Received: 3 January 2017 | Revised: 12 March 2017 | Accepted: 16 April 2017
DOI: 10.1002/aqc.2795

WILEY

SHORT COMMUNICATION

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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Funding information
Danish rod and net fish licence funds; European Union AMBER project (Adaptive Management of Barriers in European Rivers).

Abstract

1. The majority of rivers around Europe have been modified in one way or another, and no longer have an original, continuous flow from source to outlet. The presence of weirs and dams has altered habitats, thus affecting the wildlife that lives within them. This is especially true for migrating rheophilic fish species, which, in addition to safe passage, depend on gradient and fast-flowing waters for reproductive success and early development.
2. Thus far, research has focused on investigating the impacts of weirs and dams on fish passage, with less attention paid to the loss of habitat entrained by such infrastructure. The loss of rheophilic habitat is particularly important in lowland streams, where gradient is limited, and dams and weirs can be constructed with less effort.
3. Denmark is considered a typical lowland country, where the landscape around streams and rivers has been modified by agriculture and other human activities for centuries, leaving management practitioners wondering how much change is acceptable to maintain sustainable fish populations and fisheries practices.
4. With examples from Denmark, this paper attempts to conceptualize the loss in habitat as a result of barriers in lowland streams and rivers, and the repercussions that such alterations may have on rheophilic fish populations. Furthermore, the need for management to address habitat loss and its related consequences concurrently with the improvement of fish passage is emphasized.

KEYWORDS
catchment management, fish, hydropower, impoundment, indicator species, river, river management, stream

1 | INTRODUCTION

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

Many countries lack a complete inventory of water barriers and those that do typically register large barriers only (e.g. the United States National Inventory of Dams for dams higher than 10 m). In Denmark, the Ministry of Environment and Food has recently generated an inventory of barriers to implement the EC Water Framework Directive (Council of the European Communities, 2000). Although quite comprehensive, even this inventory is unlikely to account for all Danish barriers, given that smaller weirs and especially culverts often remain unregistered. While freshwater managers have remedied some of the negative consequences of barriers associated with fish passage (e.g. through fish ladders, fish passes, etc.), most of the habitat changes caused by damming are still present and thus still threaten stream and river ecosystem sustainability. The need to take action is pressing given that river ecosystems are in the poorest condition of all ecosystems across the globe (WWF, 2016). To date, most attention has been given to the impacts of barriers on fish passage (both upstream and downstream movements; Aarestrup & Koed, 2003), and finding ways to establish minimum flows to sustain fluvial habitat (Rood et al., 2005). While this approach has merit for management, it ignores some basic problems: it does not account for the loss of habitat in the 'ponded' zone that results from damming, and it typically ignores the small-scale migrations and movements of less well-known species (Larinier, 2001). Moreover, current management schemes tend to neglect effects on other aquatic organisms, such as plants and invertebrates, which are also affected by the presence of obstacles (Merritt & Wohl, 2005; Palmer, Arensburger, Botts, Hakenkamp, & Reid, 1995).

This paper briefly describes the important consequences of barriers for rheophilic fish species (i.e. species that live in fast-moving, oxygen-rich water), with greater focus on the quantity of habitat lost owing to a loss in gradient, and lowland rivers and streams given that gradient is a limiting factor for rheophilic fish reproduction and development in such watercourses. We attempt to conceptualize the loss in habitat as a result of barriers, and present a 'quick and dirty' method that could be applied to management scenarios that aim to restore the river continuum and natural habitats for rheophilic fish species.

2 | HABITAT CHANGES AS A CONSEQUENCE OF BARRIERS

Barriers result in fragmentation and decoupling of hydrological, geomorphological and ecological aspects of a river, thereby modifying habitat and restricting movement between them (Lucas & Baras, 2000; McCluney et al., 2014; Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff et al., 1997; Ward & Stanford, 1983, 1995). Specifically, the upstream section becomes a 'ponded zone' and the length of this zone depends on the height of the dam and the watercourse gradient (Petts, 1984; Poff et al., 1997; Stanford et al., 1996; Figure 1). In turn, this completely changes the river habitat upstream of the barrier, by increasing the homogeneity of substrates and vegetation (Nilsson & Jansson, 1995; Poff, Olden, Merritt, & Pepin, 2007), increasing the depth, reducing current speed, reducing oxygenation, causing sedimentation and changing water temperatures (Petts, 1984; Poff & Hart, 2002). The downstream habitat also becomes altered, but this paper focuses primarily on the upstream geomorphological changes induced by barriers.

3 | LOWLAND STREAMS AND RIVERS: CASE STUDIES FROM DENMARK

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

In Denmark, a country consisting solely of lowland landscapes, rivers are typically small, and have shallower gradients than those in more mountainous countries. While a river in Norway, for example, can easily provide a drop of 500 m, even the larger Danish rivers typically rise below 100 m above sea level. Steep gradients are therefore a limited resource in Denmark. Nonetheless, much of the wildlife in Danish rivers relies on these scarce habitats (especially rheophilic fish), making them especially important to protect. Within lowland rivers, the areas where the gradient is (relatively) steep offer greater potential for harnessing water power, often leading to the establishment of more than a single dam throughout the river course. For example, the River Grejs (Vejle, Denmark) runs for approx. 15 km, and has a total drop of 55 m from source to outlet, with 11 dams established by 1986.

An altered flow regime caused by dams affects the wildlife present, typically reducing biodiversity (Bunn & Arthington, 2002;

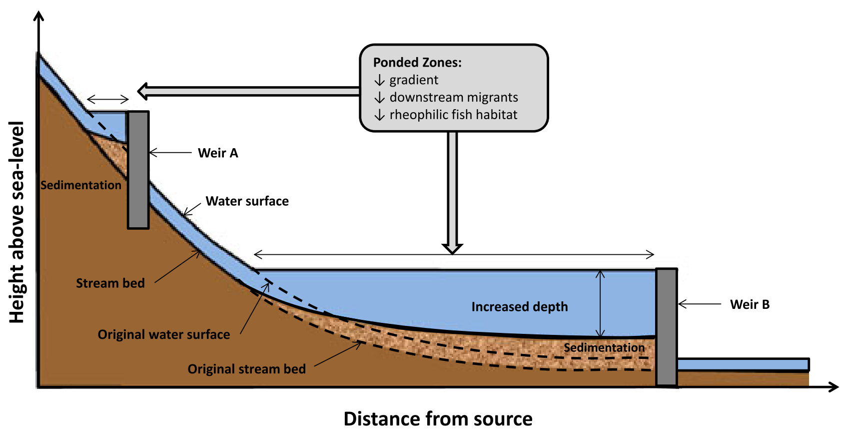

FIGURE 1 Effects of dams on rivers. Conceptualized diagram of the effects of dams on rivers showing two identical weirs (i.e. same stemmed height) (A and B). The ponded zone differs depending on the gradient of the river. As the gradient typically decreases, and the river size increases, from source to outlet, a similar sized weir closer to the outlet will have a larger ponded zone, both in length and surface area. downward-pointing arrows (↓) represent a decrease

Power, Dietrich, & Finlay, 1996) and population size of migratory species (Hubbs & Pigg, 1976; Zhong & Power, 1996). This is especially true for rheophilic species (Hoffman & Dunham, 2007). Hence, an increase in water level (i.e. increased depth) and a decrease in water velocity may be used as indicators of the loss in geomorphological variability and thus a river's ability to maintain biodiversity, as well as a rough measure of potential rheophilic habitat loss. This is important because a relatively large proportion of species that inhabit freshwater streams require relatively fast-flowing and oxygen-rich water with varied substrate conditions in order to thrive; the most common threat to freshwater species (i.e. fish, amphibians, reptiles, mammals and birds) is habitat loss and degradation from human activities (Freyhof & Brooks, 2011).

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

Recognizing the consequences of barriers on freshwater ecosystems has led to the pursuit of mitigation strategies. For example, some municipal and government agencies have put in place new infrastructure to address environmental concerns (e.g. periodic high flows, fish ladders; Auer, 1996). A common approach is the installation of nature-like fish passes. These bypasses can be useful in allowing fish to move upstream and downstream of a barrier (Calles & Greenberg, 2005) but do not remedy the underlying habitat alterations caused by barriers (Dadswell, 1996), and have been found to have limited success (Bunt, Castro-Santos, & Haro, 2012). Recent evidence suggests that dam removal provides an efficient management tool for ecological restoration of freshwater ecosystems (reviewed in Bednarek, 2001), and should be considered where possible. In fact, regardless of how much knowledge there is on individual species, complete dam removal restores habitat quality, quantity *and* connectivity, thus restoring previously lost habitat (Pess, McHenry, Beechie, & Davies, 2008), enabling rheophilic fish populations to re-establish and also enabling fish to migrate (both at small and large scales).

4 | CONCEPTUALIZING HABITAT LOSS: APPLICATIONS FOR MANAGEMENT

Table 1 provides data for three Danish rivers varying in size from 3 m to 40 m in width and from 20 km to 149 km in length. These data comprise the total drop from spring to outlet, the summed drop resulting from barriers, the total length of the river, and the summed length of the ponded zone, and were used as a rough estimate of vertical and horizontal habitat loss. This information was chosen as it is typically easy to obtain and to apply to management strategies. We acknowledge that the habitat loss may not be proportional to the loss in gradient (as this approach suggests). In fact, the relationship between habitat loss and gradient is likely to be more complex, especially if barriers are present further upstream, but this approach has merit to address rapidly some of the present management concerns.

This approach shows that a large proportion of the potential rheophilic habitat is lost in the ponded zones (Table 1). The River Gudenaa, the longest river in Denmark, was historically one of the most important Danish rivers with large populations of anadromous salmonids. It has seven barriers in the main stem predominantly for hydropower generation, yielding a total relative loss of the potential spawning and juvenile development habitat of 36% (Table 1). This loss increases to approximately 60% if the upper 10% of the watercourse is excluded where the river is narrow, the gradient is significantly steeper, and salmon production is historically non-existent. The smaller rivers Villestrup and Omme, on the other hand, have barriers established for fish farming or for driving old water mills, but nonetheless result in a similar loss in habitat. Furthermore, this estimated habitat loss is probably underestimated at fish farm sites, because the stretch of the river between a weir and the outlet of a fish farm is often several hundreds of metres apart, with very little water flow during a large part of the year. The habitat quality in these stretches is limited as a consequence of the reduced water flow alone, but may also represent an area of high predation (Jepsen, Aarestrup, Økland, & Rasmussen, 1998; Poe, Hansel, Vigg, Palmer, & Prendergast, 1991; Ruggerone, 1986).

The three rivers discussed above run mainly through agricultural land. However, rivers running through urban areas may be subjected to even more severe habitat loss (Birnie-Gauvin, Peiman, Gallagher, de Bruijn, & Cooke, 2016). For example, the River Mølleaa is approximately 13 km long, and flows through northern Copenhagen into the

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

River (no. of dams)	Total drop from source to outlet (m)	Summed drop from barriers (m)	Vertical habitat loss (%)	Total river length (km)	Summed ponded zones (km)	Horizontal habitat loss (%)
Villestrup (6)	22	8.8	40	20.0	5.8	29
Omme (14)	75	17.7	24	55.0	11.35	21
Gudenaa (7)	69	24.9	36	149.0	-*	-*

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

Øresund strait. The river has nine dams, which together remove an estimated 75% of the river gradient. There is virtually no natural gradient left, and thus no adequate habitat for rheophilic species.

5 | CONCLUSIONS

The productive potential of rheophilic species in lowland rivers is greatly reduced by the presence of dams and weirs. Typical management interventions aim to address issues concerning fish passage, but often omit any consideration of the habitat that has already been lost as a result of barriers for which empirical data are lacking (Abell, 2002). Given the relatively limited gradient available in Danish rivers (and in lowland rivers across the world in general) and the potential habitat loss associated with the latter, the overall effects of water barriers on habitat should be included in assessments of watercourses. These actions should be undertaken concurrently with the improvement of fish passage and other typical management-related challenges. To improve the state of regulated lowland rivers may mean that many of these river obstacles need to be removed in order to reinstate the former gradient and habitat, and at the same time re-establish faunal passage.

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

ACKNOWLEDGEMENTS

This research was funded by the Danish rod and net fish licence funds and the European Union (AMBER project).

REFERENCES

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, *12*, 169–176.

Abell, R. (2002). Conservation biology for the biodiversity crisis: A freshwater follow-up. *Conservation Biology*, *16*, 1435–1437.

Alexandre, C. M., & Almeida, P. R. (2010). The impact of small physical obstacles on the structure of freshwater fish assemblages. *River Research and Applications*, *26*, 977–994.

Auer, N. A. (1996). Response of spawning lake sturgeons to change in hydroelectric facility operation. *Transactions of the American Fisheries Society*, *125*, 66–77.

Bednarek, A. T. (2001). Undamming rivers: A review of the ecological impacts of dam removal. *Environmental Management*, *27*, 803–814.

Birnie-Gauvin, K., Peiman, K. S., Gallagher, A. J., de Bruijn, R., & Cooke, S. J. (2016). Sublethal consequences of urban life for wild vertebrates. *Environmental Reviews*, *24*, 416–425.

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, *30*, 492–507.

Bunt, C. M., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*, 457–478.

Calles, E. O., & Greenberg, L. A. (2005). Evaluation of nature-like fishways for re-establishing connectivity in fragmented salmonid populations in the river Emån. *River Research and Applications*, *21*, 951–960.

Council of the European Communities. (2000). Council Directive 200/60/EC of the European Parliament and of the Council of 23 October, 2000 establishing a framework for community action in the field of water policy. *Official Journal of the European Communities*, *L327*, 1–73.

Dadswell, M. J. (1996). *The removal of Edwards Dam, Kennebec River, Maine: Its effects on the restoration of anadromous fishes. Draft environmental impact statement, Kennebec River, Maine*. Nova Scotia, CA: Acadia University.

Dynesius, M., & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, *266*, 753–762.

Freyhof, J., & Brooks, E. (2011). *European Red List of freshwater fishes*. Luxembourg: Publications Office of the European Union.

Gibson, R. J. (1993). The Atlantic salmon in fresh water: Spawning, rearing and production. *Reviews in Fish Biology and Fisheries*, *3*, 39–73.

Gibson, A. J. F., Bowlby, H. D., & Amiro, P. G. (2008). Are wild populations ideally distributed? Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*, 1667–1680.

Hoffman, R., & Dunham, J. (2007). *Fish-movement ecology in high-gradient headwater streams: Its relevance to fish passage restoration through stream culvert barriers*(pp. 2007–1140). Virginia: US Geological Survey, OFR.

Hubbs, C., & Pigg, J. (1976). The effects of impoundments on threatened fishes of Oklahoma. *Annals of the Oklahoma Academy of Science*, *5*, 133–177.

Hunt, C. (1988). *Down by the river: The impact of federal water projects and policies on biological diversity*. Washington DC: Island Press.

Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. In J. P. Lagardere, M. L. Begout Anras, & G. Claireaux (Eds.), *Advances in invertebrates and fish telemetry* (pp. 347–353). Dordrecht, Netherlands: Springer.

Junge, C., Museth, J., Hindar, K., Kraabøl, M., & Asbjørn Vøllestad, L. (2014). Assessing the consequences of habitat fragmentation for two migratory salmonid fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*, 297–311.

Jungwirth, M. (1998). River continuum and fish migration – Going beyond the longitudinal river corridor in understanding ecological integrity. In M. Jungwirth, M. S. Schmutz, & S. Weiss (Eds.), *Fish migration and fish bypasses* (pp. 127–145). Oxford, UK: Blackwell Science.

Jungwirth, M., Muhar, S., & Schmutz, S. (2000). Fundamentals of fish ecological integrity and their relation to the extended serial discontinuity concept. *Hydrobiologia*, *422*, 85–97.

Koed, A., Jepsen, N., Aarestrup, K., & Nielsen, C. (2002). Initial mortality of radio-tagged Atlantic salmon (*Salmo salar* L) smolts following release downstream of a hydropower station. *Hydrobiologia*, *483*, 31–37.

Larinier, M. (2001). Environmental issues, dams and fish migration. FAO fisheries technical paper 419 (pp. 45–89). Rome, Italy.

Lucas, M. C., & Baras, E. (2000). Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries*, *1*, 283–316.

McCluney, K. E., Poff, N. L., Palmer, M. A., Thorp, J. H., Poole, G. C., Williams, B. S., … Baron, J. S. (2014). Riverine macrosystems ecology:

Sensitivity, resistance, and resilience of whole river basins with human alterations. *Frontiers in Ecology and the Environment*, *12*, 48–58.

Merritt, D. M., & Wohl, E. E. (2005). Plan dispersal along rivers fragmented by dams. *River Research and Applications*, *22*, 1–26.

Nilsson, C., & Jansson, R. (1995). Floristic differences between riparian corridors of regulated and free-flowing boreal rivers. *Regulated Rivers: Research & Management*, *11*, 55–66.

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, *308*, 405–408.

Palmer, M. A., Arensburger, P., Botts, P. S., Hakenkamp, C. C., & Reid, J. W. (1995). Disturbance and the community structure of stream invertebrates: Patch-specific effects and the role of refugia. *Freshwater Biology*, *34*, 343–356.

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

Petts, G. E. (1984). *Impounded rivers: Perspectives for ecological management*. Chichester, UK: John Wiley & Sons.

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

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., … Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, *47*, 769–784.

Poff, N. L., & Hart, D. D. (2002). How dams vary and why it matters for the emerging science of dam removal. *Bioscience*, *52*, 659–668.

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, *104*, 5732–5737.

Power, M. E., Dietrich, W. E., & Finlay, J. C. (1996). Dams and downstream aquatic biodiversity: Potential food web consequences of hydrologic and geomorphic change. *Environmental Management*, *20*, 887–895.

Rood, S. B., Samuelson, G. M., Braatne, J. H., Gourley, C. R., Hughes, F. M., & Mahoney, J. M. (2005). Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, *3*, 193–201.

Ruggerone, G. T. (1986). Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Transactions of the American Fisheries Society*, *115*, 736–742.

Stanford, J. A., Ward, J. V., Liss, W. J., Frissell, C. A., Williams, R. N., Lichatowich, J. A., & Coutant, C. C. (1996). A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management*, *12*, 391–413.

Ward, J. V., & Stanford, J. A. (1983). The serial discontinuity concept of lotic ecosystems. *Dynamics of Lotic Ecosystems*, *10*, 29–42.

Ward, J. V., & Stanford, J. A. (1995). The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research & Management*, *10*, 159–168.

Welcomme, R. L. (1985). River fisheries. FAO Fisheries Technical Paper 262. Rome, Italy.

Welcomme, R. L. (1995). Relationships between fisheries and integrity of river systems. *Regulated Rivers: Research and Management*, *11*, 121–136.

WWF. (2016). *Living Planet Report 2016: Risk and resilience in a new era*. Gland, Switzerland: WWF International.

Zhong, Y., & Power, G. (1996). Environmental impacts of hydroelectric projects on fish resources in China. *Regulated Rivers: Research and Management*, *12*, 81–98.

How to cite this article: Birnie-Gauvin K, Aarestrup K, Riis TMO, Jepsen N, Koed A. Shining a light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers, and its implications for management. *Aquatic Conserv: Mar Freshw Ecosyst*. 2017;1–5. https://doi.org/10.1002/aqc.2795