jungwirth, Muhar, & Schmutz, 2000). When barriers were first  
75 established, the potential detrimental impacts to the surrounding environment were not  
76 considered (Hunt, 1988), but it quickly became apparent that they had severe consequences to  
77 river ecosystems and the organisms that live within them (e.g., Aarestrup & Koed, 2003;  
78 Alexandre & Almeida, 2010; Dynesius & Nilsson, 1994; Junge, Museth, Hindar, Kraabøl, &  
79 Asbjørn Vøllestad, 2014; Koed, Jepsen, Aarestrup, & Nielsen, 2002).

80 Many countries lack a complete inventory of water barriers and those that do typically  
81 register large barriers only (e.g., the United States National Inventory of Dams for dams above  
82 10m). In Denmark, the Ministry of Environment and Food has recently generated an inventory of  
83 barriers to implement the EC Waterframe Directive (Council of the European Communities,  
84 2000). Although quite comprehensive, even this inventory is unlikely to account for all Danish  
85 barriers given that smaller weirs and especially culverts often remain unregistered. While  
86 freshwater management have remedied some of the negative consequences of barriers associated  
87 with fish passage (e.g., through fish ladders, fish pass etc.), most of the habitat changes due to  
88 damming are still present and thus still threaten stream and river ecosystem sustainability. The  
89 need to take action is pressing given that riverine ecosystems are in the poorest condition of all  
90 ecosystems across the globe (WWF, 2016). To date, there has been tremendous focus on the  
91 impacts of barriers on fish passage (both upstream and downstream movements; e.g., Aarestrup  
92 & Koed, 2003), and finding ways to establish minimal flow to sustain fluvial habitat (Rood et al.,

93 2005). While this approach has merit for management, it ignores some basic problems: (1) it  
94 does not account for the loss of habitat in the resulting “ponded” zone that results from  
95 damming, and (2) it typically ignores the small-scale migrations and movements of less known  
96 species (Larinier, 2001). Moreover, current management schemes tend to neglect effects on other  
97 aquatic organisms, such as plants and invertebrates, which are also affected by the presence of  
98 obstacles (Merritt & Wohl, 2005, Palmer, Arensburger, Botts, Hakenkamp, & Reid, 1995).

99 Here, we briefly describe the important consequences of barriers for rheophilic fish  
100 species (i.e., species that live in fast-moving, oxygen-rich water), with greater focus on (1)  
101 quantity of habitat lost due to a loss in gradient, and (2) lowland streams/ivers given that  
102 gradient is a limiting factor for rheophilic fish reproduction and development in such  
103 watercourses. We attempt to conceptualize the loss in habitat as a result of barriers, and present a  
104 “quick and dirty” method that could be applied to management scenarios which aim to restore  
105 the river continuum and natural habitats for rheophilic fish species.

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### 107 **Habitat changes as a consequence of barriers**

108 Barriers result in fragmentation and decoupling of hydrological, geomorphological and  
109 ecological aspects of a river, thereby modifying habitat and restricting movement between them  
110 (Lucas & Baras, 2000; McCluney et al., 2014; Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff  
111 et al., 1997; Ward & Stanford, 1983, 1995). Specifically, the upstream section becomes a  
112 “ponded zone” and the length of this zone depends on the height of the dam and the watercourse  
113 gradient (Petts, 1984; Poff et al., 1997; Stanford et al., 1996; Figure 1). In turn, this completely  
114 changes the river habitat upstream of the barrier, such as increasing homogeneity of substrates  
115 and vegetation (Nilsson & Jansson, 1995; Poff, Olden, Merritt, & Pepin, 2007), increasing depth,

116 reducing current speed, reducing oxygenation, causing sedimentation and changing water  
117 temperatures (Petts, 1984; Poff & Hart, 2002). The downstream habitat also becomes altered, but  
118 for the purpose of this paper, we focus primarily on the upstream geomorphological changes  
119 induced by barriers.

120

### 121 **Lowland streams and rivers: case studies from Denmark**

122 In lowland streams, the areas with relatively high gradients are preferentially selected to  
123 construct barriers because of their greater relative potential for energy (Hoffman & Dunham,  
124 2007). Damming effects also vary depending on the size of the watercourse and the location of  
125 the dam. Generally, a dam located closer to the source of a river will have fewer repercussions  
126 than one located further downstream (Figure 1), because the gradient of the river is typically  
127 greater in the upper regions, and therefore a smaller proportion of the watercourse is affected by  
128 the damming. Furthermore, upstream parts of a river tend to be narrower than downstream  
129 sections, thus the total damming impacts are considerably lower when a barrier is upstream  
130 (Figure 1), though may still have important consequences for local species.

131 In Denmark, a country consisting solely of lowland landscapes, rivers are typically small,  
132 and have smaller gradients than those from more mountainous countries. While a river in  
133 Norway, for example, can easily provide a drop of 500m, even the larger Danish rivers typically  
134 begin below 100m above sea level. Large gradients are therefore a limited resource in Denmark.  
135 Nonetheless, much of the wildlife in Danish rivers relies on these scarce habitats (especially  
136 rheophilic fish), making them especially important to protect. Within lowland rivers, the areas  
137 where the gradient is (relatively) large, there is greater potential for harnessing water power,  
138 often leading to the establishment of more than a single dam throughout the river course. For

139 example, River Grejs (Vejle, Denmark) runs for approx. 15km, and has a total drop of 55m from  
140 source to outlet, where a total of 11 dams were established by 1986.

141 An altered flow regime caused by dams affects the wildlife present, typically reducing  
142 biodiversity (Bunn & Arthington, 2002; Power, Dietrich, & Finlay, 1996) and population size of  
143 migratory species (Hubbs & Pigg, 1976; Zhong & Power, 1996). This is especially true for  
144 rheophilic species (Hoffman & Dunham, 2007). Hence, the increase in water level (i.e.,  
145 increased depth) and current decrease may be used as indicators of the loss in geomorphological  
146 variability and thus a river's ability to maintain biodiversity, as well as a rough measure of  
147 potential rheophilic habitat loss. This is important because a relatively large proportion of species  
148 that inhabit freshwater streams require relatively fast flowing and oxygen-rich water with varied  
149 substrate conditions in order to thrive; the most common threat to freshwater species (i.e., fish,  
150 amphibians, reptiles, mammals and birds) is habitat loss and degradation from anthropogenic  
151 activities (Freyhof & Brooks, 2011).

152 Given the extent of dam establishment in some lowland rivers, much of what used to  
153 constitute adequate habitats for these species is no longer available. For example, habitat quality  
154 indicator species in Danish rivers, such as Atlantic salmon (*Salmo salar*) and brown trout (*Salmo*  
155 *trutta*), spawn and grow (during early life stages) in stretches where habitat is typified as riffle  
156 areas with gravel or cobble substrate, with low gradients (Gibson, 1993, Gibson, Bowlby, &  
157 Amiro, 2008). Dammed rivers reduce the availability of such stretches, and have been shown to  
158 reduce overall salmonid populations (Welcomme, 1985).

159 Recognizing the consequences of barriers on freshwater ecosystems has led to the pursuit  
160 of mitigation strategies. For example, some municipal and governmental agencies have put in  
161 place new infrastructures to address environmental concerns (e.g., periodic high flows, fish

162 ladders; Auer, 1996). A common approach is the installation of nature-like fish passes. These  
163 bypasses can be useful in allowing fish to move upstream and downstream of a barrier (e.g.,  
164 Calles & Greenberg 2005) but do not remedy the underlying habitat alterations caused by  
165 barriers (Dadswell, 1996), and have been found to have limited success (Bunt, Castro-Santos, &  
166 Haro, 2012). Recent evidence suggests that dam removal provides an efficient management tool  
167 for ecological restoration of freshwater ecosystems (reviewed in Bednarek, 2001), and should be  
168 considered where possible. In fact, complete dam removal restores habitat quality, quantity *and*  
169 connectivity, thus restoring previously lost habitat (Pess, McHenry, Beechie, & Davies, 2008),  
170 enabling rheophilic fish populations to re-establish and also enabling fish to migrate (both on  
171 small and large scales), regardless of how much knowledge we have on a species.

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### 173 **Conceptualizing habitat loss: applications for management**

174 In Table 1, we provide data for three Danish rivers that vary in size from 3m to 40m in width and  
175 from 20km to 149km in length. We present the total drop from spring to outlet, the summed drop  
176 resulting from barriers, the total length of the river, and the summed length of the ponded zone.  
177 This data was then used as a rough estimate of vertical and horizontal habitat loss (Table 1). This  
178 specific information was chosen given that it is typically easily accessed and could easily be  
179 applied to management strategies. We acknowledge that the habitat loss may not be proportional  
180 to the loss in gradient (as this approach suggests). In fact, the relationship between habitat loss  
181 and gradient is likely more complex, especially if barriers are present further upstream, but this  
182 approach has merit to rapidly address some of the management concerns we are currently facing.

183         This approach shows that a large proportion of the potential rheophilic habitat is lost in  
184 the ponded zones (Table 1). River Gudena, the longest river in Denmark, was historically one of

185 the most important Danish rivers with large populations of anadromous salmonids. It has seven  
186 barriers in the main stem predominantly for hydro power generation, yielding a total relative loss  
187 of the potential spawning and juvenile development habitat of 36% (Table 1). This loss increases  
188 to approx. 60% if we exclude the upper 10% of the watercourse where the river is narrow, the  
189 gradient is significantly larger, and salmon production is historically non-existent. The smaller  
190 Rivers Villestrup and Omme, on the other hand, have barriers established for fish farming or old  
191 watermill purposes, but nonetheless result in a similar loss in habitat. Furthermore, this estimated  
192 habitat loss is likely underestimated at fish farm sites, because the stretch of the river between a  
193 weir and the outlet of a fish farm is often several hundreds of meters apart, with very little water  
194 flow during a large part for the year. The habitat quality in these stretches is limited as a  
195 consequence of the reduced water flow alone, but may also represent an area of high predation  
196 (Jepsen, Aarestrup, Økland, & Rasmussen, 1998; Poe, Hansel, Vigg, Palmer, & Prendergast,  
197 1991; Ruggerone, 1986).

198         The three rivers discussed in the above paragraph run mainly through agricultural land.  
199 However, rivers running through urban areas may be subjected to even more severe habitat loss  
200 (Birnie-Gauvin, Peiman, Gallagher, de Bruijn, & Cooke 2016). River Mølleaa is approx. 13km  
201 long, and flows through Northern Copenhagen into the Øresund strait. The river has nine dams,  
202 which together remove an estimated 75% of the river gradient. There is virtually no natural  
203 gradient left, and thus no adequate habitat for rheophilic species.

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## 205 **Conclusions**

206 The productive potential of rheophilic species in lowland freshwater rivers is greatly reduced by  
207 the presence of dams and weirs. Typical management interventions aim to address issues

208 concerning fish passage, but often omit to consider the habitat that has already been lost as a  
209 result of barriers for which we lack empirical data (Abell, 2002). Given the relatively limited  
210 gradient available in Danish rivers (and in lowland rivers across the world in general) and the  
211 potential habitat loss associated with the latter, the overall effects of water barriers on habitat  
212 should be included in assessments of watercourses. These actions should be undertaken  
213 concurrently with the improvement of fish passage and other typical management-related  
214 challenges. To improve the state of regulated lowland rivers may mean that many of these river  
215 obstacles need to be removed in order to reinstate the former gradient and habitat, which may re-  
216 establish proper fauna passage in itself.

217         The purpose of this paper was to shine a light on a problem that is often ignored in  
218 traditional fish management to this day: rheophilic habitat loss resulting from barriers. Too often,  
219 the focus of management is on fish passage alone, ignoring other important effects of damming.  
220 This may be particularly true for lowland rivers. Given the number of dams and weirs in rivers  
221 across the world, we acknowledge that acquiring complete knowledge on habitat loss and fish  
222 passage is a daunting task. However, if the majority of rheophilic-appropriate habitat is lost,  
223 improving fish passage may be pointless. We therefore suggest the use of a “quick and dirty”  
224 method (Table 1) to evaluate the potential loss in habitat as a result of barriers. This approach  
225 may provide managers with an improved overview of the state of rivers, and allow for better  
226 management strategies to be implemented. Further studies should be undertaken to evaluate the  
227 validity of the approach.

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411 **Table 1. Conceptualizing rheophilic habitat loss.** Using three Denmark rivers, the ratio of the  
 412 total drop as a result of barriers (m) to the total drop of the river from source to outlet (m) was  
 413 used as a proxy for vertical habitat loss (%). The ratio of the summed ponded zones (km) to the  
 414 total river length (km) was used as a proxy for horizontal habitat loss (%). This “quick and dirty”  
 415 approach to estimate habitat loss from barriers provides managers with a low cost and effective  
 416 method to get a rapid overview of the current state of freshwater streams and rivers, and may  
 417 enable the implementation of more effective management strategies.

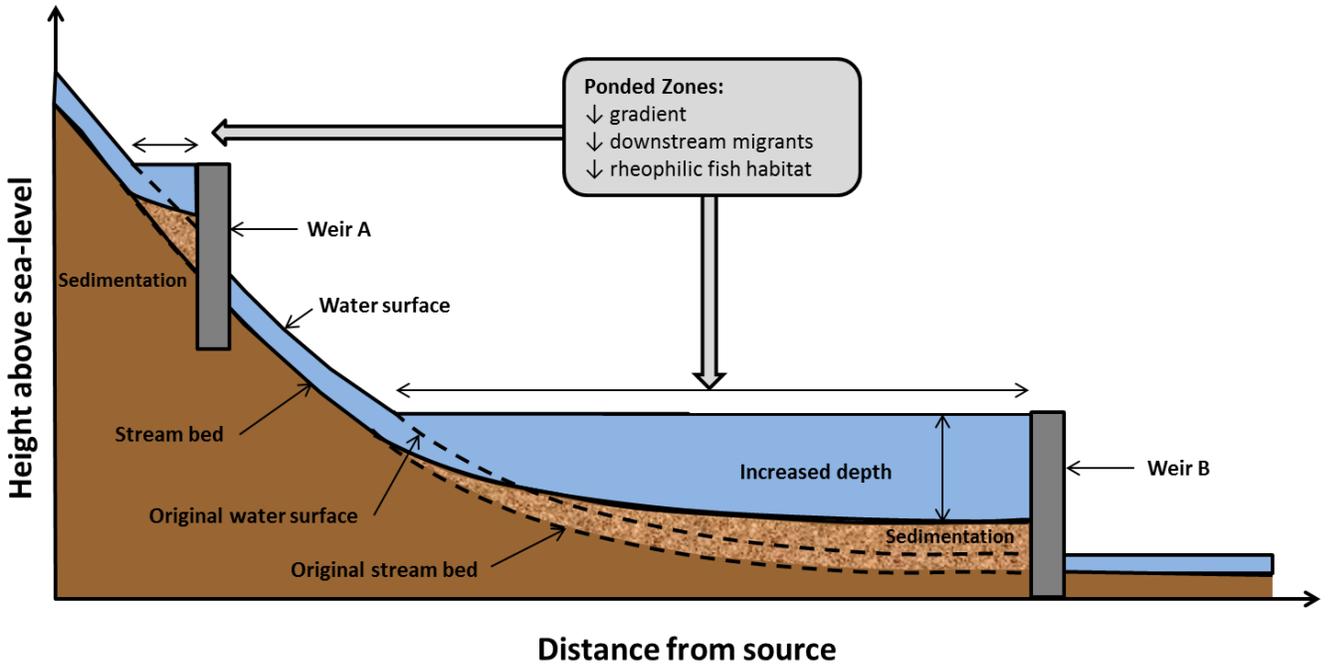
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<b>River (# of dams)</b>	<b>Total drop from source to outlet (m)</b>	<b>Summed drop from barriers (m)</b>	<b>Vertical habitat loss (%)</b>	<b>Total river length (km)</b>	<b>Summed ponded zones (km)</b>	<b>Horizontal habitat loss (%)</b>
<b>Villestrup (6)</b>	22	8.8	40	20.0	5.8	29
<b>Omme (14)</b>	75	17.7	24	55.0	11.35	21
<b>Gudena (7)</b>	69	24.9	36	149.0	-*	-*

419 \* Information not available given that the weirs and dams are too old to accurately estimate the  
 420 length of ponded zones.

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447 **Figure 1. Effects of dams on rivers.** Conceptualized diagram of the effects of dams on rivers  
 448 showing two (A and B) identical weirs (i.e., same stemmed height). Depending on the gradient  
 449 of the river, the ponded zone differs. As the gradient typically decreases, and the river size  
 450 increases, from source to outlet, a similar sized weir closer to the outlet will have a larger ponded  
 451 zone, both in terms of length and surface area. Downward-pointing arrows (↓) represent a  
 452 decrease.  
 453



454